BROOD PARASITISM, REPRODUCTIVE SUCCESS, AND SURVIVAL IN YELLOW WARBLERS.

by

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Abstract

Understanding mechanisms responsible for population declines of migratory birds requires knowledge of factors limiting population growth at all stages of the annual cycle. Interspecific brood parasites are known to have negative, short-term impacts on the reproductive success of their hosts and could have longer-term costs that reduce survival. I used an information theoretic approach to examine the age-specific costs of brood parasitism in Yellow Warblers (*Dendroica petechia*), a common host of Brown-headed Cowbirds (*Molothrus ater*) in Revelstoke, British Columbia. Age did not mitigate the costs of brood parasitism that influenced each stage of the nesting cycle and reduced annual productivity. However, there was little evidence that brood parasitism influenced the survival of yearling or older Warblers. Adult survival was influenced by climate patterns, El Niño/La Niña, that influence conditions during spring migration, demonstrating the importance of this phase of the life-cycle for population dynamics of Neotropical migrants.

Keywords: brood parasitism; breeding performance, survival; El Niño Southern Oscillation; Brown-headed Cowbird; Yellow Warbler

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1: GENERAL INTRODUCTION

Recent declines in abundance of Neotropical migratory birds have motivated efforts to identify threats that contribute to population declines (Robbins et al. 1989, Sanderson 2006, Holmes 2007, Sauer et al. 2008). Because Neotropical migrants occupy several different geographical locations and habitat types throughout their annual cycle, understanding the causes of their population declines has proven particularly challenging. Research has suggested that factors that influence conditions on the breeding grounds, especially those that limit productivity, can have significant impacts on population dynamics (Sherry and Holmes 1992, Sillett and Holmes 2005). More recently, research has suggested that conditions on wintering grounds can influence over-winter survival and therefore have significant impacts on population growth (Baillie and Peach 1992, Rappole and McDonald 1994, Sillett and Holmes 2002, Norris and Marra 2007). Additionally, there is increasing recognition that migration is the most costly period of the annual cycle and that mortality rates are higher during the migration period relative to staging periods (Sillett and Holmes 2002, Carlisle et al. 2009). Other studies considering connectivity between multiple stages within the life cycle suggest that events that occur during one stage can have carry-over effects on reproductive success and survival in subsequent periods of the annual cycle (Marra et al. 1998, Webster et al. 2002, Norris et al. 2004). This suggests that factors that occur at all stages within the annual cycle have the potential to contribute to population declines (Holmes 2007) and that a consideration of all stages is necessary to make informed management decisions for species in decline.

During the breeding season, brood parasitism is one factor that is known to impact reproductive success. Interspecific brood parasites such as Brown-headed Cowbirds lay their eggs in nests of host species, exploiting a variety of hosts that provide parental care to their unrelated parasitic young. Host adults that accept parasitized clutches can have 1) smaller clutches (Sealy 1992, Hill and Sealy 1994), 2) reduced hatching success (Petit 1991, McMaster and Sealy 1999), and 3) produce poorer quality young that may consequently have lower juvenile survival (Marvil and Cruz 1989, Zanette et al. 2005). These cumulative losses can result in an overall loss of annual productivity for parasitized adults in some, but not all host species (Klaas 1975, but see Smith 1981), and could be a factor that contributes to host population declines.

In addition to reducing reproductive success for hosts, brood parasitism is energetically costly for hosts. Hosts that accept parasitic eggs invest significantly more time and energy provisioning their brood because parasitic nestlings beg more frequently and more intensely compared to host nestlings (Lichtenstein and Sealy 1998, Dearborn et al. 1998, Sedgwick and Iko 1999, Grim and Honza 2001, Hoover and Reetz 2006, but see Rivers et al. 2010). Hosts that reject brood parasitism by abandoning or burying parasitized clutches incur time and energy costs in laying new clutches, and building more nests (Drent and Daan 1980, Gowaty 1996, Sedgwick and Iko 1999). Additionally, there is some evidence that individuals that reject parasitic eggs have a higher probability of nest predation due to retaliatory behaviour of Brown-headed Cowbirds (Zahavi 1979, Soler et al. 1995, Arcese et al. 1996, Granfors et al. 2001, Hoover and Robinson 2007), further forcing hosts to invest time and energy into renesting. Generally, reproductive effort is known to influence survival rates in many Neotropical bird species (Nur 1988), suggesting that increased energetic demands incurred due to brood parasitism may reduce adult survival. Reductions in adult survival could be an additional cost of brood parasitism that contributes to population declines of host species.

I examined the reproductive and survival costs of brood parasitism in the Yellow Warbler, a common host (>10% of nests parasitized) of the Brown-headed Cowbird brood parasite in British Columbia (Campbell et al. 2001). Yellow Warblers are small (9-10g), Neotropical migrants that breed in wet, deciduous riparian habitat in Revelstoke, B.C. (Quinlan 2009), and elsewhere in North America (Cilimburg et al. 2002). Breeding populations migrate south to wintering grounds in Mexico, Central, and South America in late July to mid August, and remain on wintering grounds until northward migration in late March to late April (Lowther 1999). Genetic and isotope data from birds captured on wintering grounds suggests that Yellow Warblers breeding in British Columbia overwinter across Mexico and Central America, migrate through western and central North America (Nevada) in the spring, and through California and New Mexico in the fall (Boulet et al. 2006). Yellow Warblers have shown broad declines across western and central breeding populations in recent years (Webb 1985, Ortega and Ortega 2000, and Sauer et al. 2008, but see Saracco et al. 2008).

In **Chapter 2**, I examined whether host Yellow Warblers could mitigate the costs of brood parasitism by learning to avoid or recognize parasitic eggs. Although results of previous studies had been mixed, studies on a variety of host species have suggested that older individuals are more likely to avoid (Brooker and Brooker 1996) or reject brood parasitism (Lotem et al. 1992, 1995, Amundsen et al. 2002, Moskát and Hauber 2007). Breeding performance has been found to improve with age in a variety of bird species.

Age-related improvements in breeding success have been attributed to prior experience that leads to individual improvement in territory selection, predator detection, and avoidance, or foraging efficiency (experience hypothesis; Curio 1983, Nol and Smith 1987, Desrochers 1992), increased reproductive effort later in life, when the expectation of future reproduction is low (restraint hypothesis; Pianka and Parker 1975), and/or selective mortality that removes poorer quality individuals from the breeding population (selective mortality hypothesis; Orians 1969, Curio 1983).

In **Chapter 2**, I also examined whether in Yellow Warbler hosts, age mitigated the reproductive costs associated with accepting a parasitic egg. If brood parasites are selecting hosts to maximize the number of parasitic young that fledge, Cowbirds would be expected to preferentially target and parasitize host individuals that are more successful at raising broods. Other studies have suggested that Cowbird and Cuckoo species select for more successful parents by cueing in on signals of high parental care quality such as nest defence, food resource availability (Smith et al. 1984, Zanette and Clinchy 2010), or nest size (Soler et al. 1995). Since reproductive success generally increases with age, I expected that older, more experienced host individuals might not suffer the same reproductive costs as yearling individuals.

In **Chapter 3**, I assessed whether male and female Yellow Warblers had reduced survival in years after receiving a Brown-headed Cowbird egg, or raising a Cowbird nestling. Other studies investigating the survival costs of brood parasitism suggested that long-term costs might be higher for hosts that are far smaller than the brood parasites (Sedgwick and Iko 1999, Hoover and Reetz 2006). I therefore predicted that the increased energetic demands associated with brood parasitism would be costly for small Yellow Warbler hosts and would reduce their survival.

In addition to studying the factors that impact survival on the breeding grounds, I examined whether large-scale climatic events expected to influence conditions at breeding and wintering grounds, and during spring migration, potentially masked or overwhelmed any survival costs associated with brood parasitism. Several studies have suggested that large-scale environmental conditions could have a significant impact on the survival of songbirds (Sillett et al. 2000, Nott et al. 2002, Mazerolle et al. 2005). I therefore predicted that climate events influencing conditions on breeding and wintering grounds or conditions encountered during migration might impact annual survival in Yellow Warblers. I predicted that the relative impacts of large-scale climatic conditions might be greater during migration or at migration stopover sites, since recent evidence suggests that this period of the annual cycle can have a large impact on annual survival (Carlisle et al. 2009). For instance mortality of Black-throated Blue Warblers (*Dendroica caerulescens*) during the spring and fall migration period is estimated to be 15 times higher than during either the summer or winter stationary period (Sillett and Holmes 2002; Carlisle et al 2009). Previous studies that examined the impacts of large-scale climatic patterns have used a variety of time periods to assess impacts. In order to examine what periods in the lifecycle El Niño/Southern Oscillation (ENSO) impacts, I evaluated competing mechanisms that are predicted to regulate survival at 3 stages of the lifecycle (**Chapter 3**). In **Chapter 4**, I discuss the costs of brood parasitism for Yellow Warblers breeding in Revelstoke, B.C., relative to other factors experienced during the annual cycle, and suggest research directions that warrant further study.

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2: AGE DOES NOT MITIGATE THE REPRODUCTIVE COSTS OF BROOD PARASITISM IN YELLOW WARBLERS

2.1 Abstract

Age is known to influence breeding performance in many passerine species. Brood parasitism is an external factor, which also influences reproductive success of host species. We used an information theoretic approach to examine the age-specific costs of brood parasitism in the Yellow Warbler (*Dendroica petechia*), a common host of Brown-headed Cowbirds (*Molothrus ater*) in Revelstoke, British Columbia. Although older Yellow Warbler females had higher breeding performance, they were as likely to be parasitized and accept Cowbird eggs as yearling females. Age did not mitigate the reproductive costs of brood parasitism that influenced each stage of the nesting cycle and reduced annual productivity. The cumulative effects of Cowbird parasitism reduced annual productivity of older females from an average of 2.7 to 1.7 and the annual productivity of yearling females from 2.0 to 0.3 fledglings. Age-structured population models incorporating the costs of brood parasitism on population growth can therefore assume the reproductive costs are similar for yearling and older females.

2.2 Introduction

Breeding performance improves with age in many bird species (Perrins and Moss 1974, Clutton-Brock 1988, Newton 1989, Sæther 1990, Green 2001) and this pattern may result from improvement in one or many aspects of reproduction. For example, older birds have been reported to have earlier nest initiation dates (Balbontin et al. 2007, Lozano et al. 1996, Caro et al. 2009), produce larger eggs (Robertson et al. 1994), lay larger clutches (Espie et al. 2000, Low et al. 2007), and have greater fledging success per nesting attempt (Perrins and Moss 1974, Reid et al. 2003), and per breeding season (Green 2001). Age-related improvement in breeding performance may result from prior breeding experience that leads to individual improvement in selecting a territory, predator detection and avoidance, or foraging efficiency (experience hypothesis; Curio 1983, Nol and Smith 1987, Desrochers, 1992), increased reproductive effort later in life, when the expectation of future reproduction is low (restrained hypothesis; Pianka and Parker 1975), and/or selective mortality that removes poorer quality individuals from the breeding population (selective mortality hypothesis; Orians 1969, Curio 1983).

Reproductive success is reduced by interspecific, obligate brood parasites such as Cuckoos (Family Cuculidae) and Cowbirds (Genus *Molothrus*) that have negative effects at several stages of the nesting cycle. Clutch sizes are reduced when a host egg is removed and replaced with brood parasitic eggs (Smith 1981, Rothstein 1982, Sealy 1995, Banks and Martin 2001, Tewksbury et al. 2002). Hatching success of remaining host eggs is lowered by host eggs being damaged by brood parasites, or by earlier hatching brood parasitic nestlings drawing parental attention away from host eggs and nestlings (Walkinshaw 1961, McMaster and Sealy 1999, Peer and Sealy 1999, Peer and

Bollinger 2000). Parasitized broods produce fewer or no host fledglings due to parasitic young outcompeting host young for food deliveries or in some cases ejecting host young from the nest (Walkinshaw 1961, Marvil and Cruz 1989, Lichtenstein and Sealy 1998, McMaster and Sealy 1999, Davies 2000, Peer and Bollinger 2000, Payne 2005, Rivers 2006, but see Rivers et al. 2010). These costs usually reduce annual productivity of hosts (Klaas 1975, Smith et al. 2002). However, in some cases parasitized individuals can compensate for their reduced fledging success by initiating additional nesting attempts (Smith 1981, Roth et al. 1996). Zanette et al. (2005) also demonstrated that brood parasitism by Brown-headed Cowbirds skewed the Song Sparrow host offspring sex ratio towards male-biased host nestling production (Zanette et al. 2005).

Despite extensive literature on age-related improvement in breeding performance, most studies examining the impact of brood parasitism have only investigated whether hosts learn to recognize and avoid brood parasitism and if older individuals are consequently less likely to be parasitized and more likely to reject parasitic eggs compared to yearling females. There studies usually find no evidence that older host females are less likely to be parasitized by either Cuckoos or Cowbirds, and in fact, contrary to predictions derived from the learning hypothesis, the reverse was often the case (Smith 1981; Smith et al. 1984; but see Sealy 1995, Brooker and Brooker 1996, and Langmore 2007). Some studies demonstrate that older females are more likely to reject a parasitic egg or nestling. Lotem et al. (1992, 1995) found that earlier breeding great reed warbler (*Acrocephalus arundinaceus*) hosts consisting of a higher proportion of adult females, were significantly more likely to reject brood parasitic Common Cuckoo (*Cuculus canorus*) eggs from their nests (but see Moskát and Hauber 2007). Similarly, Langmore et al. (2009) found that experienced Superb Fairy-wren (*Malurus cyaneus*) hosts were more likely than naïve breeding females to abandon nests containing single Cuckoo chicks, a signal of brood parasitism for hosts where brood parasitic young remove hosts eggs and nestlings. However, Amundsen et al. (2002) and Sealy (1995; but see Hobson and Sealy 1989) found no evidence that age influenced whether Bluethroats (*Luscinia svecica*) rejected Common Cuckoo eggs or Yellow Warblers rejected Brown-headed Cowbird (*Molothrus ater*) eggs.

Comparatively few studies have examined how host age influences other aspects of reproduction in parasitized hosts. In Song Sparrows (*Melospiza melodia*), brood parasitism by Brown-headed Cowbirds reduced the clutch size of first time breeders more than experienced breeders (Smith 1981). Brood parasitism also reduced the fledging success of first time breeders significantly more than older females (Smith 1981). No studies to date have examined whether host age influenced hatching success, nestling condition, or the sex ratio of host nestlings in parasitized nests.

In this study, we examined how female age influences breeding performance, brood parasitism rates and impacts of brood parasitism on Yellow Warbler hosts at different stages of the nesting cycle. We predicted that 1) the breeding performance of older females would be superior to yearling females; 2) older Yellow Warbler females would be less likely to be parasitized and more likely to reject parasitized clutches; and 3) brood parasitism would have less impact on the breeding performance of older Yellow Warbler females because older, more experienced females are likely to breed in higher quality territories and invest more in a breeding attempt. We evaluated these predictions by comparing the age-specific costs of brood parasitism by Brown-headed Cowbirds in yearling and older female Yellow Warblers. We used an observational rather than an experiment approach to allow for a relative assessment of the costs of parasitism at multiple stages of the nesting cycle. We assessed female age only because female Yellow Warblers provide all parental care prior to the hatching stage and are therefore likely to show age-related improvements in breeding performance (Desrochers and Magrath 1993; Reid et al. 2003; Low et al. 2007, but see McCleery and Perrins 1988; Green 2001) and be impacted by the reproductive costs of brood parasitism (Sealy 1995).

2.3 Methods

2.3.1 Study Sites

Our study was conducted in Revelstoke Reach, situated within the drawdown zone of Arrow Lakes Reservoir, a 240 kilometer-long reservoir system in the upper Columbia River valley separating the Monashee and Selkirk mountain ranges, east of the Kootenay region of British Columbia, Canada (N50.58’56”/W-118.20’00”). Water levels in the Arrow Lakes reservoir were controlled by hydroelectric dam operations behind the Hugh Keenleyside Dam, upstream of the city of Castlegar, British Columbia. Three study sites, each 30-39 ha, were established in the upper reaches of the floodplain (435-441 m elevation). Study sites were periodically subject to flooding in some years of the study and were representative of locally existing riparian vegetation compositions ranging from dense stands of mature black cottonwoods with a diverse understory at higher elevations (>440 m) to more isolated patches of willow at lower elevations (<438 m).

2.3.2 Study Species

The Yellow Warbler is a small (9-10g), Neotropical migrant with a wide breeding range that extends across much of North America, with northern limits defined by the presence of shrub vegetation south of the tundra (Lowther 1999). Populations of Yellow Warblers breeding in Revelstoke, BC, and elsewhere in western North America are associated with wet riparian habitats and vegetation such as willow and other low-lying shrub species, and deciduous trees such as black cottonwood (Cilimburg et al. 2002). In Western North America, Yellow Warblers begin to arrive on their breeding grounds in late April to early May and breeding extends from May until mid to late July (Campbell et al. 2001, Quinlan 2009). Males return to the breeding grounds and establish territories prior to the arrival of females (Quinlan 2009). Breeding pairs typically rear one successful brood of up to 5 fledglings per year; second broods are attempted but are rarely successful (Quinlan 2009). Females are solely responsible for nest building and provide all parental care during egg-laying and incubation (Lowther 1999). However, both males and females provision young during the nestling and post-fledging period (Lowther 1999). Breeding populations migrate south to wintering grounds in Mexico and South America in late July to mid August, and remain on wintering grounds until northward migration in late March to late April (Lowther 1999). Genetic and isotope data from birds captured on wintering grounds suggests that Yellow Warblers breeding in British Columbia overwinter across Mexico and Central America, migrate through western and central North America (Nevada) in the spring, and through California and New Mexico in the fall (Boulet et al. 2006).

Across its breeding range, the Yellow Warbler is frequently parasitized by Brown-headed Cowbirds (Schrantz 1943, McGeen 1972, Clark and Robertson 1981, Lowther 1984, Hobson and Sealy 1989). In a long-term Yellow Warbler monitoring program running from 1974 to 1991 (excluding 1977) in the Delta Marsh, Manitoba Canada (50°11'N, 98°19'W), an average of 21% (n=1885) of monitored nests were parasitized by Brown-headed Cowbirds. In British Columbia, Yellow Warblers are a common host of Brown-headed Cowbirds (Campbell et al. 2001) and parasitism rates range between 11-16% (Campbell et al. 2001). Yellow Warblers have been demonstrated to exhibit adaptations to Brown-headed Cowbirds prior to being parasitized including: nest guarding, aggressive behaviour, and alarm calls (Burgham and Picman 1989, Hobson and Sealy 1989). When parasitized, Yellow Warblers accept and continue caring for parasitic Cowbird eggs in approximately 50-60% of parasitized nests (Sealy 1995). However, Yellow Warblers are considered to be a 'rejecter' host to brood parasitism; hosts that have been demonstrated to respond to brood parasitism by abandoning the parasitized clutch, or burying the parasitic egg or the parasitized clutch, and renesting a top the parasitized clutch (Clark and Robertson 1981, Rothstein 1990, Sealy 1995, Hosoi and Rothstein 2000). Rejection is more likely to occur when Cowbird eggs are laid during the first half of the clutch initiation period, and in clutches initiated early in the breeding season (Sealy 1995). Yellow Warblers are more likely to abandon nests containing Cowbird eggs or nests where egg removal by Cowbirds has reduced clutch size below a species-specific size threshold (Rothstein 1982, Sealy 1992).

2.3.3 Monitoring Breeding Performance and Parasitism Rates

From 2004-2006 and 2008-2009, we monitored all bird breeding at the study plots at 2-3 day intervals from the time of arrival on the breeding grounds (early May) until independence of the final brood (late July). In each year of study, we successfully located and recorded the band combinations of all colour-banded birds that returned to the study area from previous years and identified unmarked individuals, presumably new to the study area. We attempted to catch all banded and unbanded breeding birds that established territories within the study sites using 12 m mist-nests combined with playbacks of Yellow Warbler songs. Males were typically caught within 3 days of their return to the study area. Females were less responsive to playbacks and were more likely to be caught later when incubating or provisioning young. When caught, all birds were fitted with a Canadian Wildlife Service-issued aluminium band and a unique combination of three colour bands. Individuals were assigned a gender and age based on plumage and feather wear (Pyle 1997). Where possible, females were classified as yearling females (second year birds in their first breeding season) or older females (after second year birds in at least their second breeding season). Females were classified as being of unknown age if they were not captured or could not be confidently aged and were subsequently omitted from the analysis. In 2008, a blood sample (~25 µL) was taken from the brachial vein of 4 male and 4 female adults of known sex using a 26.5”G needle during routine banding procedures. Blood samples were immediately transferred to and stored in 1.5mL of Longmire’s Buffer solution. These sex blood samples were later used to determine the accuracy of nestling sex determination protocols.

Nest searching and monitoring of all nesting attempts made by breeding pairs began upon arrival of females in mid-May, and ended in late July, after all nesting pairs fledged their young. Upon locating nests, we recorded the Universal Transverse Mercator (UTM) locations using handheld GPS units. Nests were subsequently checked every 1-4 days to observe clutch initiation date (defined here as the date the first egg was laid), hatch date (defined here as the day the first nestling hatched), and record clutch and brood size. When clutch initiation date was not directly observed, it was estimated by back counting from the date of hatching. We also documented occurrences and timing of egg-laying by Brown-headed Cowbirds and hatch dates of Cowbird nestlings. The timing of Cowbird egg-laying was classified into the following discrete nesting phases (adopted from Sealy 1995); pre-laying (prior to Yellow Warbler egg initiation), early-laying (one Yellow Warbler egg laid), late-laying (more than one Yellow Warbler egg laid), and post-laying (incubation or nestling stages). Parasitized Yellow Warbler females were classified as either acceptors (continued providing parental care after being parasitized) or rejecters (either abandoned the nest or buried the contents of the nest including Yellow Warbler and/or Cowbird eggs). Nests under 6 m were observed using stepladders and pole-mounted mirrors. Nests above these heights were monitored from a distance with binoculars or a spotting scope. Due to our limitations in accurately viewing the contents of nests placed at heights greater than 6m, the status of nest parasitism was considered unknown and these nests were subsequently omitted from the analysis. We assumed females fledged all young banded or observed at nests on day 7, if there were signs of fledging (flattened nest rim faeces in nest, fledglings), and parents were subsequently observed carrying food to fledglings within their territory. Nests were considered successful if they fledged at least one Yellow Warbler young. We assumed nest failure due to predation if all nestlings disappeared before reaching 7 days of age, and if there were signs of predation (egg fragments, nest destroyed or disturbed).

Where possible, nestlings were banded with a Canadian Wildlife Service-issued aluminium band, weighed to the nearest 0.10 g using a digital scale, and measured for tarsus length (from the notch in the intertarsal joint to the top of the palm) to the nearest 0.01 mm on day 7 of the 9-day nestling period, the last day young can be handled without causing premature fledging. In 2008 and 2009, a blood sample (~25 µL) was taken from the brachial vein of each nestling using a 26.5”G needle. Blood samples were immediately transferred to 1.5 mL of Longmire’s Buffer solution and 70% ethanol in 2008 and 2009, respectively and were later stored at -40°C until used to determine nestling sex.

2.3.4 Nestling Condition and Sex Ratio

Nestling condition was estimated using the residuals from a mass versus tarsus regression for all nestlings. This regression explained 83% of the variance in nestling mass. We determined the gender of nestlings with a polymerase chain reaction (PCR)-based technique, using two sets of primers provided by SIGMA-ALDRICH® (Griffiths et al. 1998, Fridolfsson and Ellegrin 1999). Primers 2550F and 2718R amplified a section of the W chromosome present in females. Primers 2987F and 3112R amplified a region of the Z chromosome present in males and females. PCR products were separated in 1.5% agarose gel, run in standard TBE buffer, and visualized by ethidium bromide staining. Known males were recognized in agarose electrophoresis as displaying a single PCR product while females showed two different products. This protocol was then applied to all nestling blood samples and the sex ratio of nestlings per brood was identified.

2.3.5 Statistical Analysis

We developed a series of candidate model sets to examine how female age influenced brood parasitism (parasitized or not), the response of Yellow Warbler females to brood parasitism (accept or reject), and how female age and brood parasitism influenced six measures of breeding performance. The six measures (clutch size, nest success, number fledged, nestling condition, nestling sex ratio, and annual productivity) were selected to account for the losses due to brood parasitism at each stage of reproduction. We examined clutch size to determine losses at the laying and incubation stage due to Cowbirds removing host eggs. Nest success was evaluated to determine whether parasitized nests were more likely to fail during egg laying, incubation, or nestling stages due to increased activity and noise near the nest. We examined the number of host young fledged from successful nests to assess whether the presence of a Cowbird nestling increased host nestling mortality. Nestling condition and sex ratio were evaluated to determine whether increased competition over resources differentially affected the survival of male versus female host nestlings. Annual productivity was examined to determine whether females parasitized with a Cowbird egg at least once per breeding season produced fewer young compared to unparasitized females. Previous studies suggested that parasitized broods had reduced hatching success. However, we were not able to assess whether the proportion of Yellow Warbler eggs that hatched was influenced by brood parasitism because a high percentage of the nests we monitored either failed entirely or fledged full broods, making our hatching ratio disproportionately skewed to 0 or 1.

The candidate model set examining whether nests were parasitized (parasitism) included all combinations of three variables: year (YEAR), clutch initiation date (DATE), and female age (AGE; yearling or older). The candidate model set examining whether parasitized females rejected parasitized nests (rejection response) included all combinations of variables: DATE, AGE, and nesting stage the parasitic egg was laid (STAGE; pre-laying, 1 egg laid, 2 or more eggs laid, and incubation or later). Model sets examining clutch size, nesting success, and number of young fledged included whether parasitized or not (PAR), YEAR, DATE, AGE, and a female age*parasitism interaction term (PAR*AGE). Nestling condition and sex ratio candidate model sets were simplified to include three variables due to smaller sample sizes: AGE, PAR, and PAR*AGE. The nestling condition analysis included an additional term adjusting for brood size, which was used as a null model (BSIZE). The annual productivity candidate model set included: YEAR, AGE, PAR, PAR*AGE. In all candidate models, the date variable included a linear and squared term grouped together (DATE + DATE^2) because we expected passerine breeding performance to peak mid-season, and be diminished both early and late in the breeding season. The parasitism, rejection response, and nesting success analyses were treated as logistic regressions, and sex ratio was treated as binomial responses, with x successes from y trials, using a logit link function. Clutch size, number fledged, nestling condition, and annual productivity were treated as linear responses and were examined using a generalized linear model with a normal error distribution. We initially explored factors influencing breeding performance and female response to parasitism using a mixed modelling approach, since individual females (26%) had multiple nesting attempts within a year and were monitored in multiple years of the study. We specified female identity as a random factor. However, there was little variance associated with the female identity term (the standard errors of the variance component were large compared with the mean), so we simplified the analysis by dropping the random term from all analyses.

Akaike Information Criterion (AIC) values for small sample sizes (AIC_c) were derived manually for each model using the output of generalized linear models and logistic regressions computed in SAS® 9.2 and SPSS version 17. AIC_c values were used in all analyses because the sample sizes divided by the number of models in the candidate sets were always less than 40 (Burnham and Anderson 2002, Anderson 2008). For all analyses we calculated the variance inflation factor (ĉ) for the global model using the formula:

$$\hat{c} = x^2 / df$$

where χ^2 is the Pearson chi squared (generalized linear models) or the Hosmer and Lemeshow chi squared (logistic regression) and df is the degrees of freedom. AIC_c and Quasi-AIC_c ($QAIC_c$; AIC_c corrected for over-dispersion) values were calculated to give a measure of the level of fit of the data to the model weighted by the number of parameters in the model and when appropriate, the variance inflation factor. $QAIC_c$ values were used when the ĉ value exceeded 1.0 (nestling condition and annual productivity analyses; Burnham and Anderson 2002, Anderson 2008). Delta (Δ) (Q)AIC_c values were calculated as the differences between the (Q)AIC_c of each model and that of the most parsimonious model (model with the lowest AIC_c or $QAIC_c$). For each analysis, candidate models were then ranked relative to one another using AIC_c weights (w_i). Models with high w_i values were the best-supported by the datasets. Parameter estimates and their associated unconditional standard errors were also calculated to assess the relative influences of the variables present in competing models. AIC_c parameter likelihoods were calculated as the sum of the w_i of all competing models in which the parameter occurred. AIC parameter estimates (importance values) were calculated as the mean estimate (across all competing models) of each parameter weighted by the w_i of each model in which the parameter was included. AIC unconditional standard errors were calculated as the standard error of each parameter weighted by the AIC_c weight of each candidate model in which the parameter occurred.

2.4 Results

We monitored the breeding performance of 19 Yellow Warbler pairs in 2004, 24 in 2005, 36 in 2006, 38 in 2008, and 36 in 2009 (n =152 pair-years). Reproductive success and parasitism rates varied by year; therefore we did not pool data among years. On average, 51% of females in any year were older birds (range=18% in 2004 to 71% in 2005). Females initiated nests between May 25th and July 4th and laid clutches that contained two – five eggs (mean ± SD =4.0 ± 0.9). Cowbirds parasitized 18% of Yellow Warbler nests (n=158), contributed to 1% of nest failures, and in all cases parasitized nests contained a single Cowbird egg. Overall, 57% (n=145), including 11 parasitized nests, fledged and successful nests contained 3.1 ± 1.6 fledglings (n=82). Of the nests that failed, predation was the predominate cause of failure (76%, n=145). Females initiated between 1 and 4 clutches per year, occasionally fledging two broods (n=3). Annual productivity per female averaged 2.1 ± 1.9 fledglings (n=117).

2.4.1 Parasitism

We found no evidence that yearling females were more susceptible to Cowbird parasitism than older Yellow Warbler females. In fact, older females were slightly more likely to be parasitized than yearling females (n=158; Figure 2-1, Table 2-1, Appendix A, B). Cowbird parasitism rates also varied between years, being lowest in 2004 (9%, n=11) and highest in 2005 (31%, n=29; Table 2-1, Appendix A, B). The term year was in all three strongly supported models (Table 2-1, Appendix A) and had high parameter likelihoods (0.791; Appendix B). Female age was present in one of the three strongly supported models and two of the three moderately ranked models ($\Delta AIC_c < 4$; Table 2-1, Appendix A), but the parameter likelihood for age was only moderate (0.484) and had large standard errors (Appendix B). The parameter estimate for female age was positive, suggesting that older females are slightly more likely to be parasitized (Appendix B). The date terms were present in one of the three strongly supported models (Table 2-1, Appendix A) and one of the moderately supported models, but the parameter likelihood for the date terms were low (0.289) and the weighted parameter likelihoods had large standard errors (Appendix B), indicating that there was little seasonal variation in Brown-headed Cowbird parasitism.

2.4.2 Rejection Response

Yellow Warbler females abandoned or buried 26.9% (n=26) of nests that were parasitized by Cowbirds. There was some support for the hypothesis that older females are more likely to reject a nest parasitized by Cowbirds (Figure 2-1) since the model containing the term female age was one of two models that received strong support ($\Delta AIC_c < 2$, Table 2-1, Appendix A, B). However, the null model received more support than the model that included the female age term (w_i=0.369 versus w_i=0.293; Table 2-1, Appendix A) and female age had only moderate parameter likelihoods (0.437) and the weighted parameter likelihoods had large standard errors (Appendix B). None of the other 5 candidate models received strong support. The parameter likelihoods for the terms date and the stage at which a nest was parasitized were all low (0.253 and 0.106, respectively; Appendix B) suggesting these terms had little influence on the response of female Yellow Warblers.

2.4.3 Clutch Size

Clutch sizes in parasitized nests were, on average, 0.7 eggs (n=145) smaller than in unparasitized nests, and there was some evidence that the reduction in clutch size was greater for older compared to yearling Yellow Warblers (Figure 2-2a). Clutch size also declined as the season progressed and varied between years, being smaller in 2004 and larger in 2006 (Table 2-2, Appendix C, D). Three of the 19 candidate models received strong support ($\Delta AIC_c < 2$). The highest ranked model (w_i=0.478) that contained date, year, female age, parasitism, and female parasitism*female age received almost twice the level of support as the next best model (w_i = 0.255; Table 2-2, Appendix C). The temporal variables (date and year) were included in all three strongly supported models (Table 2-2, Appendix C) and had high weighted parameter likelihoods (1.000 and 0.971, respectively; Appendix D). The parasitism and female age variables were included in two of the three strongly supported models (Table 2-2, Appendix C) and also had high parameter likelihoods (1.000 and 0.756 respectively; Appendix D). The female age*parasitism interaction term was included in the best model (Table 2-2, Appendix C) but he weighted parameter likelihoods had large standard error (Appendix D) indicating that it did not have a strong influence on clutch size.

2.4.4 Nesting Success

Nesting attempts by yearling Yellow Warbler females were less likely to successfully fledge young than nesting attempts by older females (n=145; Figure 2-2b). Cowbird parasitism also reduced the probability that a nest would fledge young, but there was little support for the hypothesis that older females are better able to mitigate the effects of parasitism (Figure 2-2b, Table 2-2, Appendix C). Nest success also decreased as the season progressed and varied between years, being high in 2004 and low in 2006 and 2008 (Table 2-2, Appendix C). In our analysis, five of the 19 candidate models received strong support. The temporal variables date and year were included in all five strongly supported models (Table 2-2, Appendix C) and had high parameter likelihood values (0.824 and 0.969, respectively; Appendix D). Female age and parasitism terms were both included in three of the five strongly supported models (Table 2-2, Appendix C) and had moderate parameter likelihoods (0.559 and 0.579, respectively) but the weighted parameter likelihoods had high standard error (Appendix D). The female age*parasitism interaction term was included in only one of the five best-supported models (Table 2-2, Appendix C), but the weighted parameter likelihoods had high standard error (Appendix D). Our analysis therefore provided little support for the relationship between nest success and the interaction between the parasitism and female age.

2.4.5 Number Fledged

Older Yellow Warbler females fledged more offspring on average from successful nests than yearling females (n=82; Figure 2-2c). Cowbird parasitism reduced the number of young fledged from successful nests (Figure 2-2c). In our analysis, one of the 19 candidate models received strong support. The highest supported model (w_i=0.667) that contained date, female age, parasitism, and female age*parasitism received six times more support than the next best model (w_i=0.112) that included the additional term year but did not include the female age*parasitism term (Table 2-2, Appendix C). All the terms in the top model consequently had high parameter likelihoods (0.908, 0.923, 1.000, 0.755, respectively; Appendix D). The year term was not included in any high-ranking model (Table 2-2, Appendix C), had a low parameter likelihood (0.187), and the weighted parameter likelihoods had high standard error (Appendix D).

2.4.6 Nestling Condition

We found no evidence that Cowbird parasitism had an effect on the average condition of Yellow Warbler nestlings per brood (n=81), or that older females raised offspring that were in better condition than yearling females (Figure 2-2d, Appendix C, D). If anything, average nestling condition was higher in parasitized broods raised by yearling females (Figure 2-2d). There was a high level of model uncertainty indicated by all five models in the candidate set receiving strong support. The highest ranked model included brood size and female age (w_i=0.289) and the parameter likelihoods for these terms were high (1.000, and 0.728 respectively; Table 2-2, Appendix D). The weighted parameter estimates indicated that nestling condition declined with brood size and was higher in broods raised by young females (Appendix D). The term parasitism and moderate to low parameter likelihoods (0.549) and for the terms parasitism and age*parasitism, the weighted parameter likelihoods had high standard errors (Appendix D).

2.4.7 Nestling Sex Ratio

We found little evidence that female age, Cowbird parasitism, or the interaction between female age and parasitism had a strong affect on the sex ratio per Yellow Warbler brood (n=44; Figure 2-2e, Table 2-2, Appendix C, D). In our analysis, the null model was the best-supported model in the candidate set (w_i=0.314; Table 2-2, Appendix C). However, four of five candidate models received strong support indicating that there was a high level of model uncertainty due to the limited amount of data from parasitized nests (Table 2-2, Appendix C). Parameter likelihoods were moderate (0.501; Appendix D) for the parasitism term (the lone term ranking as the second best supported model) but low for the female age and female age and parasitism interaction term (0.429 and 0.101, respectively; Appendix D). Taken together, this suggests that parasitism has little effect on nestling sex ratio.

2.4.8 Annual Productivity

Older females had higher annual productivity than yearling Yellow Warbler females. Cowbirds reduced the annual productivity of females that were parasitized at least once during a breeding season, but there was only limited support for the hypothesis that Cowbirds had less impact on older females (n=117; Figure 2-2f, Table 2-2, Appendix C, D). Three of the ten candidate models received strong support. The highest ranked model included the terms female age and parasitism (w_i=0.274; Table 2-2, Appendix C), and the parameter likelihoods for these terms were high (0.683 and 0.792 respectively; Appendix D). The parasitism term was also included in the second ranked model (w_i=0.176). The third ranked model having essentially the same ranking as the second model (w_i=0.170) included the female age*parasitism interaction term (Table 2-2, Appendix C) but the weighted parameter likelihoods for the interaction term had high standard errors (Appendix D) indicating that the effects of female age and parasitism on annual productivity were additive. The year term was not included in any of the models that received strong support (Table 2-2, Appendix C) and the term had high standard error (Appendix D) suggesting that year had relatively little importance in predicting annual productivity.

2.5 Discussion

This study, like many other studies that have examined age effects on breeding performance of birds, found that older Yellow Warbler females had higher annual breeding success than yearling females. Age-related improvements in productivity resulted from improvement at several stages of the nesting cycle as older females laid larger clutches, had higher nesting success, and fledged more young per successful nest. Our results were consistent with other studies that have shown age related variation in clutch initiation date (Balbontin et al. 2007, Lozano et al. 1996, Caro et al. 2009), egg sizes (Robertson et al. 1994), clutch size (Espie et al. 2000, Low et al. 2007), and fledging success per nesting attempt (Perrins and Moss 1974, Reid et al. 2003) and per breeding season (Green 2001). Counter to our predictions however, we found no evidence that older Yellow Warbler females mitigated the reproductive costs of brood parasitism by Brown-headed Cowbirds.

Brood parasitism is known to have negative impacts on host breeding performance at several stages of the breeding cycle. Previous studies, on a large range of host species, demonstrated that parasitized nests have smaller clutches after brood parasites remove host eggs (Smith 1981, Rothstein 1982, Sealy 1995, Banks and Martin 2001, Tewksbury et al. 2002), reduced hatching (Walkinshaw 1961, McMaster and Sealy 1999, Peer and Sealy 1999, Peer and Bollinger 2000) and fledging success (Walkinshaw 1961, Marvil and Cruz 1989, Lichtenstein and Sealy 1998, McMaster and Sealy 1999, Davies 2000, Peer and Bollinger 2000, Payne 2005, Rivers 2006). Similarly, we found that Yellow Warblers that were parasitized by Brown-headed Cowbirds had smaller clutch sizes (presumably due to Cowbirds removing host eggs). Although we did not directly measure hatching success, lower nest success in parasitized nests suggested the presence of a Brown-headed Cowbird egg and/or nestling might increase activity near the nest, and subsequently influence predation rates. Our results indicated that fewer host young were fledged from nests containing parasitic young. Losses at the fledging stage were greater than losses in clutch size suggesting host nestling mortality, presumably due to competitive disadvantages in the presence of Cowbird nestlings. Previous studies have found that reproductive losses per nest due to brood parasitism decrease the annual productivity of hosts (Klaas 1975; Smith et al. 2002). Other studies showed host species compensated for reproductive losses due to parasitism by initiating more breeding attempts per year following nest failure or rejection (Smith 1981), and re-nested at times when Cowbird frequencies are lower (Roth et al. 1996). Our study was consistent with the former; female Yellow Warblers parasitized at least once during the breeding season reared fewer young to independence annually compared to unparasitized females.

Despite evidence that intensely begging Cowbird nestlings outcompeted host offspring for parental food deliveries, empirical evidence that host nestlings were in poorer condition when raised alongside Cowbirds is mixed (Smith 1981, Weatherhead 1989, Clotfelter and Yasukaw 1999, Chace et al. 2000, Rivers et al. 2010). However, some evidence suggested that only female host nestlings were at a competitive disadvantage in obtaining food resources (Zanette et al. 2005). Results of this observational study provided little evidence that Yellow Warbler nestlings were in poorer condition when raised with a Brown-headed Cowbird nestling. We also failed to find evidence that competition between nest mates in parasitized Yellow Warbler nests led to female biased mortality that skewed the nestling sex ratio. Reasons why we found no evidence that brood parasitism influenced nestling condition or sex ratio include; 1) our sample sizes for parasitized broods were too small to detect differences; or 2) condition differences only become apparent once nestlings have fledged, as parents continue partitioning more food resources to brood-parasitic young relative to host young (Smith 1981); 3) condition and sex ratio alterations may be evident in some host species i.e., Song Sparrows (Smith 1981, Zanette et al. 2005) but not others; or 4) cowbirds preferentially parasitize females that will provide greater levels of parental care. We have little reason to suspect that host species having smaller body sizes relative to Cowbirds, such as Song Sparrow and Yellow Warblers would be affected differently by Cowbirds. In fact, given the size differential between Yellow Warblers and Brown-headed Cowbirds is substantially greater than that between Song Sparrows and Cowbirds, we would have expected a greater effect of parasitism on nestling condition in Yellow Warblers. Further examination of sex-specific post-fledgling survival and recruitment into the breeding population would be necessary to determine whether the prolonged effect of parents allocating more resources reduced host fledgling condition and survival to adulthood.

Based on the hypotheses for age-related improvements in breeding performance, we expected that the dichotomy in acceptance and rejection responses to parasitism would be explained by host age. Counter to predictions, our results showed no support that older Yellow Warblers are parasitized less by Cowbirds. Most age-specific studies on Cuckoo hosts found evidence that older or more experienced hosts were parasitized less often (Brooker and Brooker 1996, Langmore and Kilner 2007) and rejected brood parasitism more frequently (Lotem et al. 1992, 1995; but see Moskát and Hauber 2007, Langmore et al. 2009). However, few studies have demonstrated this to be true of Brown-headed Cowbird hosts. Unlike Cowbird nestlings, Cuckoo nestlings evict all host eggs and nestlings. Consequently, Cuckoo hosts do not successfully raise young whereas, in Cowbird-parasitized clutches, host young can potentially survive to fledge when raised alongside parasitic nest mates (Payne 1977 and this study). Based on the evolutionary equilibrium hypothesis; hosts accept when the costs of rejecting are lower than the costs of accepting parasitism, we might expect the evolution of rejection strategies to be more advantageous and 'fine tuned' for Cuckoo hosts relative to Cowbird hosts (Roskaft et al. 1990, Payne and Payne 1998; Lorenzana and Sealy 1999; Davies 2000).

Our predictions that with time and experience, hosts would learn strategies to avoid and deal with brood parasitism was developed from the perspective of the host and assumed that hosts had the ability to adapt strategies that minimize the costs of parasitism. Alternatively, Cowbirds might preferentially parasitize older and higher quality parents. Other studies on Song Sparrow (Smith et al. 1984) and Magpie (*Pica*

pica; Soler et al. 1995) hosts found similar results suggesting that Cowbird and Cuckoos select for more successful parents by cueing in on condition signals such as nest defence and nest size. This suggests that brood parasitism events might be non-random and that individuals with higher breeding performance, such as older individuals might be differentially impacted by brood parasitism (Krüger 2007). Our study suggests that Cowbirds do not have a strong preference for high quality hosts since older Yellow Warbler females were parasitized only slightly more often than yearlings.

We expected that once parasitized by Brown-headed Cowbirds, older females that accepted host eggs would be less impacted by the reproductive costs of brood parasitism compared to yearling Yellow Warbler females. Contrary to our predictions, our analysis suggested that older females suffered similar cumulative costs of brood parasitism as yearling females. There was also little indication that older females parasitized at least once during the breeding season were better able to compensate for net losses in annual productivity across other nesting attempts. Our results were contrary to results from a study by Smith (1981) that found that for older Song Sparrow breeders, annual productivity was less reduced by brood parasitism compared to younger breeders. However, Song Sparrows are multi-brooded, rearing up to four broods of 1-4 young per year (Smith and Roff 1980, Zanette et al. 2005), whereas Yellow Warblers typically produce only one successful brood per breeding season. Older Song Sparrows might therefore be better able to compensate for reduced fecundity in parasitized nests by subsequently raising more broods (Smith 1981, Nol and Smith 1987), whereas older Yellow Warbler females have less reproductive opportunity to do so per breeding season.

In summary, this study found that brood parasitism reduced the reproductive success of yearling and older Yellow Warblers. Other studies suggested that parasitism rates and/or responses to parasitism are non-random with respect to female age in a suite of host species (Victoria 1972, Smith 1981, 1984, Lotem 1992, Brooker and Brooker 1996, Langmore and Kilner 2007, Payne and Payne 1998). Alternative studies have demonstrated little evidence that age or experience influences anti-parasitic strategies (Brooker and Brooker 1996, Sealy 1995, Payne and Payne 1998, Amundsen et al. 2002), suggesting that the dynamics between hosts and parasites might be species-specific. Future studies should examine whether the relatively short-term costs of brood parasitism on reproductive success have longer-term carry-over effects on future adult survival.

2.6 Figures

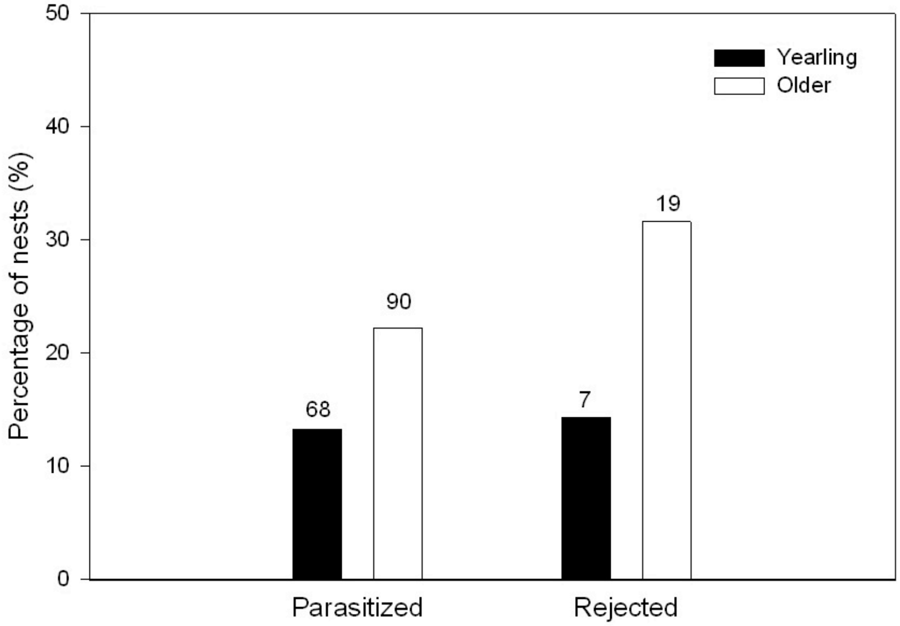

Figure 2-1. The percentage of parasitized (n=158) Yellow Warbler nests and the percentage of brood parasitized nests that were rejected (n=26) through abandonment or egg burial for yearling (closed bar) and older females (open bar) across the five study years (2004-2006, 2008-2009). Numbers above the bars represent the number of nests within each female age category.

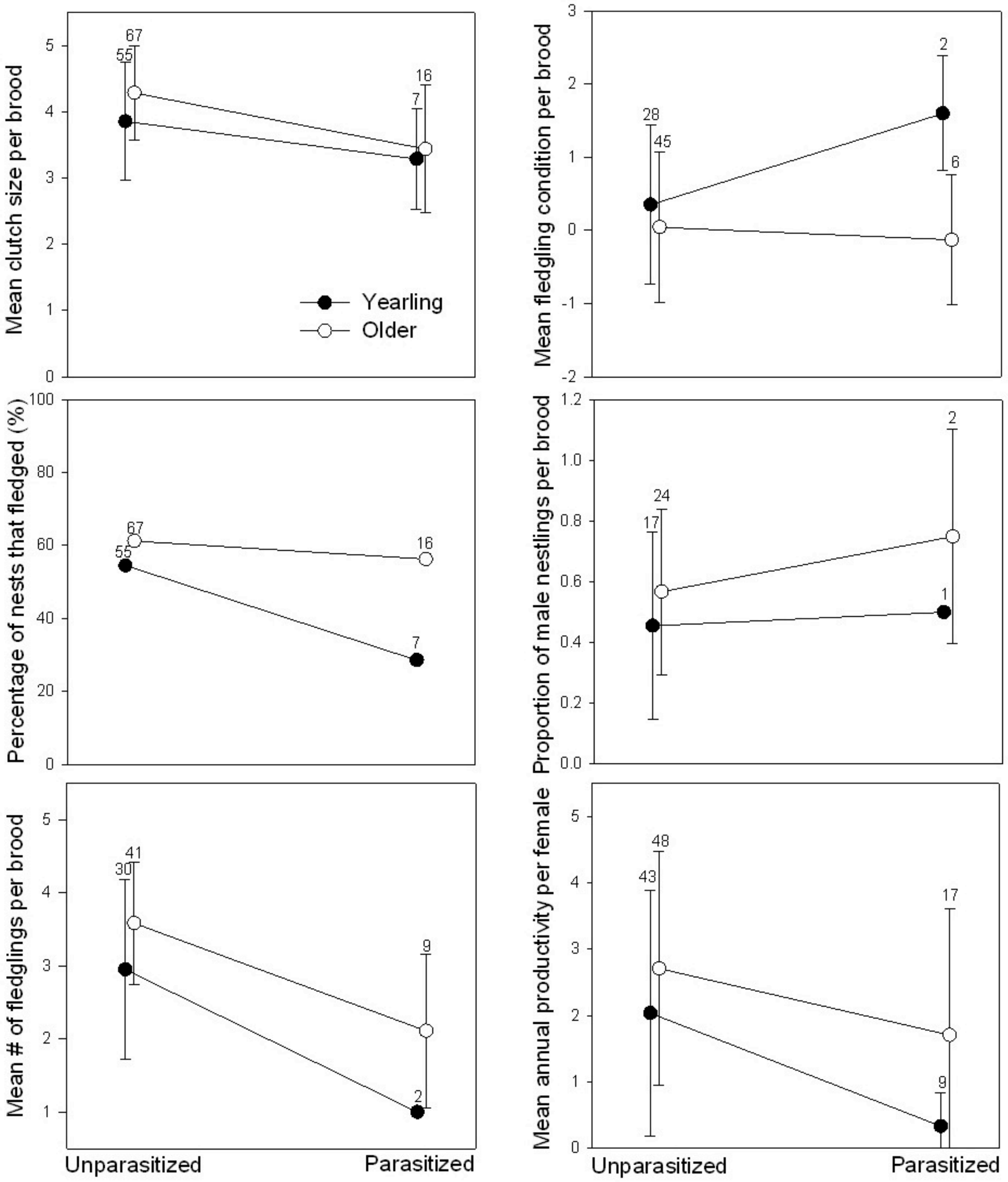

Figure 2-2. Breeding performance (±SD) of yearling (open circle) and older (closed circle) females in parasitized and unparasitized Yellow Warbler broods across the five study years (2004-2006, 2008-2009). The 6 measures of breeding performance assessed included; (a) mean number of host eggs laid per brood (n=145); (b) percentage of fledged Yellow Warbler nests (n=145); (c) mean number of fledglings produced from successful nests (n=82); (d) mean condition of fledglings per brood (n=81); (e) mean proportion of males out of the number of nestlings sampled from a brood (n=81); and (f) annual productivity per female (n=117). Numbers above the bars represent the number of nests (a-e) or females (f) within each category.

2.7 Tables

Table 2-1. Summary of top ranked AIC*c* models (ΔAIC_c <2) predicting brood parasitism and rejection response of parasitized Yellow Warbler females breeding in Revelstoke, British Columbia between 2004-2006 and 2008-2009. Parasitism (n=158) was assessed in relation to host female age (AGE; yearling or older), nest initiation date and nest initiation date squared (DATE + DATE^2), and YEAR. Rejection response (n=26) was examined in relation to AGE, DATE + DATE^2, and nesting stage (STAGE; pre-laying, 1 egg laid, more than 2 eggs laid, incubation or later). Other notations include: interaction (*) and additive effects (+) between factors. AIC_c is Akaike's information criterion adjusted for small sample size, ΔAIC_c is the difference in AIC_c value from that of the top ranked model, w_i is the Akaike weight, and *K* is the number of parameters in the model +1 for intercept. Candidate models are listed by ΔAIC_c.

Model	***K***	**AIC*c***	**ΔAIC*c***	w_i
Parasitism:				
YEAR	5	147.247	0.000	0.309
YEAR + AGE	6	147.672	0.425	0.250
DATE + DATE^2 + YEAR	7	148.995	1.748	0.129
Rejection response:				
NULL	1	30.444	0.000	0.369
AGE	2	30.903	0.459	0.293

Table 2-2. Summary of top ranked (Q)AIC$_c$ models (Δ(Q)AIC$_c$ <2) examining breeding performance of Yellow Warbler females in Revelstoke, British Columbia between 2004-2006 and 2008-2009. Breeding performance measures [clutch size (n=145), nesting success (n=145), number fledged (n=82), fledgling condition (n=81), proportion male (n=44), and annual productivity (n=117] were assessed in relation to DATE and DATE^2, YEAR, AGE, whether parasitized (PAR). Fledgling condition was also assessed in relation to brood size (BSIZE). QAIC$_c$ is adjusted for over-dispersion. See Table 2-1 for additional explanations of parameters.

Model	***K***	**(Q)AIC$_c$**	**Δ(Q)AIC$_c$**	**w$_i$**
Clutch Size[a]:				
DATE + DATE^2 + YEAR + AGE + PAR + PAR*AGE	11	313.965	0.000	0.478
DATE + DATE^2 + YEAR + AGE + PAR	10	315.223	1.258	0.255
DATE + DATE^2 + YEAR + PAR	9	315.356	1.391	0.238
Nesting Success:				
DATE + DATE^2 + YEAR	7	189.669	0.000	0.193
DATE + DATE^2 + YEAR + PAR	8	189.745	0.076	0.186
DATE + DATE^2 + YEAR + AGE + PAR	9	190.108	0.439	0.155
DATE + DATE^2 + YEAR + AGE	8	190.168	0.499	0.151
DATE + DATE^2 + YEAR + AGE + PAR + PAR*AGE	10	190.645	0.976	0.119
Number fledged[a]**:**				
DATE + DATE^2 + AGE + PAR + PAR*AGE	7	230.204	0.000	0.667
Fledgling condition[b]**:**				
BSIZE + AGE	5	227.710	0.000	0.289
BSIZE + AGE + PAR + PAR*AGE	7	227.855	0.146	0.268
BSIZE + AGE + PAR	6	228.764	1.054	0.170
NULL	4	222.860	1.150	0.162
BSIZE + PAR	5	222.640	1.930	0.110
Proportion male:				
NULL	2	101.347	0.000	0.314
PAR	3	101.741	0.395	0.257
AGE	3	102.399	1.053	0.185
AGE + PAR	4	102.923	1.576	0.143
Annual productivity[b]**:**				
AGE + PAR	5	157.786	0.000	0.274
PAR	4	158.671	0.884	0.176
AGE + PAR + PAR*AGE	6	158.738	0.952	0.170

[a] The number of parameters in the model +1 for intercept and + 1 for model variance.

[b] The number of parameters in the model +1 for intercept, +1 for model variance and +1 for variance inflation factor.

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3: YELLOW WARBLER SURVIVAL: ASSESSING THE IMPACTS OF BROOD PARASITISM AND LARGE-SCALE CLIMATIC CONDITIONS

3.1 Abstract

Understanding the mechanisms responsible for population declines of Neotropical birds requires knowledge of factors that limit population growth at all stages of the annual cycle. Interspecific brood parasites such as Brown-headed Cowbirds (*Molothrus ater*) are known to have negative, short-term consequences on the reproductive success of their hosts. However, few studies have examined the long-term survival costs for parasitized hosts. We colour-banded, resighted, and monitored Yellow Warblers (*Dendroica petechia*) over seven breeding seasons in Revelstoke, British Columbia to assess whether adults that were parasitized and raised Brown-headed Cowbirds nestlings had reduced survival. Survival was lower for yearling (0.349) than for older Yellow Warblers (0.620), but was not influenced by brood parasitism or gender. An examination of large-scale climatic patterns, El Niño/La Niña, suggested that Yellow Warbler survival was influenced by conditions during spring migration prior to breeding, demonstrating the importance of this phase of the life-cycle for population dynamics of this Neotropical migrant.

3.2 Introduction

Birds that reproduce only by laying their eggs in nests of host species, and exploit hosts that provide parental care to unrelated parasitic young comprise 1% of bird species (Davies 2000). Biological hosts of some of these brood parasites are currently undergoing population declines, causing concern that brood parasites may be posing a significant threat to their hosts. For example, 73% of declining North American bird species (n=229) are hosts of Brown-headed Cowbirds (*Molothrus ater*; Oretega et al. 2005a). Although direct evidence is often lacking, Brown-headed Cowbirds have been regarded as a conservation threat, particularly for five host species that are classified as endangered in North America including: Kirtland's Warbler (*Dendroica kirtlandii*), Southwestern Willow Flycatcher (*Empidonax traillii extimus*), Least Bell's Vireo (*Vireo bellii pusillus*), Black-capped Vireo (*V. atricapilla*), and Golden-cheeked Warbler (*D. chrysoparia*; Morrison and Hahn 2002, Ortega et al. 2005b).

In addition to other conservation threats for host species, Brown-headed Cowbirds may contribute to current population declines by reducing host productivity. Hosts that accept parasitized clutches have 1) smaller clutches (Sealy 1992, Hill and Sealy 1994, **Chapter 2**); 2) reduced hatching success (Petit 1991, McMaster and Sealy 1999); and 3) fledglings that are in poorer condition (Marvil and Cruz 1989, Zanette et al. 2005). The cumulative losses due to brood parasitism can result in an overall loss of annual productivity for some host species (Klaas 1975, **Chapter 2**; but see Smith 1981).

Despite wide acceptance among researchers that brood parasitism has significant short-term annual reproductive costs for hosts, few studies have examined whether brood parasitism has a long-term cost. Brood parasitism imposes an energetic cost that may reduce adult survival in hosts. Hosts that accept parasitic eggs invest significantly more time and energy provisioning their brood because parasitic nestlings beg more frequently and more intensely compared to host nestlings (Lichtenstein and Sealy 1998, Dearborn et al. 1998, Sedgwick and Iko 1999, Grim and Honza 2001, Hoover and Reetz 2006; but see Rivers et al. 2010). Hosts that reject brood parasitism by abandoning or burying parasitized clutches incur time and energy costs in laying new clutches, and building more nests (Drent and Daan 1980, Gowaty 1996, Sedgwick and Iko 1999). Additionally, there is some evidence that individuals that reject parasitic eggs have a higher probability of nest predation due to the retaliatory behaviour of brood parasites (Zahavi 1979, Soler et al. 1995, Arcese et al. 1996, Granfors et al. 2001), further prompting hosts to invest time and energy into renesting.

Six studies to date have examined whether brood parasitism by Brown-headed Cowbirds reduces adult survival of their hosts but results from these studies are mixed. Grzybowski (1991) found that receiving a parasitic Brown-headed Cowbird egg reduced adult survival in Black-capped Vireos (*Vireo atricapillus*). Conversely, Willow Flycatchers (*Empidonax traillii adastus*) that were parasitized with a Cowbird egg did not have reduced survival (Sedwick and Iko 1999). Hoover and Reetz (2006) found that adult survival was negatively correlated with the number of Brown-headed Cowbird young raised by double-brooding, male Protonotary Warblers (*Protonotaria citrea*) but see Hoover 2003). In contrast, studies by Smith (1981) and Payne and Payne (1998) found that Song Sparrow (*Melospiza melodia*) and Indigo Buntings (*Passerina cyanea*) that raised Brown-headed Cowbird nestlings had similar return rates as unparasitized adults.

Studies investigating the survival costs associated with brood parasitism suggest that long-term costs may be higher for hosts that are far smaller than brood parasites (Sedgwick and Iko 1999, Hoover and Reetz 2006). However, these studies estimated survival using return rates (the proportion of banded individuals returning in subsequent years, of those marked), rather than using models that estimate and incorporate recapture probabilities into survival estimates. Survival estimates based on return rates could be negatively biased (Martin et al. 1995, Sandercock 2007) and may not be accurate enough to detect survival costs of brood parasitism in some host species. Alternatively, return rate estimates could potentially overestimate the survival costs if parasitized individuals were more likely to change breeding sites. Thus, there is need to reassess the effects of brood parasitism on survival using more robust analysis techniques that incorporates resighting probabilities

An additional explanation to explain why some studies found no effect of parasitism on adult survival is that other factors encountered during the lifecycle may have greater effects on adult survival compared to brood parasitism. For example, several studies suggested that large-scale environmental conditions El Niño/La Niña could have a significant impact on the survival of songbirds (Sillett et al. 2000, Nott et al. 2002, Mazerolle et al. 2005). Climate events influencing conditions at stopover sites and on migration had a large impact on the annual survival of Black-throated Blue Warblers (*Dendroica caerulescens*). In the Black-throated Blue Warbler, mortality during the spring and fall migration period is estimated to be 15 times higher than during either the summer or winter stationary period (Sillett and Holmes 2002; Carlisle et al 2009).

In the current study, we assessed whether a small (9-10g), typically single-brooded host, the Yellow Warbler, had lower survival in years after being parasitized by a Brown-headed Cowbird. We conduct separate analyses to examine the survival costs associated with receiving a parasitic egg and raising a parasitic nestling. We also examine whether survival costs associated with brood parasitism vary with sex and age because these factors are known to impact survival of songbirds in other studies (Cilimburg et al. 2002, Stutchbury et al. 2009). Finally, we evaluate whether large-scale climate conditions (El Niño/La Niña) expected to influence conditions at three stages of the annual cycle affect adult survival, potentially masking or overwhelming any survival costs associated with brood parasitism.

3.3 Methods

3.3.1 Study Sites

Our study was conducted in Revelstoke Reach, situated within the drawdown zone of Arrow Lakes Reservoir, a 240 kilometer-long reservoir system in the upper Columbia River valley separating the Monashee and Selkirk mountain ranges, east of the Kootenay region of British Columbia, Canada (N50.58’56”/W-118.20’00”). Water levels in the Arrow Lakes reservoir were controlled by hydroelectric dam operations behind the Hugh Keenleyside Dam, upstream of the city of Castlegar, British Columbia. Three study sites, each 30-39 ha, were established in the upper reaches of the floodplain (435-441 m elevation). Study sites were periodically subject to flooding in some years of the study and were representative of locally existing riparian vegetation compositions ranging from dense stands of mature black cottonwoods with a diverse understory at higher elevations (>440 m) to more isolated patches of willow at lower elevations (<438 m).

3.3.2 Study Species

The Yellow Warbler is a small (9-10g), Neotropical migrant with a wide breeding range that extends across much of North America, with northern limits defined by the presence of shrub vegetation south of the tundra. (Lowther 1999). Populations of Yellow Warblers breeding in Revelstoke, BC, and elsewhere in western North America are associated with wet riparian habitats and vegetation such as willow and other low-lying shrub species, and deciduous trees such as black cottonwood (Cilimburg et al. 2002). In Western North America, Yellow Warblers begin to arrive on their breeding grounds in late April to early May and breeding extends from May until mid to late July (Campbell et al. 2001, Quinlan 2009). Males return to the breeding grounds and establish territories prior to the arrival of females (Quinlan 2009). Breeding pairs typically rear one successful brood of up to 5 fledglings per year; second broods are attempted but are rarely successful (Quinlan 2009). Females are solely responsible for nest building and provide all parental care during egg-laying and incubation (Lowther 1999). However, both males and females provision young during the nestling and post-fledging period (Lowther 1999). Breeding populations migrate south to wintering grounds in Mexico and South America in late July to mid August, and remain on wintering grounds until northward migration in late March to late April (Lowther 1999). Genetic and isotope data from birds captured on wintering grounds suggests that Yellow Warblers breeding in British Columbia overwinter across Mexico and Central America, migrate through western and central North America (Nevada) in the spring, and through California and New Mexico in the fall (Boulet et al. 2006).

Across its breeding range, the Yellow Warbler is frequently parasitized by Brown-headed Cowbirds (Schrantz 1943, McGeen 1972, Clark and Robertson 1981, Lowther 1984, Hobson and Sealy 1989). In a long-term Yellow Warbler monitoring program running from 1974 to 1991 (excluding 1977) in the Delta Marsh, Manitoba Canada (50°11'N, 98°19'W), an average of 21% (n=1885) of monitored nests were parasitized by Brown-headed Cowbirds. In British Columbia, Yellow Warblers are a common host of Brown-headed Cowbirds (Campbell et al. 2001) and parasitism rates range between 11-16% (Campbell et al. 2001). Yellow Warblers have been demonstrated to exhibit adaptations to Brown-headed Cowbirds prior to being parasitized including: nest guarding, aggressive behaviour, and alarm calls (Burgham and Picman 1989, Hobson and Sealy 1989). When parasitized, Yellow Warblers accept and continue caring for parasitic Cowbird eggs in approximately 50-60% of parasitized nests (Sealy 1995). However, Yellow Warblers are considered to be a 'rejecter' host to brood parasitism; hosts that have been demonstrated to respond to brood parasitism by abandoning the parasitized clutch, or burying the parasitic egg or the parasitized clutch, and renesting atop the parasitized clutch (Clark and Robertson 1981, Rothstein 1990, Sealy 1995, Hosoi and Rothstein 2000). Rejection is more likely to occur when Cowbird eggs are laid during the first half of the clutch initiation period, and in clutches initiated early in the breeding season (Sealy 1995). Yellow Warblers are more likely to abandon nests containing Cowbird eggs or nests where egg removal by Cowbirds has reduced clutch size below a species-specific size threshold (Rothstein 1982, Sealy 1992).

3.3.3 Yellow Warbler Captures and Resightings

In each year of study, we located and recorded the band combinations of all colour-banded birds that returned to the study area from previous years. We also attempted to catch all banded and unbanded breeding birds that established territories within the three study sites using 12-m mist nests combined with playbacks of Yellow Warbler songs. Males were typically caught within 3 days of their return to the study area. Females were less responsive to playbacks and were more likely to be caught later when incubating or provisioning young. When caught, unbanded birds were fitted with a Canadian Wildlife Service-issued aluminium band and a unique combination of three colour bands. Individuals were assigned a gender and age based on plumage and feather wear (Pyle 1997). Where possible (93%, n=215), adults were classified as yearling (second year birds in their first breeding season) or older females (after second year birds in at least their second breeding season). We classified the remaining 15 individuals as yearling birds because they could not be classified as older birds based on plumage and because once the majority of the breeding population had been banded, birds entering the study population were more likely to be young birds (57%; n=152 based on birds from 2006 onward).

3.3.4 Monitoring Reproduction, Parasitism, and Assigning Breeding Status

From 2004-2006 and 2008-2009, we monitored all study plots at 2-3 day intervals from the time of arrival on the breeding grounds (early May) until independence of the final brood (late July). Monitoring was less intensive in 2007 when we visited the sites from the 5th-21st of May and the 14th-28th of June in order to resight and band breeding birds. In all years except 2007, we attempted to monitor all breeding attempts initiated by banded individuals (approximately 30 pairs per year, range =19-38). Most nests were found during the early stages of nest building stage and laying (76%, n=197). Nests were subsequently checked every 1-4 days to observe clutch initiation date (defined here as the date the first egg was laid), hatch date (defined here as the day the first nestling hatched), and record clutch and brood size. When clutch initiation date was not directly observed, it was estimated by backcounting from the date of hatching. We assumed nests fledged all young banded or observed at nests on day 7, if there were signs of fledging (flattened nest rim feces in nest, fledglings), and if parents were subsequently observed carrying food to fledglings within their territory. Nests were considered successful if they fledged at least one Yellow Warbler young. We assumed nest failure due to predation if all nestlings disappeared before reaching 7 days of age, and if there were signs of predation (egg fragments, nest destroyed or disturbed).

We also documented occurrences and timing of egg-laying by Brown-headed Cowbirds and hatch dates of Cowbird nestlings. We classified individuals as 1) having been parasitized by a Brown-headed Cowbird (if a Brown headed Cowbird egg was laid in one or more clutches initiated during the breeding season; 2) having raised a Brown-headed Cowbird nestling (if a Brown-headed Cowbird nestling hatched from a parasitized clutch); or 3) not known to have been parasitized or to have raised a Brown-headed Cowbird. The latter category may include some individuals that were parasitized since the contents of nests at heights greater than 6m were not assessable and the status of these nests was monitored with binoculars.

We distinguished between breeding birds and transient birds in all years. We considered breeding birds to be those that established territories, attempted to form pair bonds, and bred at one of our sites in at least one year of study. Transient birds were captured at the study site during banding operations but were not resighted on subsequent days and did not initiate breeding attempts at our sites. Transient birds were subsequently excluded from the survival analysis.

3.3.5 Statistical Analysis

Adult annual survival (φ) and recapture (*P*) rates were estimated using methods described by Lebreton et al. (1992) and Cooch and White (2009) with program MARK version 5.1 (White and Burnham 1999). We defined φ as the probability that a Yellow Warbler survived and returned to our study sites between consecutive years of study and *p* as the probability of encountering a Yellow Warbler if alive and at our study sites. We began our analysis by first defining our global (most parameterized) model (Burnham and Anderson 2002). Our global model allowed survival rates to vary with gender, yearling birds in their first breeding season to differ from older birds in at least their second breeding season, and between each year of the study. Our global model allowed recapture rates to vary with gender and between years with extensive study (2004-2006 and 2008-2009) and the year with less extensive study (2007) since resighting and monitoring efforts were reduced in 2007. Our global model was therefore described as:

$$\phi(g + a + t + g * a + g * t + g * a + g * a * t)\ P(g + t/2007 + g * t/2007)$$

where *g*=gender, *a*=age, *t*=time-dependence, and *t/2007* is time dependence with 2007 differing from all other years.

We assessed the goodness-of-fit for the global model by estimating the variance inflation factor (ĉ) using the parametric bootstrap and median procedures implemented in program MARK (White and Burnham 1999, Cooch and White 2009). Parametric bootstrap and median procedures estimated ĉ to be 1.4 and 1.1, respectively, suggesting that our global model fit our data adequately (Burnham and Anderson 2002). We used the higher, more conservative, estimate of ĉ to correct for over-dispersion in the data before comparing models in our candidate models sets (Burnham and Anderson 2002). Results were also compared using the smaller ĉ value (1.1). We restricted our candidate models to the global model plus nested models, following the approach of Lebreton et al. (1992). We first modelled recapture rates to determine the best model structure for the recapture rate. We then modelled survival rates with candidate models containing sex, age, time, and all possible interactions, and a model with constant survival over time (denoted as ".") to serve as a null model (Cooch and White 2009).

To determine whether Brown-headed Cowbird brood parasitism explained additional variation in apparent survival probabilities, we compared models with the parasitism covariates (parasitized by a Brown-headed Cowbird egg or not; denoted *BHCOe*, and raised a Brown-headed Cowbird nestling or not; denoted *BHCOn*) and possible interactions with sex (*s*) and age (*a*). There were some uncertainties about individuals that were classified as 'not parasitized' because nests that were placed greater than 6m were visible only with binoculars. We therefore re-ran the *BHCOe* analysis with three factors (known to be parasitized, not parasitized, and unknown parasitism history). We similarly re-ran the *BHCOn* analysis with three factors (known to have raised a Cowbird nestling, did not raise a Cowbird nestling, not known to have raised a Cowbird nestling). Re-analysis did not change our conclusions about the impacts of parasitism on adult survival so only the results of the initial analyses are presented.

Finally, we examined whether environmental covariates could explain additional temporal variation in survival estimates. We used mean standardized values of the Southern Oscillation Index (SOI) over three time periods ($SOI_{Nov\text{-}Feb}$, $SOI_{May\text{-}Aug}$, and $SOI_{Mar\text{-}May}$) that influence conditions at different stages of the annual cycle (Figure 3-1) as a measure of El Niño/Southern Oscillation (ENSO) covariates in our candidate model set (Philander 1990, NOAA 2010). Variation in Yellow Warbler survival was examined in relation to the best-supported survival model and models that contained each SOI time period independently. Due to small sample sizes, no interactive terms or additive SOI terms were included in the candidate models. Large, negative SOI values are associated with El Niño conditions, whereas large, positive SOI values are associated with La Niña events. El Niño events in the winter and spring (November to February) are associated with warm, dry conditions in British Columbia (Ropelewski and Halpert 1986), leading to earlier spring flowering (Beaubien and Freeland 2000) and higher insect availability (Swetnam and Betancourt 1998) in the subsequent breeding season. We therefore predicted that mean $SOI_{Nov\text{-}Feb}$ would be negatively related to survival. La Niña conditions in the summer (May to August) are statistically correlated with an increase in summer monsoon rainfall on wintering grounds along the continental coast of Mexico (Caso et al. 2007), presumably leading to greater primary productivity and higher insect availability during the winter. We therefore predicted that mean $SOI_{May\text{-}Aug}$ would be positively related to survival. Finally, El Niño events in early spring (March to May) are associated with light southerly winds (Nott et al. 2002) that are favourable for migration (Richardson 1990). We therefore predicted that mean $SOI_{Mar–May}$ would be negatively related to survival.

We used Akaike's Information Criterion (AIC; Burnham and Anderson 2002), corrected for small sample sizes (AIC_c) and over-dispersion ($QAIC_c$), as computed by Program MARK, to test the relative support of competing models. $\Delta(Q)AIC_c$ values were calculated as the differences between the $QAIC_c$ of each model and that of the most parsimonious model (model with the lowest $QAIC_c$). For each analysis, candidate models were then ranked relative to one another using $QAIC_c$ weights (w_i). Models with high w_i values were the best-supported by the datasets. Parameter estimates and their associated unconditional standard errors were also calculated to assess the relative influences of the variables present in competing models. $QAIC_c$ parameter likelihoods were calculated as the sum of the w_i of all competing models in which the parameter occurred. $QAIC_c$ parameter estimates were calculated as the mean estimate (across all competing models) of each parameter weighted by the w_i of each model in which the parameter was included. AIC unconditional standard errors were calculated based on the standard error of each parameter weighted by the AIC_c weight of each competing model in which the parameter occurred. We calculated survival estimates based on the best-supported candidate model, as well as model-averaged survival estimates.

3.4 Results

During the 6-year period of study, 215 (111 females, 104 males) locally breeding adult Yellow Warblers were banded within our study area. Collectively, these individuals contributed 141 between-year recaptures for a total of 356 encounter histories. Fifty-nine percent of females and fifty-five percent of males were banded as yearling birds. Brown-headed Cowbirds were observed to parasitize between 9% and 44% of breeding pairs a year (mean = 19%, n=118 pairs). However, across all years, relatively few pairs raised a nestling Cowbird (9%, n=118 pairs; range 0% in 2004, 12% in 2006).

3.4.1 Survival and Recapture Probabilities

Recapture probabilities were best modelled with the inclusion of a gender term and no time dependence. Of the 5 models tested, the model containing the gender term obtained nearly twice the support of the next highest ranked model, which included a gender term and allowed for recapture probabilities in 2007 to differ from all other years (w_i= 0.468 versus 0.262; Table 3.1). The best model estimated that the recapture probabilities (± SE) were lower for females (0.629 ± 0.110) than males (0.895 ± 0.052).

In the survival analysis, three models out of the 16 tested models received high support ($\Delta QAIC_c < 2$). Each high-ranking model contained the age term (Table 3-1, Appendix E, F). The highest ranked model, which contained only age, received more than twice the support of the next highest ranked (w_i = 0.413; Table 3-1, Appendix E, F). The second ranked model which contained age and gender, received essentially the same support as the next highest ranked model, which contained age and time (w_i = 0.201 and 0.163, respectively; Table 3-2, Appendix E). Combined, the three models that received highest support ($\Delta QAIC_c < 2$) accounted for 77% of the overall support. Model ranking was sensitive to the ĉ value used to correct for over-dispersion. Four models in the candidate model set received strong support when using the smaller of the two calculated ĉ values (ĉ=1.1). The highest ranked model that included the age and time terms received the same level of support as the second ranked model that contained the age term (w_i = 0.289 versus 0.226, respectively; results not shown). The third and fourth highest ranked models included the gender term with age and time, and the gender term with age, respectively, but had the combined overall support of only 29%. Together, model ranking using conservative and small ĉ values provide strong support for the age and time parameters, and relatively little support for the gender parameter. Yearlings had lower survival compared to older Yellow Warblers, and females had lower survival than males (Appendix F). Model averaged survival estimates based on most conservative estimate of ĉ (1.4), indicated survival estimates (± SE) ranged between 0.299 ± 0.114 in 2007 and 0.67 ± 0.136 in 2004 for yearlings, and between 0.318 ± 0.100 in 2007 and 0.697 ± 0.124 in 2004 for older Yellow Warblers (Figure 3-2).

3.4.2 Survival and Brood Parasitism Covariates

There was little evidence that survival was reduced in yearling or older individual that were parasitized with a Brown-headed Cowbird egg (Table 3-2, Appendix F, G). The model containing the additive effect of age and parasitized with Brown-headed Cowbird egg had strong support ($\Delta QAIC_c < 2$) of the 12 models tested, but had far less support than the top-ranked model that contained only the age parameter (w_i=0.135 versus 0.308, respectively; Table 3-2, Appendix G). An additional four models with the Brown-headed Cowbird egg covariate received moderate support (ΔQAICc < 4). The remaining five models containing the Brown-headed Cowbird egg covariate having essentially no support (ΔQAICc < 4; Table 3.4). Although the Brown-headed Cowbird egg covariate was present in one model that received high support, standard errors were high (0.405) and confidence intervals for this parameter bound zero (Appendix F), suggesting the parameter may be present as a spurious covariate (Guthery et al. 2005) in the model receiving high support.

Model selection indicated little support that raising a brown-headed Cowbird nestling reduced the survival of yearling or older Yellow Warbler individuals (Table 3-2, Appendix F, G). Models that received high support (ΔQAICc < 2) included age, the additive effect of gender and age, and the additive effect of age and time, together accounting for 65% of the overall model support when $\hat{c}$ was 1.4 (Table 3-2, Appendix G). Three of the nine models containing the Brown-headed Cowbird covariate received moderate support (ΔQAICc < 4), but together accounted for only 23% of the overall support, and standard errors for the covariate were high (0.610), and bounded zero (Appendix F).

3.4.3 Survival and Environmental Covariates

There was a strong effect of both age and $SOI_{Mar-May}$ on annual survival of adult Yellow Warblers (w_i =0.708; Figure 3-3, Table 3-2, Appendix F, G). Beta-estimates for the top-ranking model indicated a negative effect of SOI (-0.619) that was consistent with our prediction that ENSO affects survival conditions during the spring migration period of the lifecycle (Appendix F). The model containing $SOI_{Mar-May}$, the only model to receive high support ($\Delta QAIC_c < 2$) out of the 5 models tested, had approximately 7 times more support than the next highest ranked model that included the age parameter (w_i =0.708 vs. 0.127, respectively; Table 3-2, Appendix G). There was no support (ΔQAICc >4) for either of the other environmental covariate models ($SOI_{Nov-Feb}$ and $SOI_{May-Aug}$). Furthermore, Beta-estimates for $SOI_{May-Aug}$ model were negative (-0.185; Appendix F), and therefore inconsistent with our predictions that conditions on wintering grounds during La Niña events are favourable for overwintering Yellow Warblers.

3.5 Discussion

Our analysis of a seven-year mark-recapture dataset provided evidence that survival of adult Yellow Warblers varies with age and time, but little evidence that local survival varies with sex or is reduced as a result of brood parasitism. Model weighted parameter estimates indicated that the local survival of yearling birds is 26% less than older birds (0.349 versus 0.620). Many other studies have found that survival increased with age in birds (Lack 1966, Sæther 1990, Brown and Roth 2002, Kostecke and Cimprich 2008). Yearling Yellow Warblers might be expected to have lower survival because they are outcompeted by older individuals for high quality habitat (Marra and Holmes 2001). Age related survival could also arise because of juvenile inexperience in predator avoidance, foraging, and social interactions (Brown 1975, Slater 1983, Wunderle 1991). Alternatively, variation in survival might reflect differences in the dispersal behaviour of yearling and older birds. Breeding dispersal is often related to reproductive success (Payne and Payne 1993, Haas 1998), and yearling birds with higher failure rates (**Chapter 2**) may therefore be more likely to disperse than older birds. We have observed little annual breeding dispersal between three study sites that are separated by 1-20 km (1% individuals, n=75 monitored ≥ 2 years). However, we are unable to rule out the possibility that age variation in survival is driven by differences in dispersal rates. Because breeding dispersal can bias estimates of survival in Yellow Warblers (Cilimburg et al. 2002), we suggest that our survival estimates for yearling birds be treated more cautiously than estimates for older birds.

Long-term studies frequently document variation in adult survival across years (Mazerolle 2005, Kostecke and Cimprich 2008, Salgago-Ortiz 2008). The model averaged parameter estimates in our study suggested that survival of yearling birds varied between 0.299 ± 0.114 to 0.439 ± 0.157, and for older birds varied from 0.561 ± 0.099 to 0.697 ± 0.124. Variation in annual survival is similar to previous studies of *Dendroica* species, which ranged between 0.480 ± 0.050 and 0.600 ± 0.060 (Yellow Warbler; Mazerolle 2005), and 0.318 ± 0.045 and 0.545 ± 0.060 (Black-throated Blue Warbler; Sillett and Holmes 2002). Annual variation in survival has been attributed to large-scale environmental patterns (Mazerolle 2005, Nott et al. 2002, Sillett and Holmes 2002). However, previous studies have used a variety of time periods to assess environmental impacts. Our model suggested that ENSO impacts on migration have a greater effect than ENSO effects on breeding and wintering stages. Similarly, Nott et al. (2002) found that ENSO events that influence conditions during spring migration can influence annual survival. Our results provide additional evidence to the argument that migration is the most limiting period of the annual lifecycle (Carlisle et al. 2009).

Our results show ENSO impacts on survival based on a relatively short time series. Other survival studies range in length from nine or ten years (Nott et al. 2002 and Mazerolle et al. 2005, respectively), to significantly longer (37 years; see Anders and Post, 2006). Due to the relatively small time series for our study (seven years), our results should be treated as preliminary and interpreted with caution. We do however view our method of evaluating survival impacts of ENSO at multiple stages of the annual cycle to be superior to drawing conclusions from one time period within the annual cycle. In the current study, we did not examine the impacts of survival during fall migration and suggest that this phase of the lifecycle requires further consideration. The small time series has limited our ability to increase the number of competing models to include additive effects of SOI at multiple stages within the annual cycle.

Adult survival is generally found to be higher for males relative to females in many small songbird species (reviewed by Breitwisch 1989, Brown and Roth 2002, Sillett and Holmes 2002). Survival rates of male Yellow Warblers have also been reported to be higher than females (Mitra 1999, Cilimburg et al. 2002, but see Mazerolle et al. 2005). Sex specific differences in survival rates may result from 1) unequal costs associated with reproduction on the breeding ground (Breitwisch 1989, Visser and Lessels 2001); 2) competitive exclusion from optimal foraging habitat during migration (Yong et al. 1998), or on wintering grounds (Marra 2000, Marra and Holmes 2001); and 3) a consequence of higher breeding dispersal (Martin and Li 1992, Cilimburg et al. 2002). Our results however, do not provide convincing evidence that survival rates vary with sex in Yellow Warblers. This is consistent with previous work on Yellow Warblers in the Delta Marsh, Manitoba, Canada (Mazerolle et al. 2005).

Our study provides little evidence that being parasitized with a Brown-headed Cowbird egg imposes a significant survival costs on Yellow Warblers. One other study has failed to detect a significant effect of brood parasitism (received a Cowbird egg) on survival (e.g. Sedgwick and Iko 1999). Only one study, conducted on Black-capped Vireo, has concluded that receiving a parasitic egg reduced survival (Grzybowski 1991). However, this study has since been criticized for basing results on correlative evidence that return rates were low in years when parasitism rates were high, rather than based on return rates of parasitized relative to unparasitized individuals (Grzybowski 1991, Hoover, 2003). One explanation for why parasitism may not impose a cost that can be detected using survival models even though it frequently causes females to abandon a clutch and initiate a new breeding attempt (Clark and Robertson 1981, Guigueno and Sealy 2010) is that higher quality individuals expected to have higher survival are preferentially targeted by Cowbirds. However, evidence that Cowbirds selectively target older, and potentially higher quality, parents is limited (**Chapter 2**). Alternatively, we might not detect an impact of parasitism on survival because other factors can have similar consequences. Nests can be abandoned due to disturbance or predators (Rothstein 1975, Clark and Robertson 1981) and females can initiate second and third breeding attempts after previous attempts are depredated (Lowther 1999).

We expected that Yellow Warblers would be more likely to suffer survival costs as a result of brood parasitism if they hatched and raised a Brown-headed Cowbird nestling. Studies suggest that provisioning parasitic young can significantly increase the energetic expenditure of small hosts (Trine et al. 1998, Kilpatrick 2002, Kilner 2003, Hoover and Reetz 2006), such as Yellow Warblers. Hoover and Reetz (2006) found that survival rates of male Prothonotary Warblers were 2.7 times lower for males that raised three or more Cowbird young than males that raised no parasitic young. However, our study found no evidence that Yellow Warblers that reared Brown-headed Cowbird young had reduced survival. Survival effects may not have been detected in our study because the costs of raising one parasitic nestling are small and unlike the Prothonotary Warbler, Yellow Warblers never raised more than one Brown-headed Cowbird per year. Survival effects of parasitism may have existed, but were undetectable because the number of pairs raising nestlings was low (between 0 and 13% of pairs per year, n=118). Greater effects of ENSO that influence all birds in our population during spring migration may have masked the survival costs of raising a parasitic nestling. The later point could be possible since in the Black-throated Blue Warbler, mortality during migration was fifteen times greater then while on staging grounds (Sillett and Holmes 2002).

In summary, although Brown-headed Cowbirds are known to influence the productivity of many host species (Klaas 1975; Smith et al. 2002), including the Yellow Warbler (**Chapter 2**), we found little evidence that brood parasitism by Brown-headed Cowbird has additional long-term costs on Yellow Warbler survival. We acknowledge this conclusion assumes that Cowbirds to not actively seek out high quality hosts and differences in the quality of hosts that are parasitized and unparasitized do not confound estimates of the costs of parasitism. Apparent survival of Yellow Warblers was impacted by large-scale environmental patterns that occurred during spring migration. We advocate that studies attempting to examine the impacts of ENSO on survival should evaluate competing mechanisms that are predicted to regulate survival at various stages of the lifecycle, as we have attempted in the current study. Future studies are needed to determine ENSO impacts during fall migration and to evaluate whether large-scale climate conditions can have additive effects throughout the annual cycle.

3.6 Figures

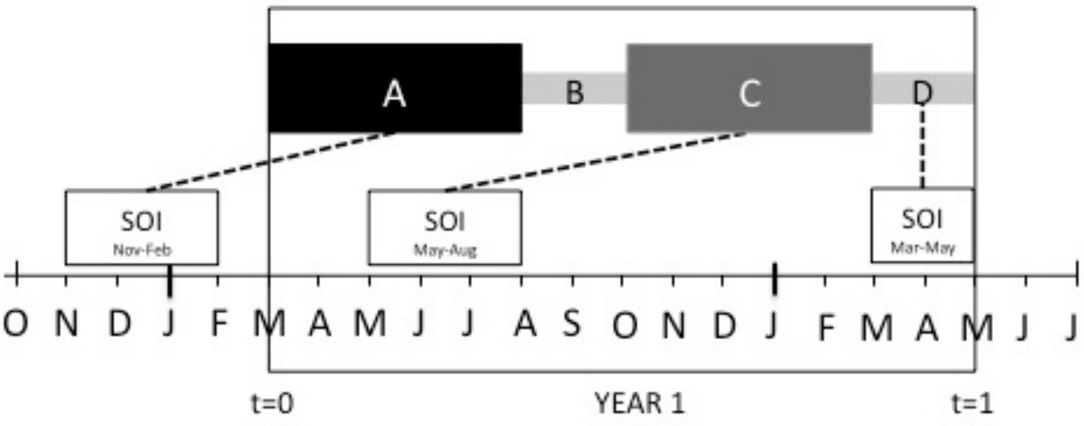

Figure 3-1. Chronology of three competing ENSO indices analyzed in relation to the Yellow Warbler survival time period. The x-axis delimits a 22-month time period. Survival in "Year 1", is monitored by resighting birds on breeding grounds in May at time (*t*)=0, to breeding grounds in May *t*=1 and is inclusive of survival across four stages in the lifecycle (closed boxes; breeding grounds (A), during fall migration (B), on wintering grounds (C), and spring migration (D)). The three El Niño/Southern Oscillation phases (ENSO; open boxes) tested corresponded to mean monthly Southern Oscillation Index (SOI) values indicated. Each SOI phase was predicted to impact different staging grounds utilized by Yellow Warblers in "Year 1" (dotted lines).

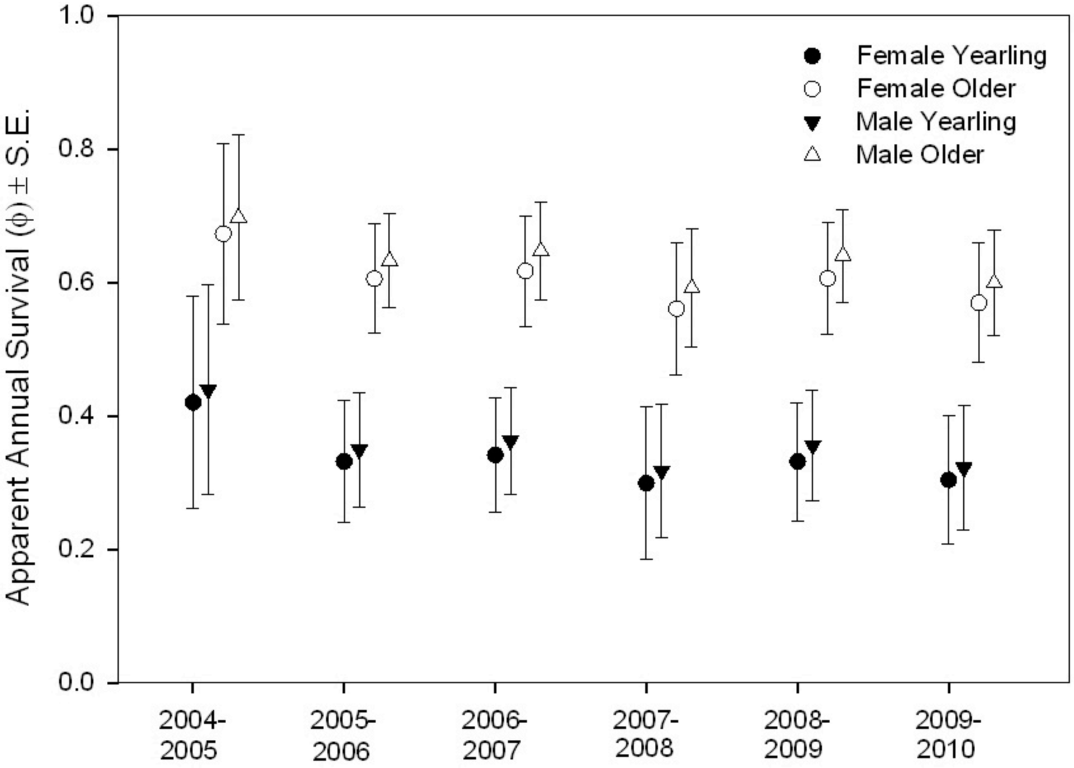

Figure 3-2. Adult survival (φ) of yearling females (closed circles) and males (closed triangles), versus older females (open circles) and males (open triangles) Yellow Warblers (n=215) in the study population in Revelstoke, British Columbia, between 2004-2010. Error bars denote 95% confidence intervals based on annual model-averaged survival estimates derived with an over-dispersion (ĉ) value of 1.4.

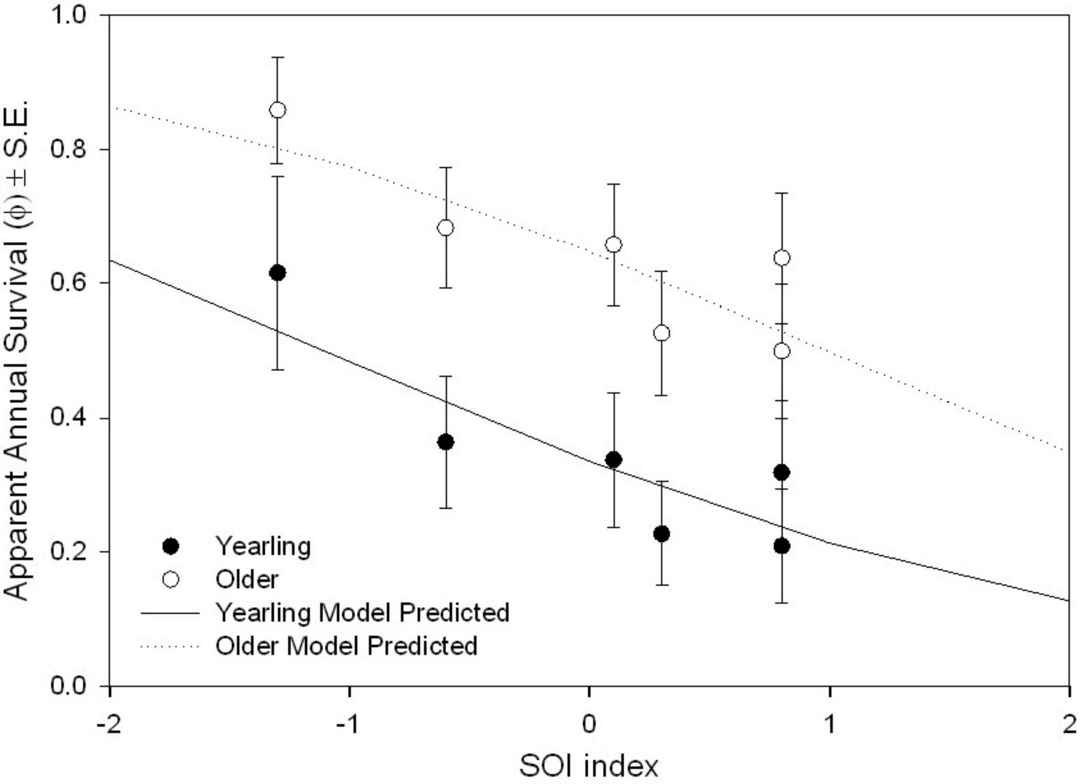

Figure 3-3. Model predictions for yearling (solid line) and older (dashed line) Yellow Warblers based on the model that received strongest support [$\varphi(a+SOI_{Mar–May})$ $P(g)$] and real estimates of apparent survival for yearling (closed circles) and older (open circles) Yellow Warblers (n=215) in the study population at in Revelstoke, British Columbia, between 2004-2010. Model parameters denoted as follows: *a* (age class; yearling or older) and $SOI_{Mar - May}$ (environmental covariate; mean Southern Oscillation Index between March and May). Highly negative and highly positive SOI values represent El Niño and La Niña events, respectively. Error bars denote 95% confidence intervals based on annual model-average survival estimates derived with an over-dispersion (ĉ) of 1.4.

3.7 Tables

Table 3-1. Summary of strongly supported ($\Delta QAIC_c<2$) models predicting recapture probability (*P*) and annual survival (φ) of Yellow Warblers (n=215) in the study population in Revelstoke, British Columbia, between 2004-2010 as estimated from program MARK (White and Burnham 2009). Model parameters denoted as follows: *a* (age class; yearling or older), g (gender; male or female), *t* (varies through time by year), *t/2007* (varies through time with 2007 differing from other years of study), "." (constant through time, * (interaction between factors), and + (additive effect between factors). QAIC*c* is Akaike's information criterion adjusted for small sample size and corrected for over-dispersion (ĉ), $\Delta QAIC_c$ is the difference in $QAIC_c$ value from that of the top ranked model, w_i is the Akaike weight, QDeviance is the model deviance corrected for ĉ and *K* is the number of parameters in the model +1 for intercepts. Candidate models are listed by $\Delta QAIC_c$ and were derived with a ĉ of 1.4.

Model	**$QAIC_c$**	**$\Delta QAIC_c$**	***K***	**QDeviance**	**$QAIC_c$ w_i**
Recapture probability (*P*):					
φ(*g*+*a*+*t*+*g***a*+*g***t*+*a***t*+*g***a***t*) *P*(*g*)	387.999	0.000	26	331.288	0.468
φ(*g*+*a*+*t*+*g***a*+*g***t*+*a***t*+*g***a***t*) *P*(*g*+*t/2007*)	389.164	1.164	27	330.073	0.262
Survival probability (φ):					
φ(*a*) *P*(*g*)	364.215	0.000	4	356.090	0.411
φ(*g*+*a*) *P*(*g*)	365.658	1.444	5	355.470	0.200
φ(*a*+*t*) *P*(*g*)	366.066	1.851	9	347.495	0.163

Table 3-2. Summary of strongly supported ($\Delta QAIC_c<2$) models predicting the effects of brood parasitism and environmental covariates on survival (φ) of Yellow Warblers (n=215) in the study population in Revelstoke, British Columbia, between 2004-2010 as estimated from program MARK (White and Burnham 2009). Model coding and column headings defined in Figure 3-1 except: *BHCOe*, (parasitism covariate; parasitized with a Brown-headed Cowbird egg), *BHCOn* (parasitism covariate; raised a Brown-headed Cowbird nestling), and $SOI_{Mar\,-\,May}$ (environmental covariate; mean Southern Oscillation Index between March and May). Candidate models are listed by $\Delta QAIC_c$ and were derived with a ĉ of 1.4.

Model	**$QAIC_c$**	**$\Delta QAIC_c$**	**K**	**QDeviance**	**QAICc w_i**
Survival (φ) and parasitism covariate (*BHCOe*):					
φ(*a*) *P*(*g*)	364.215	0.000	4	356.090	0.308
φ(*g*+*a*) *P*(*g*)	365.658	1.444	5	355.470	0.150
φ(*a*+*BHCOe*) *P*(*g*)	365.863	1.648	5	355.675	0.135
φ(*a*+*t*) *P*(*g*)	366.066	1.851	9	347.495	0.122
Survival (φ) and parasitism covariate (*BHCOn*):					
φ(*a*) *P*(*g*)	364.215	0.000	4	356.090	0.342
φ(*g*+*a*) *P*(*g*)	365.658	1.444	5	355.470	0.166
φ(*a*+*t*) *P*(*g*)	366.066	1.851	9	347.495	0.135
Survival (φ) and environmental covariate (*SOI*):					
φ($a+SOI_{Mar\,-\,May}$) *P*(*g*)	360.773	0.000	5	350.585	0.708

3.8 Reference List

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4: GENERAL CONCLUSIONS

The general decline of Neotropical migrant species has prompted research into which stages during the annual cycle are limiting or regulating populations (Robbins et al. 1989, Sanderson 2006, Holmes 2007, Sauer et al. 2008). Understanding mechanisms responsible for population declines of migratory birds requires knowledge of factors that may limit population growth across multiple stages of the annual lifecycle (Holmes 2007, Carlisle et al. 2009). Interspecific brood parasitism is one factor that is known to reduce the reproductive success of host individuals, and has been implicated as a possible cause of decline for host species.

I used an observational approach to examine the impacts of a common interspecific brood parasite, the Brown-headed Cowbird on adult Yellow Warbler breeding performance and survival. Brown-headed Cowbirds parasitized 18% (n=158) of Yellow Warbler nests and in all cases parasitized nests contained a single Cowbird egg. Cowbird eggs hatched in 41% of parasitized nests (n=27) and parasitic young fledged in 55% (n=11) of nests that hatched Cowbirds. Yellow Warblers were successful in fledging host young in 31% of nests where the parasitic egg did not hatch (n=16), and 64% of nests with parasitic young (n=11). Brood parasitism impacted reproductive success at each stage of the nesting cycle and reduced average annual productivity per female from 2.4 to 1.2 fledglings (n=117; **Chapter 2**). Brood parasitism was expected to reduce the survival of Yellow Warblers, a host that is on average 31-40 grams smaller than Brown-headed Cowbirds (Lowther 1993, 1999). I found little evidence that brood parasitism influenced Yellow Warbler survival, although it is possible that my estimates of the costs of parasitism are confounded by Cowbird preferences for high quality hosts (**Chapter 3**); survival estimates for females that were parasitized with a Brown-headed Cowbird egg were 2% lower than unparasitized females.

Brown-headed Cowbirds appeared to have a relatively small impact on Yellow Warblers compared to other factors. In this study, the average percentage of nests that were parasitized (18%, n=158) was similar to Yellow Warbler parasitism rates recorded elsewhere (21%, n=1885; Sealy 1992, 1995), but nest failure attributed to brood parasitism was low (1%, n=145). There was no detectable effect of brood parasitism on adult survival. In contrast, nest predation rates were high (43%) and accounted for 76% (n=145) of nest failures. No direct predation events on adults were ever observed by researchers, but a total of eight incidences of mate switching were recorded throughout the breeding season (n=184 breeding pairs). Mate switching could have occurred due to predator-driven adult mortality, however, mate switching can also occur while both pairs are alive, as a strategy to maximize fitness by mating with a new partner (Ramsey, 2000, Green et al. 2004). Brown-headed Cowbirds could be responsible for some or all predation events as Cowbirds are known to depredate host nests that are too far advanced in the nesting phase to be parasitized (Arcese et al. 1996; Granfors 2001) and can exhibit Mafia-like retaliatory behavior towards hosts that reject their eggs (Zahavi 1975, Hoover and Robinson 2007). However, preliminary evidence obtained in 2008 from 7 cameras monitoring visits to fake or inactive Yellow Warbler nests for between 7 to 30 days per camera during the period when Brown-headed Cowbirds were laying eggs suggested American Crows (*Corvus brachyrhynchos*) were the predominate predators. No

Cowbirds were detected at or near the nests (n=18 avian visitors) by cameras. Additionally, predation and parasitism rates varied across years (range: 8-29%, and 8-44% if nest, respectively) but were not correlated as would be expected if brood parasites were the dominant nest predator (r_s=0.30, p=0.31, n=5). We therefore suggest that Brown-headed Cowbirds are not likely to be significant Yellow Warbler nest predators. This conclusion is consistent with a study by McLaren and Sealy (2000) that examined the relationship between predation and parasitism in seven populations of Yellow Warblers (Ontario, Michigan, Colorado, Montana, and Manitoba) and found no evidence of a correlation.

I expected brood parasitism rates to decline with host age since breeding performance is known to increase with age in many species (Clutton-Brock 1988, Sæther 1990, Green 2001). However, brood parasitism rates would be expected to increase with host age if Brown-headed Cowbirds selectively targeted higher quality parents to raise their eggs as demonstrated in other studies (Smith et al. 1984, Soler et al. 1995, Zanette et al. 2010). My results were more consistent with the later prediction. Older Yellow Warbler females laid larger clutches, fledged a greater number of young per nesting attempt and per breeding season, and there was some evidence to suggest that older females were parasitized slightly more frequently than younger females.

Generally, the degree to which brood parasitism impacts local host populations depends on the preference parasites have for selecting a particular host species (Robinson et al. 1995; Smith 1999), abundance of brood parasites in the area (Smith 1999), and the vulnerability and severity for which a particular host species is impacted by the costs of parasitism (Smith 1999). The negative impacts brood parasitism has on individual host fitness, and reproductive success alone are unlikely to have consequences at the population level unless average reproductive success per host is approaching a level where adult production is not high enough to balance adult mortality, and populations are not rescued by immigration from source populations (Smith et al. 1996; Rogers et al. 1997; Smith 1999). Demographic data from the current study can be applied to Pulliam's (1988) basic model for estimating population growth:

$$\lambda = P_A + P_J\beta$$

where λ is the finite rate of increase within a patch ($\lambda > 1$ depicts a source population having positive population growth), P_A is the adult survival rate, P_J is the survival rate of fledglings (often assumed to be 50% that of adults; May and Robinson 1985), and β is the is the annual productivity per breeding individual. In the current thesis, I have estimated P_A (**Chapter 3**) and β (**Chapter 4**) for the study population of Yellow Warblers. Demographic parameters from this study population, weighted for the proportion of yearling and older females within our population (average 40% and 60% respectively) can be used to examine the impacts that current rates of brood parasitism (18%) have on population growth. Although lacking an estimate of P_J, I assume that based on previous literature P_J conservatively ranges between 50%-100% that of P_A (May and Robinson 1985, Kostecke and Cimprich 2008). Results from this preliminary calculation suggest that at all estimated values of P_J, λ is less than 1. Even when the negative effects of parasitism on annual productivity are removed, λ remains very low unless juvenile survival is as great as that of adults. This suggests that factors other than parasitism are limiting the growth rate of this population.

Large-scale variation in climate measured using El Niño/Southern Oscillation (ENSO) values encountered during spring migration had a detectable effect on Yellow Warbler survival (**Chapter 3**). Survival rates varied from 0.86 ± 0.08 to 0.50 ± 0.10 for older adults during El Niño and La Niña conditions, respectively. This result was similar to Nott et al. (2002) and confirms the importance of the migration period in the lifecycle of small songbirds. The small time series of this analysis (seven years) limited our ability to evaluate additional competing models and include additive effects of the Southern Oscillation Index (SOI) at multiple stages within the annual cycle. The approach taken in this study was indirect and assumed that ENSO is correlated with conditions at the spatial scale relevant to our population of Yellow Warblers. An alternative approach would be to directly measure factors such as food availability during El Niño and La Niña years at locations that correspond to where this population, breeds, overwinters, and utilizes during migration. Having this information would confirm that ENSO predictions were reflective of local conditions.

This thesis estimates age specific adult reproductive success and apparent survival parameters that are required to construct age structured population models. However, fledgling survival estimates have not yet been obtained for this population. Robust estimates of juvenile survival are generally difficult to obtain for migratory species especially when natal dispersal is high and local recruitment rates are low (Gardali et al. 2003, Kostecke and Cimprich 2008). Due to limited data on fledgling survival rates, many studies attempting to assess population dynamics use a conservative estimate such as one third (Temple and Cary 1988) or one half (Greenberg 1980, May and Robinson 1985) that of adult survival rates. Until more accurate estimates of juvenile survival become available from long-term data sets, indirect estimates could be used along with parameters provided in this thesis to model how changes in parasitism rates would impact population growth. The population of Yellow Warblers breeding in Revelstoke Reach, like many other populations, uses riparian habitat that is impacted by water use decisions made by hydroelectric operations. In the current study, between 6%-12% of Yellow Warbler nests failed due to flooding in years when water levels rise prior to the end of breeding season. Efforts could therefore be made to examine how changes in the reservoir operations that further reduce annual productivity will impact population growth. Additional models could be developed to identify the critical level of flooding that reduces per capita reproduction below the populations' source/sink threshold.

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APPENDICES

Appendix A. Support for Δ(Q)AIC$_c$ models predicting parasitism and rejection response of parasitized Yellow Warbler females breeding in Revelstoke, British Columbia between 2004-2006 and 2008-2009. Parasitism (n=158 nests) was assessed in relation to host female age (AGE; yearling or older), nest initiation date and nest initiation date squared (DATE + DATE^2), and YEAR. Rejection response (n=26 nests) was examined in relation to AGE, DATE + DATE^2, and nesting stage (STAGE; pre-laying, 1 egg laid, more than 2 eggs laid, incubation or later, incubation or later). AIC$_c$ is Akaike's information criterion adjusted for small sample size, ΔAIC$_c$ is the difference in AIC$_c$ value from that of the top ranked model, w$_i$ is the Akaike weight, and *K* is the number of parameters in the model +1 for intercept. Candidate models are listed by ΔAIC$_c$.

Model	***K***	**AIC$_c$**	**ΔAIC$_c$**	**w_i**
Parasitism:				
YEAR	5	147.247	0.000	0.309
YEAR + AGE	6	147.672	0.425	0.250
DATE + DATE^2 + YEAR	7	148.995	1.748	0.129
DATE + DATE^2 + YEAR + AGE	8	149.443	2.197	0.103
AGE	2	149.577	2.330	0.096
NULL	1	150.670	3.424	0.056
DATE + DATE^2 + AGE	4	151.638	4.391	0.034
DATE + DATE^2	3	152.479	5.232	0.023
Parasitism response:				
NULL	1	30.444	0.000	0.369
AGE	2	30.903	0.459	0.293
DATE + DATE^2	3	32.503	2.059	0.132
DATE + DATE^2 + AGE	4	33.052	2.609	0.100
STAGE	4	34.402	3.959	0.051
AGE + STAGE	5	35.199	4.755	0.034
DATE + DATE^2 + STAGE	6	37.392	6.948	0.011
DATE + DATE^2 + AGE + STAGE	7	37.827	7.383	0.009

Appendix B. Importance values (parameter likelihoods), model-weighted parameter estimates and associated unconditional standard errors (SE) explaining parasitism (n=158 nests) and rejection response to parasitism (n=26 nests) for yearling and older female Yellow Warblers nesting in Revelstoke, British Columbia between 2004-2006 and 2008-2009. See Appendix A for explanation of model coding.

Model Parameter	**Parameter likelihood**	**Weighted parameter estimate**	**Unconditional SE**
Parasitism:			
INTERCEPT	1.000	-9.641	23.942
DATE	0.289	0.101	0.298
DATE^2	0.289	0.000	0.014
YEAR (2004)	0.791	-0.579	0.867
YEAR (2005)	0.791	0.678	0.676
YEAR (2006)	0.791	0.473	0.430
YEAR (2008)	0.791	-0.363	0.476
AGE (Older)	0.484	0.111	0.185
Rejection response:			
INTERCEPT	1.000	31.644	69.807
DATE	0.253	-0.413	0.876
DATE^2	0.253	0.001	0.003
AGE (Older)	0.437	0.240	0.436
STAGE (Pre-laying)	0.106	-0.011	0.116
STAGE (Laying ≤1 egg)	0.106	0.045	0.134
STAGE (Laying >2 eggs)	0.106	0.014	0.091

Appendix C. Support for Δ(Q)AIC$_c$ models predicting 6 measures of breeding performance for Yellow Warbler females breeding in Revelstoke, British Columbia between 2004-2006 and 2008-2009. Breeding performance measures included: clutch size (n=145), nesting success (n=145), number fledged (n=82), fledgling condition (n=81), proportion male (n=44), and annual productivity (n=117]. Model coding and column headings defined in Appendix A except: BSIZE (the number of host nestlings in the brood prior to fledge date), QAIC$_c$ is AIC$_c$ for over-dispersion, Δ(Q)AIC$_c$ is the difference in (Q)AIC$_c$ value from that of the top ranked model.

Model	K	AIC$_c$	ΔAIC$_c$	w$_i$
Clutch Size[a]:				
DATE + DATE^2 + YEAR + AGE + PAR + PAR*AGE	11	313.965	0.000	0.478
DATE + DATE^2 + YEAR + AGE + PAR	10	315.223	1.258	0.255
DATE + DATE^2 + YEAR + PAR	9	315.356	1.391	0.238
DATE + DATE^2 + AGE + PAR + PAR*AGE	7	320.003	6.038	0.023
DATE + DATE^2 + PAR	5	323.026	9.061	0.005
DATE + DATE^2 + YEAR	8	332.980	19.015	0.000
DATE + DATE^2 + YEAR + AGE	9	333.587	19.622	0.000
DATE + DATE^2 + AGE	5	339.849	25.884	0.000
DATE + DATE^2	4	340.008	26.043	0.000
YEAR + AGE + PAR	8	343.858	29.893	0.000
YEAR + AGE + PAR + PAR*AGE	9	344.491	30.526	0.000
YEAR + PAR	7	348.350	34.385	0.000
AGE + PAR	4	352.130	38.165	0.000
AGE + PAR + PAR*AGE	5	352.771	38.806	0.000
YEAR + AGE	7	358.655	44.690	0.000
PAR	3	359.035	45.069	0.000
YEAR	6	361.445	47.480	0.000
AGE	3	366.951	52.986	0.000
NULL	2	371.111	57.146	0.000
Nesting Success:				
DATE + DATE^2 + YEAR	7	189.669	0.000	0.193
DATE + DATE^2 + YEAR + PAR	8	189.745	0.076	0.186
DATE + DATE^2 + YEAR + AGE + PAR	9	190.108	0.439	0.155
DATE + DATE^2 + YEAR + AGE	8	190.168	0.499	0.151
DATE + DATE^2 + YEAR + AGE + PAR + PAR*AGE	10	190.645	0.976	0.119
YEAR + AGE + PAR	7	192.664	2.995	0.043
YEAR + AGE	6	192.861	3.192	0.039
YEAR + AGE + PAR + PAR*AGE	8	192.917	3.248	0.038
YEAR	5	193.943	4.273	0.023
YEAR + PAR	6	194.005	4.336	0.022
DATE + DATE^2	3	196.384	6.714	0.007
DATE + DATE^2 + PAR	4	196.567	6.897	0.006
DATE + DATE^2 + AGE	4	197.210	7.540	0.004
DATE + DATE^2 + AGE + PAR + PAR*AGE	6	197.827	8.158	0.003
AGE	2	198.524	8.854	0.002
AGE + PAR	3	198.526	8.856	0.002
NULL	1	198.544	8.874	0.002
PAR	2	198.759	9.089	0.002
AGE + PAR + AGE + PAR	4	198.868	9.198	0.002
Number fledged[a]:				
DATE + DATE^2 + AGE + PAR + PAR*AGE	7	230.204	0.000	0.667
DATE + DATE^2 + YEAR + AGE + PAR	10	233.781	3.577	0.112
DATE + DATE^2 + PAR	5	234.761	4.557	0.068
DATE + DATE^2 + YEAR + AGE + PAR + PAR*AGE	11	235.261	5.057	0.053
AGE + PAR	4	235.545	5.340	0.046
AGE + PAR + PAR*AGE	5	236.447	6.242	0.029
YEAR + AGE + PAR	8	238.701	8.496	0.010
DATE + DATE^2 + YEAR + PAR	9	239.274	9.070	0.007
YEAR + AGE + PARASITISM + PAR*AGE	9	240.001	9.797	0.005
PAR	3	242.658	12.454	0.001
YEAR + PAR	7	244.973	14.769	0.000
DATE + DATE^2 + AGE	5	246.410	16.206	0.000
DATE + DATE^2	4	248.109	17.904	0.000
DATE + DATE^2 + YEAR + AGE	9	250.207	20.002	0.000

DATE + DATE^2 + YEAR	8	252.221	22.017	0.000
AGE	3	254.633	24.429	0.000
NULL	2	257.121	26.916	0.000
YEAR + AGE	7	257.710	27.506	0.000
YEAR	6	260.185	29.981	0.000
Fledgling condition[b]:				
BSIZE + AGE	5	227.710	0.000	0.289
BSIZE + AGE + PAR + PAR*AGE	7	227.855	0.146	0.268
BSIZE + AGE + PAR	6	228.764	1.054	0.170
NULL	4	222.860	1.150	0.162
BSIZE + PAR	5	222.640	1.930	0.110
Proportion male:				
NULL	2	101.347	0.000	0.314
PAR	3	101.741	0.395	0.257
AGE	3	102.399	1.053	0.185
AGE + PAR	4	102.923	1.576	0.143
AGE + PAR + PAR*AGE	5	103.610	2.263	0.101
Annual productivity[b]:				
AGE + PAR	5	157.786	0.000	0.274
PAR	4	158.671	0.884	0.176
AGE + PAR + PAR*AGE	6	158.738	0.952	0.170
AGE	4	159.989	2.203	0.091
YEAR + AGE + PAR	9	160.244	2.458	0.080
NULL	3	160.285	2.499	0.079
YEAR + PAR	8	161.343	3.557	0.046
YEAR + AGE + PAR + PAR*AGE	10	161.384	3.598	0.045
YEAR + AGE	8	162.831	5.044	0.022
YEAR	7	163.489	5.703	0.016

[a] The number of parameters in the model +1 for intercept and + 1 for model variance.

[b] The number of parameters in the model +1 for intercept, +1 for model variance and +1 for variance inflation factor.

Appendix D. Importance values (parameter likelihoods), model-weighted parameter estimates and associated unconditional standard errors (SE) explaining 6 measures of breeding performance [clutch size (n=145), nesting success (n=145), number fledged (n=82), fledgling condition (n=81), proportion male (n=44), and annual productivity (n=117] for yearling and older female Yellow Warblers nesting in Revelstoke, British Columbia between 2004-2006 and 2008-2009. See Appendix A for explanation of model coding.

Model Parameter	**Parameter likelihood**	**Weighted parameter estimate**	**Unconditional SE**
Clutch Size:			
INTERCEPT	1.000	34.019	15.971
DATE	1.000	-0.332	0.196
DATE^2	1.000	0.001	0.001
YEAR (2004)	0.971	-0.616	0.238
YEAR (2005)	0.971	-0.223	0.181
YEAR (2006)	0.971	0.079	0.166
YEAR (2008)	0.971	-0.010	0.163
AGE (Older)	0.756	0.154	0.148
PAR	1.000	-0.548	0.288
PAR*AGE	0.501	-0.275	0.356
Nesting Success:			
INTERCEPT	1.000	62.626	54.433
DATE	0.824	-0.735	0.660
DATE^2	0.824	0.002	0.002
YEAR (2004)	0.969	1.376	0.678
YEAR (2005)	0.969	0.238	0.394
YEAR (2006)	0.969	-0.874	0.387
YEAR (2008)	0.969	-0.207	0.352
AGE	0.559	0.142	0.207
PAR	0.579	-0.175	0.241
PAR*AGE	0.162	0.040	0.090
Number fledged:			
INTERCEPT	1.000	39.231	28.660
DATE	0.908	-0.419	0.349
DATE^2	0.908	0.001	0.001
YEAR (2004)	0.187	0.008	0.077
YEAR (2005)	0.187	-0.041	0.104
YEAR (2006)	0.187	0.003	0.069
YEAR (2008)	0.187	-0.006	0.067
AGE	0.923	0.552	0.265
PAR	1.000	-1.571	0.671
PAR*AGE	0.755	0.168	0.691
Fledgling condition:			
INTERCEPT	1.000	1.048	0.360
AGE (Older)	0.728	-0.236	0.249
PAR	0.549	0.154	0.504
PAR*AGE	0.268	-0.371	0.622
BSIZE	1.000	-0.227	0.099
Proportion male:			
INTERCEPT	1.000	0.045	0.224
AGE (Older)	0.429	0.071	0.198
PAR	0.501	3.300	5.235
PAR*AGE	0.101	-2.838	5.102
Annual productivity:			
INTERCEPT	1.000	2.008	0.330
YEAR (2004)	0.210	0.223	0.393
YEAR (2005)	0.210	0.193	0.341
YEAR (2006)	0.210	-0.009	0.105
YEAR (2008)	0.210	0.011	0.101
AGE	0.683	0.528	0.457
PAR	0.792	-1.090	0.664
PAR*AGE	0.216	0.147	0.321

Appendix E. Support for ΔQAIC$_c$ models predicting recapture probability (P) and annual survival (φ) of Yellow Warblers (n=215) in the study population in Revelstoke, British Columbia, between 2004-2010 as estimated from program MARK (White and Burnham 2009). Model parameters denoted as follows: *a* (age class; yearling or older), g (gender; male or female), *t* (varies through time by year), *t/2007* (varies through time with 2007 differing from all other years of study), "." (constant through time, * (interaction between factors), + (additive effect between factors). QAIC*c* is Akaike's information criterion (AIC) adjusted for small sample size and corrected for over-dispersion ($\hat{c}$), ΔQAIC$_c$ is the difference in QAIC$_c$ value from that of the top ranked model, w_i is the Akaike weight, QDeviance is the model deviance corrected for $\hat{c}$ and K is the number of parameters in the model +1 for intercepts. Candidate models are listed by ΔQAIC$_c$ and were derived with a $\hat{c}$ of 1.4.

Model	**QAIC$_c$**	**ΔQAIC$_c$**	**K**	**QDeviance**	**QAIC$_c$ w_i**
Recapture probability (*P*):					
$\varphi(g+a+t+g*a+g*t+a*t+g*a*t)\ P(g)$	387.999	0.000	26	331.288	0.468
$\varphi(g+a+t+g*a+g*t+a*t+g*a*t)\ P(g+t/2007)$	389.164	1.164	27	330.073	0.262
$\varphi(g+a+t+g*a+g*t+a*t+g*a*t)\ P(.)$	390.772	2.772	25	336.424	0.117
$\varphi(g+a+t+g*a+g*t+a*t+g*a*t)\ P(g+t/2007+g*2007)$	391.473	3.474	28	329.987	0.082
$\varphi(g+a+t+g*a+g*t+a*t+g*a*t)\ P(t/2007)$	391.793	3.794	26	335.082	0.070
Survival probability (φ):					
$\varphi(a)\ P(g)$	364.215	0.000	4	356.090	0.411
$\varphi(g+a)\ P(g)$	365.658	1.444	5	355.470	0.200
$\varphi(a+t)\ P(g)$	366.066	1.851	9	347.495	0.163
$\varphi(g+a+t)\ P(g)$	367.320	3.105	10	346.619	0.087
$\varphi(g+a+g*a)\ P(g)$	367.464	3.249	6	355.200	0.081
$\varphi(g+a+t+g*a)\ P(\mathrm{g})$	369.396	5.182	11	346.553	0.031
$\varphi(g+a+t+g*t)\ P(g)$	371.863	7.648	15	340.310	0.009
$\varphi(.)\ \mathrm{P}(g)$	373.141	8.926	3	367.067	0.005
$\varphi(a+t+a*t)\ P(g)$	373.362	9.147	14	344.007	0.004
$\varphi(g+a+t+g*a+g*t)\ P(g)$	374.076	9.861	16	340.309	0.003
$\varphi(g)\ P(g)$	374.837	10.623	4	366.712	0.002
$\varphi(g+a+t+a*t)\ P(\mathrm{g})$	374.865	10.650	15	343.311	0.002
$\varphi(g+a+t+g*a+a*t)\ P(g)$	376.982	12.767	16	343.216	0.001
$\varphi(t)\ P(g)$	378.474	14.259	8	362.018	0.000
$\varphi(g+t)\ P(g)$	379.172	14.957	9	360.601	0.000
$\varphi(g+a+t+g*t+a*t)\ P(g)$	380.250	16.035	20	337.487	0.000
$\varphi(g+a+t+g*a+g*t+a*t)\ P(g)$	382.478	18.263	21	337.428	0.000
$\varphi(g+t+g*t)\ P(g)$	385.800	21.585	14	356.445	0.000
$\varphi(g+a+t+g*a+g*t+a*t+g*a*t)\ P(g)$	387.999	23.785	26	331.288	0.000

Appendix F. β-Estimates (vector of parameters representing each level of a factor in the models), standard errors (SE) and 95% confidence intervals (CI) for models that received high support ($\Delta QAIC_c<2$) in the survival analysis (φ) of Yellow Warblers in the study population (n=215) in Revelstoke British Columbia between 2004-2010 (estimated from program MARK; White and Burnham 2009). Model coding and column headings defined in Appendix E except: *BHCOe*, (parasitism covariate; parasitized with a Brown-headed Cowbird egg), *BHCOn* (parasitism covariate; raised a Brown-headed Cowbird nestling), and *SOI* (environmental covariate; mean Southern Oscillation Index for the time period indicated in subscript). Candidate models are listed by $\Delta QAIC_c$ and were derived with a ĉ of 1.4.

Model	**β-Estimates**	**SE**	**95% CI**	
			Low	High
φ(*a*) P(*g*):				
φ Intercept	-0.606	0.272	-1.140	-0.072
φ *a* (Yearling)	0.479	0.191	-0.104	0.854
φ(*g+a*) *P*(*g*):				
φ Intercept	0.298	0.288	-0.266	0.862
φ *g* (Male)	0.265	0.331	-0.384	0.914
φ *a* (Yearling)	-1.080	0.319	-1.706	-0.455
φ(*a+t*) *P*(*g*):				
φ Intercept	-1.223	0.440	-2.086	-0.360
φ *a* (Yearling)	1.327	0.352	0.638	2.016
φ *t1* (2004)	1.693	0.701	-0.318	3.068
φ *t2* (2005)	0.462	0.539	-0.593	1.518
φ *t3* (2006)	0.663	0.514	-0.344	1.670
φ *t4* (2007)	-0.108	0.542	-1.169	0.954
φ *t5* (2008)	0.548	0.533	-0.496	1.592
φ(*a+BHCOe*) *P*(*g*):				
φ Intercept	0.521	0.203	0.123	0.918
φ *a* (Yearling)	-1.086	0.323	-1.719	-0.454
φ *BHCOe*	-0.263	0.405	-1.058	0.531
φ(*a+*$SOI_{Mar\text{-}May}$) *P*(g):				
φ Intercept	0.610	0.209	0.199	1.020
φ *a*	-1.294	0.350	-1.980	-0.609
φ $SOI_{Mar\text{-}May}$	-0.619	0.279	-1.165	-0.073

Appendix G. Summary of strongly supported ($\Delta QAIC_c<2$) models predicting the effects of brood parasitism and environmental covariates on apparent annual survival (φ) of Yellow Warblers (n=215) in the study population at sites in Revelstoke, British Columbia, between 2004-2010 (estimated from program MARK; White and Burnham 2009). Model coding and column headings defined in Appendix E except: *BHCOe*, (parasitism covariate; parasitized with a Brown-headed Cowbird egg), *BHCOn* (parasitism covariate; raised a Brown-headed Cowbird nestling), and *SOI* (environmental covariate; mean Southern Oscillation Index for the time period indicated in subscript). Candidate models are listed by $\Delta QAIC_c$ and were derived with a ĉ of 1.4.

Model	**$QAIC_c$**	**$\Delta QAIC_c$**	**K**	**QDeviance**	**QAICc w_i**
Survival (φ) and parasitism covariate (*BHCOe*):					
$\varphi(a)\ P(g)$	364.215	0.000	4	356.090	0.308
$\varphi(g+a)\ P(g)$	365.658	1.444	5	355.470	0.150
$\varphi(a+BHCOe)\ P(g)$	365.863	1.648	5	355.675	0.135
$\varphi(a+t)\ P(g)$	366.066	1.851	9	347.495	0.122
$\varphi(a+t+BHCOe)\ P(g)$	366.979	2.764	10	346.279	0.077
$\varphi(s+a+BHCOe)\ P(g)$	367.302	3.088	6	355.038	0.066
$\varphi(a+BHCOe+a*BHCOe)\ P(g)$	367.838	3.623	6	355.574	0.050
$\varphi(a+t+BHCOe+a*BHCOe)\ P(g)$	368.950	4.735	11	346.106	0.029
$\varphi(g+a+BHCOe+g*BHCOe)\ P(g)$	369.165	4.950	7	354.812	0.026
$\varphi(g+a+BHCOe+a*BHCOe)\ P(g)$	369.288	5.073	7	354.935	0.024
$\varphi(g+a+BHCOe+g*BHCOe+a*BHCOe)\ P(g)$	371.366	7.151	8	354.910	0.009
$\varphi(g+a+BHCOe+g*BHCOe+a*BHCOe+g*a*BHCOe)\ P(g)$	372.549	8.334	9	353.978	0.005
Survival (φ) and parasitism covariate (*BHCOn*):					
$\varphi(a)\ P(g)$	364.215	0.000	4	356.090	0.342
$\varphi(g+a)\ P(g)$	365.658	1.444	5	355.470	0.166
$\varphi(a+t)\ P(g)$	366.066	1.851	9	347.495	0.135
$\varphi(a+BHCOn)\ P(g)$	366.258	2.043	5	356.070	0.123
$\varphi(g+a+BHCOn)\ P(g)$	367.716	3.501	6	355.452	0.059
$\varphi(a+t+BHCOn)\ P(g)$	368.049	3.831	10	347.345	0.050
$\varphi(a+BHCOn+a*BHCOn)\ P(g)$	368.334	4.119	6	356.070	0.044
$\varphi(g+a+BHCOn+a*BHCOn)\ P(g)$	369.689	5.474	7	355.335	0.022
$\varphi(g+a+BHCOn+g*BHCOn)\ P(g)$	369.796	5.581	7	355.442	0.021
$\varphi(a+t+BHCOn+a*BHCOn)\ P(g)$	370.012	5.797	11	347.169	0.019
$\varphi(g+a+BHCOn+a*BHCOn+s*BHCOn+g*a*BHCOn)\ P(g)$	371.200	6.985	9	352.628	0.010
$\varphi(g+a+BHCOn+a*BHCOn+g*BHCOn)\ P(g)$	371.779	7.564	8	355.323	0.008
Survival (φ) and environmental covariate (SOI):					
$\varphi(a+SOI_{Mar-May})\ P(g)$	360.773	0.000	5	350.585	0.708
$\varphi(a)\ P(g)$	364.215	3.442	4	356.090	0.127
$\varphi(a+SOI_{May-Aug})\ P(g)$	365.690	4.917	5	355.502	0.061
$\varphi(a+SOI_{Nov-Feb})\ P(g)$	365.920	5.147	5	355.732	0.054
$\varphi(a+t)\ P(g)$	366.066	5.293	9	347.495	0.050