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ARTICLE

Age-dependent costs of cowbird parasitism in Yellow Warblers (*Setophaga petechia*)

C.A. Rock, S.P. Quinlan, M. Martin, and D.J. Green

Abstract: Brood parasitism by Brown-headed Cowbirds (*Molothrus ater* (Boddaert, 1783)) often reduces the reproductive success of their hosts. We examined whether the ability of females to avoid or mitigate the costs of brood parasitism improved with age in a population of Yellow Warblers (*Setophaga petechia* (L., 1766)) breeding near Revelstoke, British Columbia, between 2004 and 2011. Cowbirds parasitized 18% of Yellow Warbler nesting attempts and females rejected 24% of parasitized nests, principally by deserting the nest and initiating a new breeding attempt. We found no evidence that older females were better at avoiding parasitism or more likely to reject parasitized nests than yearlings. On average, brood parasitism reduced clutch sizes by 0.8 eggs, had no effect on nest success, but reduced the number of young fledged from successful nests by 1.3 offspring. Despite age-related improvement in some measures of breeding performance, the costs of brood parasitism at each period of the breeding cycle did not vary with age. There was, however, some evidence, that brood parasitism reduced the annual productivity (total number of young fledged) of older females less than the annual productivity of yearlings suggesting that the cumulative costs of brood parasitism varied with age.

Key words: Yellow Warbler, *Setophaga petechia*, brood parasitism, age, Brown-headed Cowbird, *Molothrus ater*.

Résumé : Le parasitisme de couvée par le vacher à tête brune (*Molothrus ater* (Boddaert, 1783)) entraîne souvent une réduction du succès de reproduction des hôtes. Nous avons vérifié si la capacité des femelles à éviter ou atténuer les coûts du parasitisme de couvée augmentait avec l'âge dans une population de parulines jaunes (*Setophaga petechia* (L., 1766)) nidifiant près de Revelstoke (Colombie-Britannique), de 2004 à 2011. Des vachers ont parasité 18 % des tentatives de nidification de parulines jaunes et les femelles ont rejeté 24 % des nids parasités, principalement en désertant le nid et en entreprenant une nouvelle tentative de nidification. Aucune observation ne suggère que les femelles plus âgées éviteraient plus efficacement le parasitisme ou seraient plus susceptibles de rejeter un nid parasité que des femelles d'un an. En moyenne, le parasitisme de couvée se traduisait par une réduction de la taille des couvées de 0,8 œuf, n'avait aucun effet sur le succès du nid, mais faisait diminuer de 1,3 le nombre de jeunes envolés de nids où la nidification avait été un succès. Malgré une amélioration associée à l'âge de certaines mesures de la performance de reproduction, les coûts du parasitisme de couvée à chaque période du cycle de reproduction ne variaient pas selon l'âge. Certaines données indiquent toutefois que la réduction de la productivité annuelle (nombre total de jeunes envolés du nid) découlant du parasitisme de couvée était plus faible pour les femelles plus âgées que pour les femelles d'un an, ce qui porte à croire que les coûts cumulatifs du parasitisme de couvée variaient en fonction de l'âge. [Traduit par la Rédaction]

Mots-clés : paruline jaune, *Setophaga petechia*, parasitisme de couvée, âge, vacher à tête brune, *Molothrus ater*.

Introduction

Breeding performance improves with age in many bird species (Newton 1989; Sæther 1990) and this pattern may result from improvement in one or many aspects of reproduction. For example, older birds have been reported to initiate clutches earlier (Lozano et al. 1996; Balbontín et al. 2007), produce larger eggs (Robertson et al. 1994), lay larger clutches (Espie et al. 2000; Low et al. 2007), and fledge more young 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 advancement in selecting a territory, predator detection and avoidance, or foraging efficiency (experience hypothesis; Curio 1983; Nol and Smith 1987), 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).

Reproductive success of many birds is reduced by obligate brood parasites such as cuckoos (family Cuculidae) and cowbirds (genus *Molothrus* Swainson, 1832) that have negative effects at several stages of the nesting cycle. Clutch sizes are reduced when a host egg is removed by brood parasites (Smith 1981; Rothstein 1982; Sealy 1992). Hatching success of remaining host eggs is lowered when host eggs are damaged by brood parasites, or earlier hatching brood parasitic nestlings that draw parental attention away from host eggs (Walkinshaw 1961; Peer and Sealy 1999; Peer and Bollinger 2000). Parasitized broods produce fewer or no host fledglings when parasitic young outcompete host young for food deliveries or eject host young from the nest (Lichtenstein and Sealy 1998; Peer and Bollinger 2000; Rivers 2007; but see Rivers et al. 2010). These costs usually reduce the total number of fledglings raised by hosts over the course of the breeding season (Klaas 1975; Lorenzana and Sealy 1999; Smith et al. 2002). The presence of parasitic young may also reduce the postfledging survival of host offspring (Rasmussen and Sealy 2006; but see Smith 1981), further increasing the cumulative costs of brood parasitism.

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Studies investigating age-specific impacts of brood parasitism have typically asked whether older hosts are less likely to be parasitized than younger hosts because they occupy better territories, select better nest sites or are more effective at defending their nest, and more likely to eject parasitic eggs or reject parasitized nests as they learn to recognize parasitic eggs. These studies usually found no evidence that older host females were less likely to be parasitized by either cuckoos or cowbirds, and in fact, the reverse was often the case (Smith 1981; Brooker and Brooker 1996; Langmore and Kilner 2007; but see Sealy 1995). Some studies demonstrated that older females were more likely to reject a parasitic egg or nestling. Lotem et al. (1992, 1995) found that earlier breeding Great Reed Warbler (*Acrocephalus arundinaceus* (L., 1758)) hosts consisting of a higher proportion of adult females were significantly more likely to reject brood parasitic Common Cuckoo (*Cuculus canorus* L., 1758) eggs from their nests (but see Moskát and Hauber 2007). However, Amundsen et al. (2002) and Sealy (1995) found no evidence that age influenced whether Bluethroats (*Luscinia svecica* (L., 1758)) rejected Common Cuckoo eggs or Yellow Warblers (*Setophaga petechia* (L., 1766)) rejected Brown-headed Cowbird (*Molothrus ater* (Boddaert, 1783)) eggs, respectively.

A few studies have examined age-specific costs of brood parasitism on other aspects of breeding performance. Smith (1981) found that brood parasitism reduced the clutch size of yearling and adult Song Sparrows (*Melospiza melodia* (A. Wilson, 1810)) by 0.5 and 0.6 eggs, respectively, but had no effect on the proportion of eggs producing 6-day-old young or juvenile survival to independence for either age class. However, other studies examining the influence of host age on the costs of parasitism at each stage of the nesting cycle and the cost of parasitism over the breeding season are scant. In this study, we examined how female age influences brood parasitism rates, the response to nest parasitism, and the impacts of brood parasitism on clutch size, nesting success, brood size and condition at fledging, and annual productivity in Yellow Warblers. We expected that cowbirds would parasitize both older and yearling hosts but predicted that (*i*) older female Yellow Warblers would be less likely to be parasitized and more likely to reject parasitized clutches and (*ii*) brood parasitism would have less impact on the breeding performance of older Yellow Warblers.

Materials and Methods

Study species and location

The Yellow Warbler is a small (9–10 g) 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. Females are solely responsible for nest building and provide all parental care during egg laying and incubation. However, males regularly feed incubating females and both males and females provision young during the nestling and postfledging period (Lowther et al. 1999). Our study was conducted in Revelstoke Reach, situated within the drawdown zone of Arrow Lakes Reservoir, a 240 km reservoir system in the upper Columbia River valley separating the Monashee and Selkirk mountain ranges, east of the Kootenay region of British Columbia, Canada (50°58′56″N, 118°20′00″W). Yellow Warblers breeding in Revelstoke Reach are associated with wet riparian habitats containing willow and other low-lying shrub species and deciduous trees such as black cottonwood. Breeding pairs typically rear one successful brood of up to five fledglings per year; second broods are attempted but are rarely successful (Quinlan and Green 2012).

Yellow Warblers are parasitized by Brown-headed Cowbirds across much of their breeding range with parasitism rates varying from 16% to 77% where their distributions overlap (Scott and Lemon 1996; Lowther et al. 1999; Campbell et al. 2001). Females accept and continue caring for cowbird eggs in approximately 50% of parasitized nests (Sealy 1995). Yellow Warblers can reject brood parasitism by burying the eggs or abandoning the nest (Clark and Robertson 1981; Sealy 1992). Rejection is more likely to occur when cowbird eggs are laid before or on the day that a host initiates their own clutch, or when host clutch size is reduced to two or fewer eggs (Clark and Robertson 1981; Sealy 1995; Guigueno and Sealy 2010).

Monitoring breeding performance and parasitism rates

We monitored all Yellow Warblers breeding at three approximately 30 ha sites in Revelstoke Reach from 2004 to 2006 and from 2008 to 2011. We attempted to catch all breeding individuals that established territories within the study sites (19–38 pairs per year). Males were typically caught within 3 days of arriving at the site and females were caught on arrival or during the nesting period. Individuals were classified as yearlings (second year birds) or older (after second year birds) based on plumage and feather wear and feather shape (Pyle 1997). Compared with older individuals, juveniles are duller in colouration with a greenish wash, have outer primary coverts that are narrow, tapered, and relatively abraded and brown with little or no pale edging, and have outer retrices that are relatively abraded, tapered, and brownish with yellow on the inner webs that does not extend as far from the feather shaft. Females that were not captured or could not be confidently aged were omitted from the analyses.

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. Nests were typically checked every 2–3 days to record clutch initiation date (defined here as the date the first egg was laid), hatch date (defined here as the day the first nestling hatched), record clutch and brood size, and determine nest success (defined as fledging one or more host offspring). For nests that failed, we assumed that nests had been depredated if they were found empty after having previously contained at least one egg or nestling. Nest cameras ($n = 7$) monitoring fake or inactive Yellow Warbler nests identified American Crows (*Corvus brachyrhyncos* Brehm, 1822) as the dominant predator at our study site; no cowbirds were observed to visit these nests (Rock 2011). During nests checks we also noted the presence of cowbird eggs, which are similar in colour and pattern but approximately twice the volume of Yellow Warbler eggs (Sealy 1992; Guigueno and Sealy 2009). Cowbird parasitism was classified as taking place early (when nests contained zero or one host egg) or late (when nest contained two or more host eggs) in the nesting period. We subsequently recorded whether Yellow Warbler females continued to provide parental care, i.e., accept the parasitism, abandoned the nest, or buried the cowbird egg and any of their own eggs.

Nestling condition

If nests were accessible, we banded nestlings with aluminium bands issued by the Canadian Wildlife Service on day 7 of the 9 day nestling period. We also weighed nestlings to the nearest 0.10 g using a digital scale and measured tarsus length (from the notch of the intertarsal joint to the top of the palm) to the nearest 0.01 mm. Nestling condition was estimated using the residuals from a mass versus tarsus regression that explained 27% of the variance in nestling mass. We used the mean condition of nestlings on day 7 as a measure of brood condition.

Statistical analysis

We developed a series of candidate model sets to examine how female age influenced whether nests were parasitized or not, the response of female Yellow Warblers to brood parasitism (accept or reject), and how female age and brood parasitism influenced five measures of breeding performance. The five measures (final clutch size, nest success, number fledged or successful nest, nestling condition, and annual productivity) were selected to account for losses due to brood parasitism at different stages of reproduction. We recorded clutch size to identify losses at the laying or incubation stage due to cowbirds removing host eggs. Nest success was evaluated to determine whether parasitized nests that were not abandoned were more likely to fail during incubation or the nestling period due to increased activity and noise near the nest. We used the number of host young fledged from successful nests to assess whether the presence of a cowbird nestling increased host nestling mortality. Brood condition was evaluated to determine whether host nestlings that were raised with cowbird nestlings were of lower quality compared with nestlings raised in nests that were not parasitized. Finally, annual productivity was examined to determine whether females parasitized with a cowbird egg at least once per breeding season produced fewer fledged young compared with unparasitized females.

The candidate model set examining whether nests were parasitized included models with all combinations of three terms: year, clutch initiation date, and female age (yearling or older). The candidate model set examining whether females rejected parasitized nests included all combinations of the three terms: date, female age, and the stage the parasitic egg was laid (early or late). The candidate model sets examining variation in clutch size, nesting success, the number of young fledged from successful nests, and annual productivity included all combinations of year, date (where appropriate), female age, parasitism (yes or no), and a female age × parasitism interaction term. The candidate model set examining variation in brood condition included brood size as a variable in all models, all combinations of year, date, male age (yearling or older), female age, parasitism, and all interactions between age and parasitism terms. Male age was excluded from most analyses because there was no evidence that male age or the interaction between male age, female age, or parasitism improved the full models in these candidate model sets (based on Q(AIC$_c$)) values, allowing us to include data from pairs where male age was unknown. As females could have multiple nesting attempts within a year (39 of 127 females) and some were monitored in multiple years of the study (24 of 127 females), we initially explored factors influencing parasitism rates, rejection rates, and breeding performance using a mixed modelling approach and included female identity as a random term. However, there was little variance associated with the female identity term and the standard errors of the variance component overlapped zero, so we dropped the random term and used generalized linear models in subsequent analyses.

Akaike's information criterion (AIC) values for small sample sizes (AIC$_c$) were derived manually for each model using the output of generalized linear models computed in SPSS version 19 (SPSS Inc., Chicago, Illinois, USA). 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). AIC$_c$ and quasi-AIC$_c$ (QAIC$_c$; AIC$_c$ corrected for overdispersion) 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 $\hat{c}$; value exceeded 1.0 (response to parasitism, nesting success, 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 data sets. AIC$_c$ parameter likelihoods were calculated as the sum of the w_i of all competing models in which the parameter occurred. Parameter estimates and their associated unconditional standard errors were also calculated to assess the relative influences of the variables present in competing models. AIC 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 as the standard error of each parameter weighted by the AIC$_c$ weight of each candidate model in which the parameter occurred.

Table 1. Summary of top-ranked AICc models (ΔAIC$_c$ < 2) examining brood parasitism and the response of female Yellow Warblers (*Setophaga petechia*) breeding in Revelstoke, British Columbia, between 2004–2006 and 2008–2011.

Model	K	(Q)AIC$_c$	ΔAIC$_c$	w_i
Parasitism				
Year	7	190.40	0.00	0.314
Year + age	8	191.37	0.97	0.194
Year + date	8	191.53	1.13	0.178
Rejection response				
Null	2	42.63	0.00	0.275
Nesting stage	3	42.94	0.31	0.234
Date	3	44.19	1.56	0.126
Date + nesting stage	4	44.53	1.90	0.106

Note: Brood parasitism (n = 218 nests) was assessed in relation to female age (yearling or older), year, and clutch initiation date (date). Rejection of parasitized nests (n = 42) was examined in relation to female age, clutch initiation date (date), and nesting stage (early or late). 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, with +1 for intercept and +1 for the variance inflation factor where necessary.

Results

Brood parasitism and the response of female Yellow Warblers

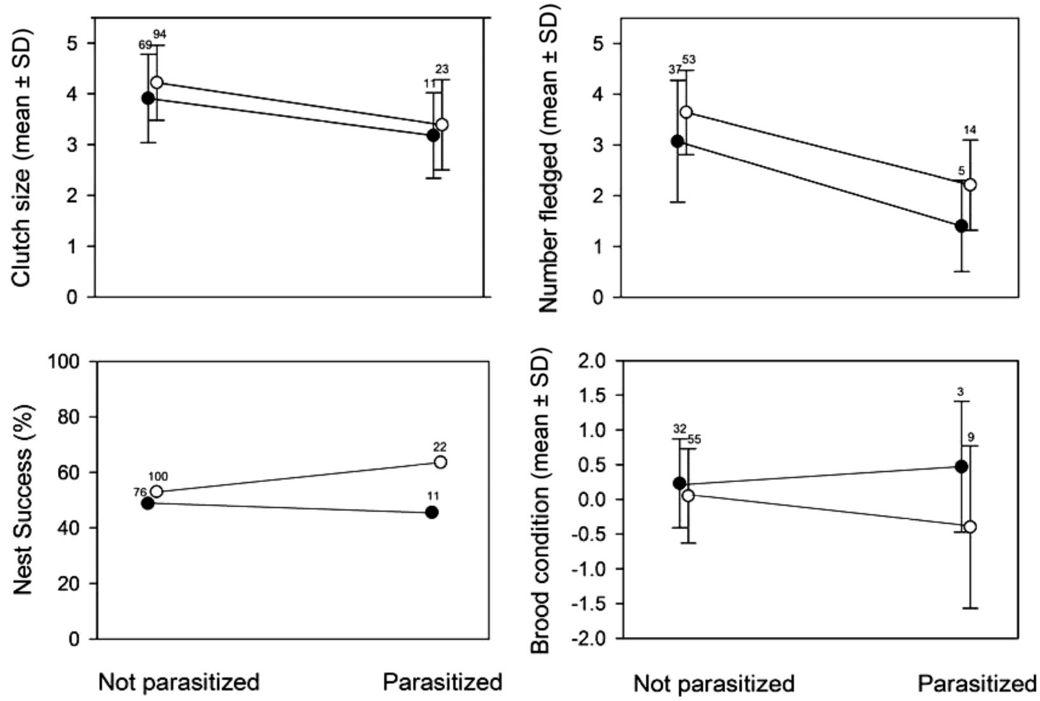
Brown-headed cowbirds parasitized 19% of Yellow Warbler nests (n = 218), and in all cases, parasitized nests contained a single cowbird egg. Cowbird parasitism rates ranged from 9% in 2004 (n = 11) to 31% in 2005 (n = 29). Counter to expectation, older females were slightly more likely to be parasitized than yearling females (21% (n = 127) versus 17% (n = 91), respectively). Year was included in all three models that received strong support (ΔAIC$_c$ < 2; Table 1), and consequently had a high parameter likelihood (0.796). Female age was included in one of the strongly supported models, but the parameter likelihood associated with this term was moderate (0.484) and the weighted parameter estimate had a large standard error (0.111 ± 0.185) suggesting female age had little effect on brood parasitism. Date was also included in one of the strongly supported models, but this term had a low parameter likelihood (0.289) suggesting there was little seasonal variation in parasitism rates.

Female Yellow Warblers buried the parasitic egg along with their own eggs (n = 1) or abandoned the parasitized nest (n = 8) in 21% of cases where a nest was parasitized by cowbirds (n = 42). Older females were somewhat less likely to reject a parasitized nest than yearling females (19% (n = 27) versus 27% (n = 15), respectively). Yellow Warblers were slightly more likely to reject a parasitized nest when the parasitic egg was laid at an early stage in the nesting period (36%, n = 14 nests, where 0–1 egg had been laid) than later in the nesting period (14%, n = 28). However, the null model received more support than models including the female age, nesting stage, or date terms (Table 1), providing little evidence that a female's response to parasitism varied with nesting stage, age, or clutch initiation date.

Impact of brood parasitism on individual nesting attempts of Yellow Warblers

Females initiated clutches between 25 May and 11 July and complete clutches contained one to six eggs. Older females laid slightly larger clutches than yearlings and clutch sizes in parasitized nests were, on average, 0.8 eggs smaller than in unparasitized nests (Fig. 1). Clutch size declined as the season progressed and

Fig. 1. Breeding performance of yearling (solid circles) and older (open circles) female Yellow Warblers (*Setophaga petechia*) parasitized or not parasitized by Brown-headed Cowbirds (*Molothrus ater*) between 2004–2006 and 2008–2011. Numbers above the bars represent the number of nests within each category.



varied between years, being smaller in 2004 and larger in 2006 (Table 2). Five of the 19 candidate models received strong support ($\Delta AIC_c < 2$). The date and parasitism terms were included in all strongly supported models and had high parameter likelihoods (1.00). The year and female age terms were both included in three of the five strongly supported models (Table 2), and had moderate parameter likelihoods (0.654 and 0.573, respectively). The female age × parasitism interaction term was included in two of the strongly supported models (Table 2), but had a low parameter likelihood (0.386) and a weighted parameter estimate with a large standard error (–0.160 ± 0.245), indicating that the cost of parasitism did not vary with age.

Overall, 52% (n = 209) of nesting attempts that were not abandoned as a result of cowbird parasitism fledged at least one nestling Yellow Warbler. Of the nests that failed, predation was the principal cause of failure (84%, n = 100). Nest success did not improve with female age and nests that were parasitized were as likely to be successful as those that were not parasitized (Fig. 1). There was considerable model uncertainty; 8 of the 19 models in the candidate set received strong support. However, the null model received more support than any other model and all terms had low parameter likelihoods suggesting that female age, parasitism by cowbirds, date, and year had little effect on the probability that females would fledge at least one nestling.

Successful nests fledged 3.2 ± 1.2 young (mean ± SD) (n = 109). On average, older females fledged 0.6 more offspring than yearling females. Cowbird parasitism reduced the number of young fledged by approximately 1.4 offspring (Fig. 1). Two of the 19 candidate models received strong support (Table 2). The highest supported model that contained the date, female age, and parasitism terms received 1.6 times the support of the next best model that also included the female age × parasitism term. All the terms in the top model consequently had high parameter likelihoods (all >0.90). There was little evidence that older females could mitigate the impact of brood parasitism; the female age × parasitism term had a low parameter likelihood (0.434) and the weighted parameter estimate was small with a large standard error (0.142 ± 0.319).

Counter to expectations, the presence of a cowbird nestling reduced slightly the condition of broods raised by older females but had no detectable effect on the condition of broods raised by young females (Fig. 1). Broods raised by older males were, however, in better condition than those raised by young males (top model, β_{ASY} ± SE = 0.36 ± 0.19 g, where ASY is after second year). Brood condition also declined as brood size increased, declined with clutch initiation date, and varied with year. Five of the 63 candidate models received strong support. The best model included female age, male age, parasitism, and the female age × parasitism interaction, in addition to the brood size, date, and year terms (Table 2). Female age and the female age × interaction were included in all five strongly supported models and had high parameter likelihoods (0.922 and 0.627, respectively). Male age was included in four of the five strongly supported models and also had a high parameter likelihood (0.799).

Impact of brood parasitism on annual productivity of Yellow Warblers

Female Yellow Warblers initiated between 1 and 4 clutches per year, occasionally fledging two broods (4 of 160 female-years). Annual productivity per female averaged 2.2 ± 1.9 fledglings. Older females produced, on average, 0.7 fledglings more than yearlings. The productivity of females that were parasitized at least once during a breeding season was reduced by approximately 1.0 fledglings, although there was some evidence that cowbirds had less impact on older females than yearlings (Fig. 2, Table 2). Two of the 10 candidate models received strong support. The highest ranked model that included the terms female age, parasitism, and the age × parasitism interaction received 1.5 times the support of the next best model that did not include the interaction term. The parameter likelihoods for the main effects of age and parasitism were high (0.871 and 0.942, respectively), although the parameter likelihood for the interaction term was lower (0.492). There was

Table 2. Summary of top-ranked (Q)AIC$_c$ models (Δ(Q)AIC$_c$ < 2) examining the breeding performance of female Yellow Warblers (*Setophaga petechia*) in Revelstoke, British Columbia, between 2004–2006 and 2008–2011.

Model	*K*	(Q)AIC$_c$	Δ(Q)AIC$_c$	w_i
Clutch size*				
Year + date + parasitism	10	436.93	0.00	0.296
Date + female age + parasitism + age × parasitism	6	437.57	0.64	0.215
Year + date + female age + parasitism	11	437.84	0.91	0.188
Year + date + female age + parasitism + female age × parasitism	12	438.04	1.11	0.170
Date + parasitism	4	438.57	1.64	0.130
Nesting success†				
Null	2	198.54	0.00	0.163
Date	3	198.83	0.29	0.141
Date + year	9	199.79	1.25	0.087
Female age	3	199.94	1.40	0.081
Year	8	200.20	1.66	0.071
Parasitism	3	200.26	1.72	0.069
Date + female age	4	200.52	1.98	0.061
Date + parasitism	4	200.53	1.99	0.060
Number fledged*				
Year + date + female age + parasitism	11	291.44	0.00	0.538
Year + date + female age + parasitism + female age × parasitism	12	292.39	0.95	0.334
Brood condition*				
Brood size + year + date + male age + female age + parasitism + female age × parasitism	14	196.85	0.00	0.144
Brood size + year + date + male age + female age + parasitism + male age × parasitism + female age × parasitism	15	197.12	0.27	0.126
Brood size + year + date + male age + female age + parasitism + male age × female age + female age × parasitism	15	198.19	1.34	0.074
Brood size + year + date + male age + female age + parasitism + male age × female age + male age × parasitism + female age × parasitism	16	198.61	1.76	0.060
Brood size + year + date + parasitism +female age + female age × parasitism	13	198.76	1.91	0.055
Annual productivity‡				
Female age + parasitism + female age × parasitism	6	323.39	0.00	0.482
Female age + parasitism	5	324.14	0.75	0.331

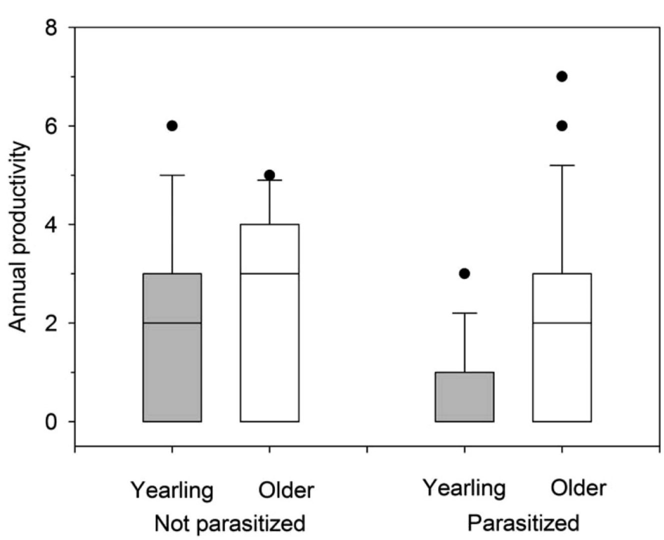
Note: Candidate models sets examined variation in clutch size (n = 197), nesting success (n = 209), number fledged (n = 109), fledgling condition (n = 99), and annual productivity (n = 160).

*K is the number of parameters in the model +1 for intercept and +1 for model variance.

†K is the number of parameters in the model +1 for intercept and +1 for variance inflation factor.

‡K is the number of parameters in the model +1 for intercept, +1 for model variance, and +1 for variance inflation factor.

Fig. 2. Boxplots comparing the annual productivity of yearling and older female Yellow Warblers (*Setophaga petechia*) parasitized or not parasitized by Brown Headed-Cowbirds (*Molothrus ater*) between 2004–2006, and 2008–2011 Boxplots show median, interquartile range (box), 10th and 90th percentiles (whiskers) and outliers (solid circles). Samples sizes from left to right are 54, 70, 13, and 23.



no evidence of unexplained temporal variation in annual productivity; the year term was not included in any of the models that received strong support.

Discussion

This study, like many other studies that have examined age effects on breeding performance of birds, found that older female Yellow Warblers had higher annual productivity than yearling females. Age-related improvements in productivity resulted from improvement at several stages of the nesting cycle as older females laid larger clutches and fledged more young per successful nest. Our results were consistent with other studies that have shown age-related variation in 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 expectations, however, we only detected age-specific costs of brood parasitism on one measure of breeding performance, the total number of young fledged during the course of the breeding season.

Brood parasitism is known to have negative impacts on host breeding performance at several stages of the breeding cycle (Lorenzana and Sealy 1999). Studies on a large range of host species have demonstrated that parasitized nests have smaller clutches (Smith 1981; Rothstein 1982; Sealy 1995; Tewksbury et al. 2002) and reduced hatching (Walkinshaw 1961; McMaster and Sealy 1999; Peer and Sealy 1999; Peer and Bollinger 2000) and fledging (Walkinshaw 1961; Marvil and Cruz 1989; McMaster and Sealy 1999; Payne 2005) success. Brood parasitism by Brown-headed Cowbirds also reduced the breeding success of Yellow Warblers in our study. Yellow Warblers with parasitized nests had smaller clutch sizes presumably because female cowbirds remove a host egg prior to laying their own. However, these parasitized nests were as likely to fledge young as nests that were not parasitized. If nests were successful, Yellow Warblers also fledged fewer young from parasitized than unparasitized nests. Losses at the end of the nestling period were greater than losses in clutch size (1.3 offspring versus 0.8 eggs). This could result because eggs were damaged during brood parasitism and failed to hatch (Peer and Sealy 1999) or because nestling mortality is higher when competing with a cowbird nestling (Lichtenstein and Sealy 1998). Female warblers that were parasitized at least once during a breeding season consequently produced, on average, 1.3 less fledglings than females that avoided brood parasitism.

Competition between host offspring and cowbird nestlings for food provided by parents during the nestling and postfledging period may reduce juvenile survival and lead us to underestimate the cumulative costs of brood parasitism by cowbirds. However, empirical evidence that host nestlings are in worse condition and have lower juvenile survival when raised alongside cowbirds is mixed. Weatherhead (1989) found that cowbird nestlings did not influence the growth rates of nestling Yellow Warblers or nestling Red-winged Blackbirds (*Agelaius phoeniceus* (L., 1766)). Smith (1981) found that the mass of nestling Song Sparrows was reduced when raised with a cowbird, but that the presence of a cowbird fledgling had no effect on juvenile survival to independence. In contrast, other studies suggest that the reproductive costs of brood parasitism extend into the postfledging period (Payne and Payne 1998; Rasmussen and Sealy 2006). We found that, after controlling for seasonal and interannual variation in nestling condition, the presence of a cowbird reduced the condition of nestlings measured 2 days prior to fledging. However, further work is required to determine if the impact of cowbirds on nestling condition or parental food allocation decisions after nestlings fledge, but prior to independence, influence the subsequent survival of juvenile Yellow Warblers (cf. Green and Cockburn 2001; Payne and Payne 1998).

We predicted that prior experience with brood parasites, or earlier arrival and the occupancy of higher quality territories, would result in older females having lower parasitism rates and higher rejection rates. Most age-specific studies on cuckoo hosts have found that older or more experienced hosts are parasitized less often (Brooker and Brooker 1996; Langmore and Kilner 2007) and reject parasitic eggs more frequently (Lotem et al. 1992, 1995; Langmore et al. 2009; but see Moskát and Hauber 2007). In contrast, studies on Brown-headed Cowbird hosts have usually found that older females, despite investing more in nest-protection behaviors (Hobson and Sealy 1989), are not less likely to be parasitized and do not have higher rejection rates than yearlings (Song Sparrow: Smith 1981; Yellow Warbler: Sealy 1995). Our results, although counter to our predictions, were consistent with previous studies in that we found no evidence that older females were less likely to be parasitized or had higher rejection rates than yearling females. Interestingly, although sample sizes are relatively small, older female Yellow Warblers were slightly less likely to reject parasitized nests than yearlings in both Manitoba (yearlings: 45%, n = 22; older: 37%, n = 54; Sealy 1995) and British Columbia (yearlings: 27%, n = 15; older: 19%, n = 27; this study).

The prediction that older Yellow Warblers would be more likely to adopt strategies that reduce parasitism rates and increase rejection rates of nests parasitized by cowbirds was developed from the perspective of the host. However, from the brood parasite's perspective, we would expect that cowbirds should preferentially parasitize older, higher quality females that are more likely to fledge young. Studies suggest that cowbirds and cuckoos that parasitize nests of Song Sparrows and Magpies (*Pica pica* (L., 1758)), respectively, may use cues such as nest defence and nest size that are correlated with the quality of individual hosts when selecting a host nest (Smith et al. 1984; Soler et al. 1995). Brood parasitism may therefore be nonrandom and high-quality older individuals that are usually more productive might be differentially impacted by brood parasitism (Krüger 2007). In our study the evidence that cowbirds preferentially parasitize older Yellow Warblers was weak. Our data therefore suggest either cowbirds do not have a strong preference for host nests built by older females or that the host nest preferences of cowbirds are counterbalanced by superior nest-protection behaviour of older Yellow Warblers (Hobson and Sealy 1989; Gill and Sealy 2004). Experimental work is required to evaluate the nest preferences of female cowbirds.

We expected that once parasitized by Brown-headed Cowbirds, older female Yellow Warblers that accepted host eggs would be less impacted by the reproductive costs of brood parasitism than yearlings. Somewhat surprisingly, brood parasitism had a similar impact on the clutch size and number of young fledged per successful nest of older and yearling females. Evidence that brood parasitism had less impact on older females was only obtained when costs were evaluated over the course of the entire breeding season. Differences in the cumulative costs of brood parasitism for older and yearling females may also be greater than estimated if older females are better at mitigating any postfledging costs of brood parasitism (see above). Unfortunately, we did not monitor juvenile survival of Yellow Warblers and cowbirds. Nevertheless, our results differ markedly from those of Smith (1981), who found that over the course of the breeding season yearling and adult female Song Sparrows that were parasitized raised the same number of independent young as unparasitized females of the same age. The difference may arise because parasitized female Song Sparrows are of higher quality and initiate more breeding attempts than unparasitized females, and female Song Sparrows are typically only parasitized in the last breeding attempt of the year. Yellow Warblers, in contrast, are rarely multibrooded and parasitism is observed in first and subsequent breeding attempts (this study).

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