Breeding Biology of Red-winged Blackbirds in the Rocky Mountains, British Columbia

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Abstract: Weather was the major factor in higher Red-winged Blackbird (*Agelaius phoeniceus*) productivity (more and larger eggs, lower egg failure rates, higher nestling survival) in 2004 compared to 2005. Nest success varied from 57% to 74%. Causes of mortality included drowning, predation, parental abandonment following predation of nest mates, hypothermia and/or lack of food associated with poor weather, and disease, pneumonia, or other bacterial infections. The diseases included three nestlings with bacterial pneumonia and one with an intestinal streptococcus infection. Two apparently healthy nestlings, when necropsied, had ventricular endocardial necrosis. Despite the adverse weather, this population had higher productivity in both years than provincial averages. This may have been partly due to the absence of predation and competition with Marsh Wrens (*Cistothorus palustris*), absence of nest site competition with Yellow-headed Blackbirds (*Xanthocephalus xanthocephalus*), and low levels of Brown-headed Cowbird (*Molothrus ater*) nest parasitism.

Keywords: Red-winged Blackbird, *Agelaius phoeniceus*, nest success, productivity, nest parasitism, egg temperature

Introduction

The Red-winged Blackbird (*Agelaius phoeniceus*), possibly the most abundant and one of the best-studied birds of North America, has a polygynous mating system in which males defend territories where several females may nest (Yasukawa and Searcy 1995). It is a hardy species, with breeding populations in the Northwest Territories, Yukon, and Alaska. Northern populations tend to have larger eggs, higher clutch and brood sizes, and faster growth because of the abundant prey and longer daylight foraging hours. For example, in Alaska, mean clutch sizes were 4.4 and 4.3 in two years of study (McGuire 1986). The diversity and availability of prey is a major determinant of productivity and starvation of nestlings is frequently reported even when prey are relatively abundant (Willson and Orians 1963; Orians 1966; Robertson 1973; Voigts 1973; Caccamise 1977; McGuire 1986; Muldal *et al.* 1986). Starvation of Red-winged Blackbird nestlings can range from < 1% (Smith 1943) to > 60% (Haigh 1968). Prey availability has large diurnal as well as seasonal variability. Many invertebrate larvae hatch according to specific thermal criteria and are synchronized with the phenology of their host or habitat plants. Orians (1966), for example, found that fewer aquatic than terrestrial prey were available in the mornings than in the afternoon and evenings, evidently because hatches occurred later in the day when weather was warmer, and Red-winged Blackbird diet reflected this diurnal variability.

Cold, wet weather can kill Red-winged Blackbird nestlings by a combination of exposure and starvation—the latter because fewer prey are available under such conditions, the female must spend more time foraging instead of incubating, and the nestlings' caloric requirements are greater (Willson and Orians 1963; Orians 1966; Fletcher and Koford 2004). Therefore, weather and starvation are closely linked in this species.

Red-winged Blackbird eggs in British Columbia are incubated for 10-11 days and the young fledge in 11-16 days (Campbell *et al*. 2001). Hatchlings are altricial: blind, naked, and helpless.

During 2003–2005 I studied selenium uptake in Red-winged Blackbirds for a mining consortium in southeast British Columbia, and later published some of the results relating to effects of selenium (Harding 2008). However, much of the breeding biology of the blackbirds and their relations to environmental conditions and to other species was not published. This paper summarizes the results of this study as they relate to the breeding biology of Red-winged Blackbirds in the Rocky Mountains of southeastern British Columbia.

Methods

Study area

We sampled 10 sites in total (Figure 1), but varied the sites in each year, according to where sufficient numbers of blackbirds were nesting. These are listed in Table 1.

Egg collections

Biological samples were collected under British Columbia scientific permits. We searched suitable habitats for nests using a canoe or chest waders. In 2003, we collected a preliminary series of Red-winged Blackbird eggs to determine if selenium uptake was occurring. In 2003 and 2004, we collected one or two eggs from nests containing at least two or three eggs, respectively. In 2005 we changed laboratories so that we could collect only one egg from nests with two or more eggs (Harding 2008). We salvaged eggs that failed to hatch for chemical analysis. Eggs were weighed (Ohaus triple beam balance scale) and measured (electronic calipers), examined for viability and possible teratogenic effects, and shipped to a laboratory for chemical analysis. Since nests are easy to locate and we sampled every nest we found that contained eggs, the sample sizes (N) in Tables 1 and 2 approximate the number of active nests in each colony. Sample sizes vary from table to table, however, because of data that could not be collected, such as a broken egg preventing accurate measurement or a nest predated before all eggs had been laid.

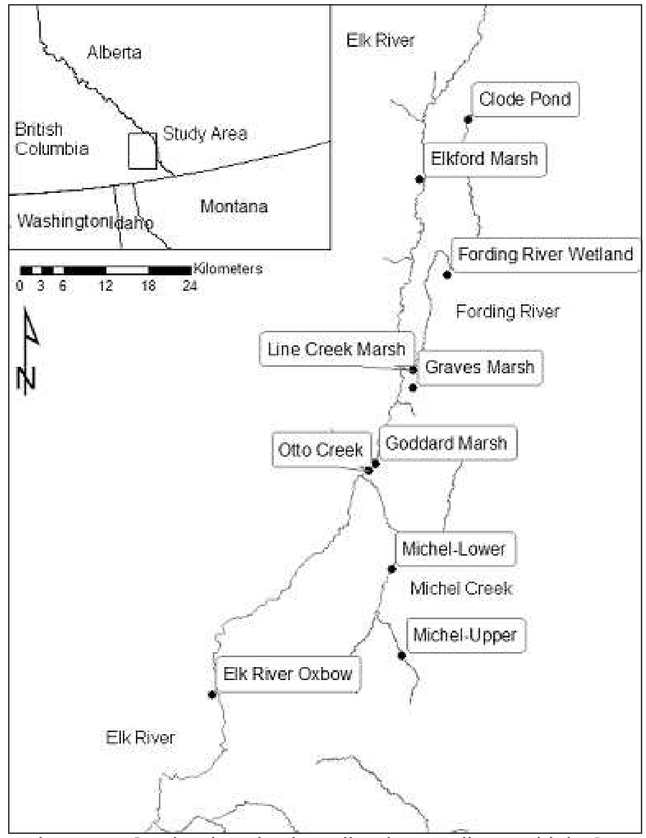

Figure 1. Study sites in the Elk River Valley, British Columbia. Otto Seep and Otto Ditch, mentioned in the text, are beside Otto Creek. Michel-Lower and Michel-Upper data were combined for analysis.

Productivity

In 2004 and 2005, we returned to each nest to count eggs and young at intervals of 3-4 days until all young had fledged. Eggshell fragments indicated predation. Eggs missing from active nests at the hatch date (calculated from the first appearance of eggs) were recorded as predated unless signs suggested otherwise, such as nests tipped over by wind. In 2005, we used a Fluke infrared thermometer (a non-contact sensor) to measure the egg temperatures to determine when incubation started and whether eggs found in the nest after the expected hatch date were still being incubated. Evidence of the cause of egg failure was recorded if seen. Examples were eggs cold and wet following rain or snow; eggs cold and absence of parents suggesting parental abandonment; and egg shells and other evidence indicating predation.

Sources of nestling mortality were recorded if evidence suggested a cause. These included nests tipped over in a manner suggesting either weather or predation; nestling remains in or near the nest suggesting predation (taking care to differentiate scavenging of dead nestlings); and dead nestlings following either severe weather episodes or parental abandonment. Nestlings found dead were submitted to the British Columbia Animal Health Centre, Abbotsford, for post-mortem examination and diagnosis, and their livers were analysed for selenium. Nestlings that disappeared before the earliest likely fledging date (i.e., 11 days post-hatch), without evidence of predation, were counted as failed and included in mortality and survival calculations.

Evidence of successful fledging included worn spots on the edge of the nest where the juveniles stood while being fed just prior to fledging, and bird droppings in the nest (females remove the juveniles' droppings while they remain in the nest, but cease to do so when they leave the nest). When nests that had previously held well-feathered, active nestlings within 1–2 days of the expected fledging date (as calculated from the hatch date) were later found empty, we recorded them has having fledged.

Prey items

In 2005, we collected prey items to analyse their selenium content and to determine whether they were predominantly aquatic or terrestrial taxa. We applied rubber bands as ligatures around one juvenile's neck in each of 34 nests, held tight with a short section of surgical tube, to prevent swallowing, similar to the method of Willson and Orians (1963), who used pipe cleaners as ligatures. We then withdrew far enough away to avoid disturbing the female, but close enough to see foraging and feeding activity, typically 20-40 m, using binoculars and a 20X spotting scope. We counted the number of times the female went to the nest with prey items and attempted to identify the prey items by taxon (Order) and source (terrestrial or aquatic). After the female had fed her nestlings about three times, but no longer than 30 minutes, we returned to the nest, extracted the prey items from the proventriculus (the anterior part of the stomach) with a small forceps, removed the ligatures, and replaced the juveniles in the nest. Then we withdrew and continued observing until the female returned to the nest and began feeding again. She usually returned to the nest within about one minute and began delivering food usually within about three minutes, but occasionally up to about 20 minutes.

Weather records

Temperature and precipitation records for Clode Pond were provided by Fording River Operations; Line Creek and Sparwood data were downloaded from Environment Canada Climate Data Archives.

Statistical analysis

I used SPSS® (SPSS Inc., Chicago, IL) for statistical analysis. Unless otherwise specified, comparisons were made using analysis of variance (ANOVA) with the Bonferonni adjustment for multiple comparisons. Hatchability, reported elsewhere (Harding 2008) was measured as "the proportion of eggs surviving to the end of incubation that hatch" (Koenig 1982). This method differentiates egg mortality that might have been caused by toxic chemicals from other causes, to the extent possible. Although a slight decrease in hatchability was detected in nests with high mean egg selenium concentrations, this was offset by an increase in hatchability in nests with unusually low mean egg selenium concentrations (selenium is an essential dietary element, but becomes toxic at high doses). For this reason, plus the absence of nestling mortalities that could be attributed solely to selenium, and the finding that selenium-exposed colonies had no episodes or rates of mortality that could not be better explained by weather events (which also occurred in non-selenium exposed colonies-Harding 2008), the possible effects of selenium are not further discussed here.

Nestling survival was measured as the percent of nestlings that survived to the fledging stage, relative to the number that hatched in each nest. Mortality, the number of nestlings that died, is not exactly the inverse of percent nestling survival, because of varying numbers of hatchlings in each nest and other reasons, although the two measures are highly correlated.

Some collected eggs were broken and could not be weighed and/or examined, and a few additional eggs were salvaged for analysis after they failed to hatch. When whole nests were destroyed, e.g., by weather or predators, before laying was complete, they were not included in subsequent observations; hence the sum of eggs that were collected, lost, incubated to full term, and failed to hatch after full incubation is always less than the number laid. Clutch size can be compared with other studies because we counted the eggs before collecting. Since the brood size, number of mortalities and the number fledged in each nest were diminished by the number of eggs collected, which was fewer in 2005 than 2004, these measures cannot be strictly compared between years, or with other studies. However, hatchability and the percent fledged are comparable because they are the proportions that hatch of the eggs incubated to full term, and that fledge of those that hatched, respectively.

Table 1. Mean egg weight (g.) per nest, 2003-2005.

Site	N (nests)	Mean	Std. Deviation	Std. Error	Min.	Max.
			2003			
Clode Pond	6	3.62	.512	.209	2.70	4.10
Goddard Marsh	6	3.37	.585	.239	2.50	3.90
Otto Creek	9	3.63	.587	.196	2.30	4.20
Fording Wetlands	3	3.87	.404	.233	3.50	4.30
Otto Seep/Ditch	2	3.40	.141	.100	3.30	3.50
Total	26	3.58	.519	.102	2.30	4.30
			2004			
Clode Pond	6	4.26	.234	.0957	4.00	4.60
Goddard Marsh	12	3.88	.425	.123	3.20	4.85
Line Creek Marsh	10	3.97	.426	.135	3.09	4.29
Otto Creek	39	4.03	.585	.0937	2.52	4.90
Graves Marsh	15	3.35	.833	.215	1.35	4.40
Fording Wetlands	12	4.40	.507	.147	3.45	5.04
Otto Seep/Ditch	14	3.71	.347	.0928	3.02	4.18
Elk R. Oxbow-Lower	4	4.60	.778	.389	3.95	5.50
Total	112	3.95	.631	.0596	1.35	5.50
			2005			
Clode Pond	9	4.05	.367	.122	3.50	4.60
Goddard Marsh	7	3.32	.993	.375	1.15	3.94
Line Creek Marsh	12	3.26	.648	.187	2.30	4.60
Otto Creek	26	3.77	.514	.101	2.73	4.96
Elkford Marsh	6	3.36	.983	.401	1.60	4.31
Graves Marsh	16	3.78	.814	.204	2.20	5.20
Michel Creek*	6	3.31	.294	.112	2.87	3.78
Fording Wetlands	10	3.77	.383	.121	3.30	4.50
Total	92	3.64	.669	.0698	1.15	5.20

*Two colonies along Michel Creek were sampled and results combined.

Results

We counted and collected eggs from 21 nests in 2003. We counted and collected eggs and monitored productivity (eggs hatched, eggs failed, nestling mortalities, and nestlings fledged) in 91 nests in 2004, and 133 in 2005: 245 nests in total.

Weather

In 2004, temperatures were generally within the long-term normal range. In June, however, when most blackbird eggs were laid, there were three excursions below the long-term normal minimum temperature for Sparwood. At Clode Pond, there was also an anomalously low minimum temperature during the second week of July, reaching 0 ºC on July 09, and a snowstorm July 07-09. Clode Pond, further north and at higher elevation, averaged 3.3 ºC cooler than Sparwood throughout the study.

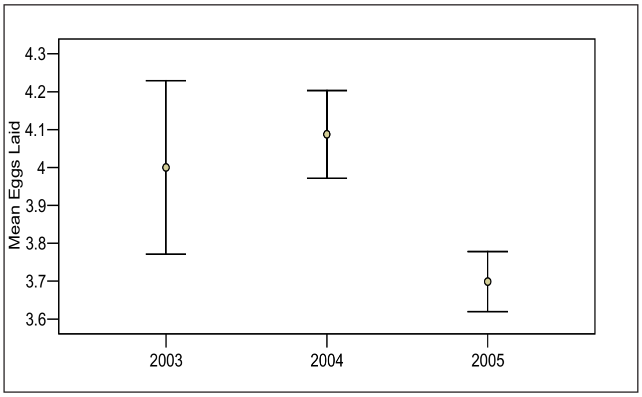

Figure 2. Mean number of eggs laid per nest, 2003-2005. Error bars are mean ± SE.

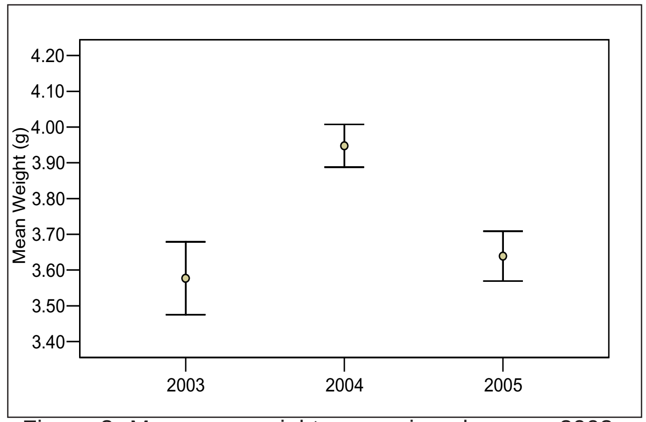

Figure 3. Mean egg weight comparison by year, 2003–2005. Error bars are mean ± SE.

Temperatures at all three weather stations were cooler than average in 2005. For example, Clode Pond had daily means of 2.9 ºC in June and 4.5 ºC in July, compared to long-term normals of 3.5 ºC and 5.6 ºC, respectively. Temperatures at Sparwood and Line Creek were likewise approximately one degree below normal. Record rainfalls occurred in June 2005 when 221 mm of total precipitation fell at Clode Pond, more than three times the long term normal of 67 mm. At Sparwood, a record 170.5 mm of precipitation fell in June 2005, compared to a normal June precipitation total of 62.8 mm. All three stations had exceptionally high precipitation June 05–07, culminating in a snowstorm June 06–07, which totaled 12.9 cm at Sparwood.

Clutch size and egg mortality

In 2003, the 21 nests had a mean clutch size of 4.0 ± SE 0.23. Of the 91 nests monitored in 2004, seven were destroyed by predators or storms and eggs were not laid in four, leaving 80 from which productivity data were collected. From these, we collected 116 eggs for analysis from 78 nests (mean = 1.5 per nest), and 18 were lost to predators or other mishaps (not counting whole nests that were destroyed). Ultimately, 170 eggs in 67 nests (mean = 2.5 per nest) were incubated to full term. Of these, 42 failed to hatch.

Of the 133 nests that we monitored at ten sites in 2005, 113 produced clutches. No eggs were produced in 20 nests that were either abandoned by the parents or destroyed by weather before egg-laying was complete. We collected 63 eggs from 112 nests (mean = 0.56 per nest). Predators, weather, nest abandonment, and other mishaps caused a further loss of 93 eggs before full incubation. Of 259 eggs incubated to full term, 48 failed to hatch.

Comparing 2003, 2004, and 2005 (Table 2), significantly ($p = 0.019$) fewer eggs were laid in 2005 (mean = 3.7 ± SE 0.080) compared to 2004 (mean = 4.1 ± SE 0.12). The differences in eggs laid between 2003 (mean = 4.0 ± SE 0.23) and both 2004 and 2005 were not statistically significant, because of the higher variability in the smaller 2003 data set (Figure 2). In each year, there were no consistent differences ($p > 0.05$) among the colonies in the number of eggs laid. Eggs were significantly heavier in 2004 than in either 2003 or 2005 (ANOVA: $p < 0.05$; Table 1; Figure 3). Egg volume was highly correlated with egg weight and is reported elsewhere (Harding 2008).

In both years, most eggs hatched over a period of about a month, beginning around June 01. First hatch dates were June 05, 2004 and May 27, 2005 (Figure 4). In 2005, the mean hatching date was June 15 with a bimodal distribution as some birds presumably re-nested after earlier, failed attempts following the June 05–07 snow storm.

Far more eggs were lost to weather and other mishaps before full incubation in 2005 (mean = 0.85 ± SE 0.13 per nest)

Table 2. Mean number of eggs laid per nest, 2003-2005.

Site	N (nests)	Mean	Std. Deviation	Std. Error	Min.	Max.
2003						
Clode Pond	4	4.25	1.708	.854	2	6
Goddard Marsh	5	3.60	.894	.400	2	4
Otto Creek	7	4.29	.488	.184	4	5
Fording Wetland	3	4.00	1.732	1.000	2	5
Otto Seep/Ditch	2	3.50	.707	.500	3	4
Total	21	4.00	1.049	.229	2	6
2004						
Clode Pond	7	4.57	.787	.297	3	5
Goddard Marsh	8	4.13	.354	.125	4	5
Line Creek	7	4.14	1.574	.595	2	7
Otto Creek	25	3.80	1.118	.224	2	6
Graves Marsh	10	4.30	1.567	.496	2	8
Fording Wetland	6	4.33	.516	.211	4	5
Otto Seep/Ditch	9	3.78	.441	.147	3	4
Elk River Oxbow	8	4.38	.744	.263	3	5
Total	80	4.09	1.034	.116	2	8
2005						
Clode Pond	11	3.91	1.136	.343	2	5
Goddard Marsh	9	3.33	1.000	.333	1	4
Line Creek	11	3.82	.751	.226	3	5
Otto Creek	38	3.68	.620	.101	2	5
Elkford Marsh	8	4.00	.756	.267	3	5
Graves Marsh	21	3.67	1.065	.232	1	5
Michel Creek*	7	3.86	.378	.143	3	4
Fording Wetland	8	3.38	1.061	.375	1	4
Total	113	3.70	.844	.079	1	5

*Two colonies along Michel Creek were sampled and results combined.

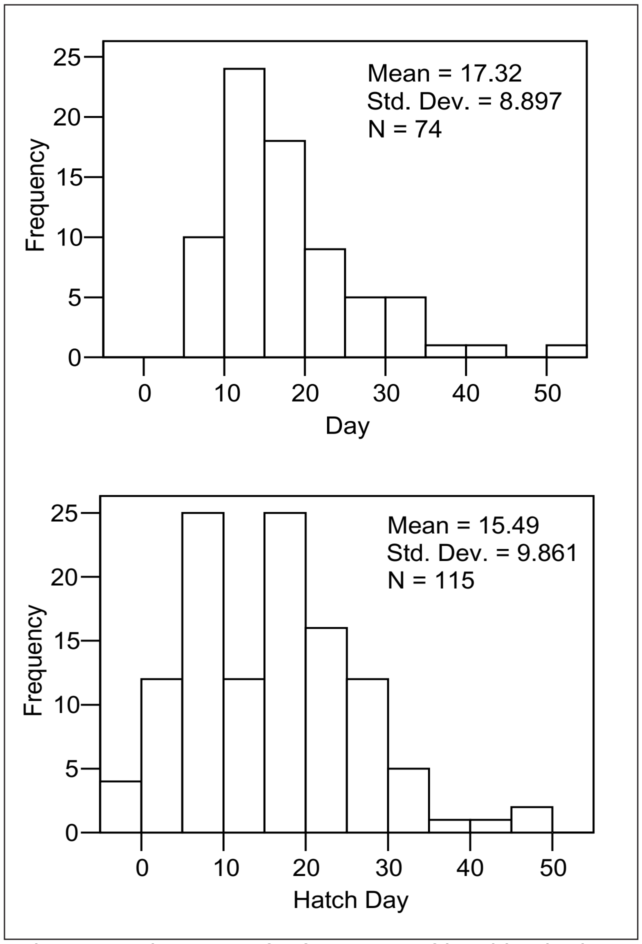

Figure 4. Histograms for frequency of hatching in days from June 01, upper 2004, lower 2005. Each bar represents five days.

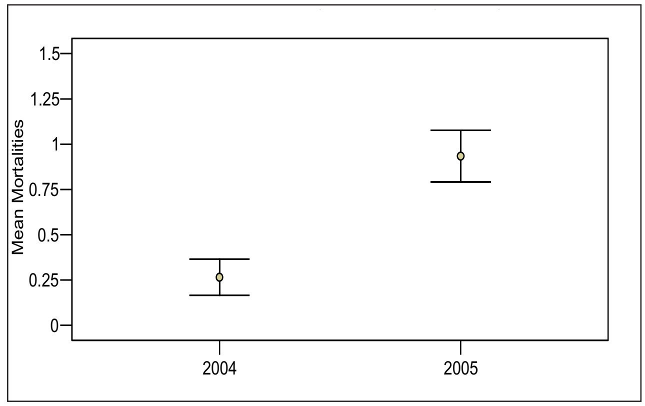

Figure 5. Mean (per nest) nestling mortalities (combining observed mortalities and those inferred because of the circumstances of their disappearance) in 2004 and 2005. Error bars are mean ± SE.

than in 2004 (mean = 0.23 ± SE 0.092). Of those incubated to full term, in both 2004 and 2005, as expected, hatchability was inversely correlated with the number of egg failures per nest (Pearson r = -0.832, $p < 0.001$ in 2005). There were no overall differences between 2004 and 2005 in the number of fully incubated eggs that failed, or, conversely, hatchability (ANOVA: $p > 0.05$).

In 2004, at Graves Marsh (Figure 1), a freezing rain on June 20 apparently killed all of the eggs. When checked on June 21, all eggs were wet and cold to the touch and there were no females present in the marsh. None of those eggs hatched, and no more were laid in those nests, although subsequently, new nests were constructed in which eggs were laid, hatched, and fledged.

In 2005 when we used the temperature sensor, incubation was usually indicated by at least one egg in the nest with a temperature of 29–32 ºC. On our second field day, June 02, we noticed that egg temperatures dropped about one degree per minute. Ambient temperature was 11 ºC and nine mm of rain fell that day at Sparwood. For this reason, we subsequently avoided examining nests on days of heavy rainfall.

In 2004, we found two Red-winged Blackbird nests (2.3%) with American Robin (*Turdus migratorius*) eggs. One of these held both cowbird and robin eggs. We found Brown-headed Cowbird eggs in 4.6% of nests in 2004 and none in 2003 or 2005; however, none of the Brown-headed Cowbird or American Robin eggs hatched.

In 2004, other marsh birds included a male Yellow-headed Blackbird (*Xanthocephalus xanthocephalus*) and a single Marsh Wren (*Cistothorus palustris*) in one of the more southerly marshes. These species, which are known nest site competitors with Red-winged Blackbirds, were not seen in 2003 and 2005.

Nestling mortality and survival

Of the 91 nests monitored in 2004, 49 fledged a mean of 2.35 ± 0.15 SE fledglings per nest (74% nest success).

In 2005, of the 133 nests monitored, 76 fledged a mean of 1.93 ± SE 0.16 fledglings (57% nest success). On a whole nest basis for which losses could be determined, predation accounted for the loss of 25 of 133 nests (18.7%), and weather for 12 (9.0%). One with nestlings was trampled by elk and three were abandoned by the parents.

As with egg failures and hatchability, nestling survival was inversely correlated with the number of mortalities per nest (Pearson r = -0.884, $p < 0.001$ in 2005). In 2005, there was significantly (ANOVA: $p < 0.001$) higher mortality (Table 3; Figure 5) and lower survival (Figure 6) of nestlings compared to 2004.

In 2004, we found seven dead nestlings. All were found two days after a late snowstorm on July 05–07. Although the pathology report did not identify a clear cause of death, they probably succumbed to hypothermia; some were in nests accompanied with live nest mates and still attended by the adult female. In 2005, we found 31 dead nestlings in or near the nests. Another 40 mortalities were inferred because they disappeared before the fledging date without evidence of predation, bringing the total of observed and inferred

Table 3. Mean number of eggs failed, number of nestling mortalities and percent nestling survival per nest, 2004-2005. Eggs failed are those that were incubated to full term (does not include eggs lost before full term); mortalities are those observed plus those inferred because they went missing before the expected fledging date; nestling survival is the percent of nestlings that fledged of those that hatched.

Site	N (nests)	Mean	Std. Deviation	Std. Error	Min.	Max.
2004						
Eggs failed						
Clode Pond	5	.20	.447	.200	0	1
Goddard Marsh	8	.50	.756	.267	0	2
Line Creek	7	1.43	1.14	.429	0	3
Otto Creek	24	.71	1.08	.221	0	4
Graves Marsh	2	1.00	1.41	1.00	0	2
Fording Wetland	5	.20	.447	.200	0	1
Otto Seep/Ditch	7	.71	1.50	.565	0	4
Elk River Oxbow	5	.40	.894	.400	0	2
Total	63	.67	1.03	.130	0	4
Nestling Mortalities (observed and inferred)						
Clode Pond	5	1.40	1.14	.510	0	3
Goddard Marsh	6	.00	.000	.000	0	0
Line Creek	3	.33	.577	.333	0	1
Otto Creek	19	.11	.315	.072	0	1
Graves Marsh	1	.00	.	.	0	0
Fording Wetland	5	.00	.000	.000	0	0
Otto Seep/Ditch	5	.00	.000	.000	0	0
Elk River Oxbow	5	.60	1.34	.600	0	3
Total	49	.27	.700	.100	0	3
Nestling survival (percent)						
Clode Pond	5	62.7	32.1	14.4	25.0	100
Goddard Marsh	6	100	.000	.000	100	100
Line Creek	3	91.7	14.4	8.33	75.0	100
Otto Creek	19	94.7	15.8	3.62	50.0	100
Graves Marsh	1	100	.	.	100	100
Fording Wetland	5	100	.000	.000	100	100
Otto Seep/Ditch	5	100	.000	.000	100	100
Elk River Oxbow	5	80.0	44.7	20.0	.00	100
Total	49	91.6	22.0	3.14	.00	100
2005						
Eggs failed						
Clode Pond	7	.43	.535	.202	0	1
Goddard Marsh	9	.67	1.00	.333	0	3
Line Creek	10	1.40	1.58	.499	0	4
Otto Creek	36	.50	.910	.152	0	3
Elkford Marsh	6	.83	1.17	.477	0	3
Graves Marsh	9	.22	.441	.147	0	1
Michel Creek	4	.25	.500	.250	0	1
Fording Wetland	4	.50	.577	.289	0	1
Total	85	.60	.978	.106	0	4
Nestling Mortalities (observed and inferred)						
Clode Pond	8	1.38	1.51	.532	0	4
Goddard Marsh	8	.25	.463	.164	0	1
Line Creek	7	1.00	1.00	.378	0	3
Otto Creek	32	.81	1.15	.203	0	4
Elkford Marsh	4	2.25	1.71	.854	0	4
Graves Marsh	9	1.22	1.39	.465	0	3
Michel Creek	4	1.25	1.89	.946	0	4
Fording Wetland	4	.00	.000	.000	0	0
Total	76	.93	1.25	.143	0	4
Nestling survival (percent)						
Clode Pond	8	45.0	49.9	17.6	.00	100
Goddard Marsh	8	84.40	35.2	12.4	.00	100
Line Creek	7	58.4	42.2	16.0	.00	100
Otto Creek	32	74.0	36.8	6.51	.00	100
Elkford Marsh	4	25.0	50.0	25.0	.00	100
Graves Marsh	9	51. 9	50.3	16.8	.00	100
Michel Creek	4	66.8	47.1	23.6	.00	100
Fording Wetland	4	1000	.000	.000	100	100
Total	76	66.4	42.4	4.9	.00	100

mortalities to 71. Most of these (77%) had hatched before June 20 when weather was cold and wet. Mortalities clustered from June 04 to June 09, a period of record rainfall and low temperatures; and June 12 to June 20, a period of extremely cold weather with a heavy rainfall on June 17. This was in contrast to 2004, when no juveniles were found dead before the July snowstorm mentioned above.

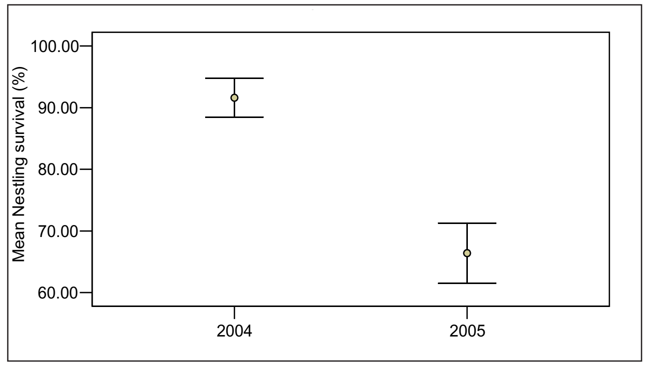

Figure 6. Mean (per nest) nestling survival (the number fledged in relation to those that hatched) in 2004 and 2005. Error bars are mean ± SE.

In 2005, proximal causes of death could be determined with a degree of confidence for 21 of 30 Red-winged Blackbird nestlings that were found dead, examined in the field, and sent to the pathology laboratory: five (17%) drowned, one (3%) died in an abandoned nest following predation of its nest mates, 11 (37%) died of hypothermia and/or lack of food associated with poor weather, and four (13%) died of disease, pneumonia, or other bacterial infections. The diseases included three nestlings with bacterial pneumonia, and one with an intestinal streptococcus infection. Two apparently healthy nestlings sacrificed for a selenium-related experiment, both from reference areas, had ventricular endocardial necrosis.

Prey items

We collected 25 prey item samples from nestlings after 34 attempts. Adult females fed their nestlings a variety of terrestrial and aquatic prey including lepidopterans (butterflies and moths) caterpillars, damselflies, dragonflies, stoneflies, dipterans (true flies), midges, and caddisflies. Females either foraged within a few meters of their nests, or flew as far as about 100 meters away to forage. They foraged by gleaning insects and other arthropod prey from rooted emergent aquatic plants, from rooted floating aquatic plants, from the water's surface, and from terrestrial trees and shrubs. Infrequently, they also captured prey by flycatching (capturing prey on the wing). After feeding their young, the females regularly removed faecal sacks and other debris from the nest.

Females delivered prey items an average of once every 10.8 minutes (SD = 4.8, n = 25). Of the prey items that could be identified to source (terrestrial or aquatic) by watching the parents forage, or to taxon (Order), 36 prey items (43%) were terrestrial and 48 (57%) were aquatic. This difference was statistically significant (χ^2, p = 0.01), but only accounted for the number of prey items and not the volume. Terrestrial prey items tended to be large (e.g., caterpillars, *Lepidop-*

tera), while most aquatic prey items were small (e.g., midges, *Chironomidae,* and caddisflies, *Trichoptera*); however, some aquatic prey were very large (e.g., damselflies, *Zygoptera*, dragonflies, *Anisoptera*, and western stoneflies, *Calineuria californica*).

Discussion

We saw no evidence that looking into the nests to count eggs and young interfered much with parental behaviour, although I did not test this empirically. As noted above, to limit exposure of eggs, we avoided disturbing nests on cold or rainy days. We did not handle the eggs or nestlings, except for a small sample of nests from which we collected prey and blood samples in 2005. The females normally returned to the nests to incubate or feed young within a minute or so of these disturbances. From these observations, it is unlikely that our observations would have had any effect on productivity.

That weather affected productivity in this study is shown by three lines of evidence: (1) smaller clutches of smaller eggs, higher egg losses, higher nestling mortality and lower nestling survival in 2005 compared to 2004, associated with below-normal temperatures and above-normal precipitation in 2005; (2) specific storms that varied in space and time when high precipitation and low temperatures were accompanied or followed shortly by high mortality of eggs or nestlings at specific colonies; and (3) Animal Health Centre diagnoses of pneumonia, other bacterial infections, and/or starvation in nestlings found dead at these times.

Our lowest clutch size, 3.7 in 2005, even though significantly lower than the mean of 4.1 we found in 2004, was still above the provincial mean of 3.4 (calculated from data given in Campbell *et al.* 2001 from nest records throughout BC). Nest success (the proportion of those found with eggs and followed to a known fate that produced at least one fledgling) was 74% in 2004 and 57% in 2005, compared to provincial average of 24% (N=275) (calculated as above from data in Campbell *et al.* 2001). Yellow-headed Blackbirds and Marsh Wrens compete with Red-winged Blackbirds for nest sites, and Marsh Wrens destroy blackbird eggs (Willson and Orians 1963; Orians 1966; Picman and Isabelle 1995; Picman *et al.* 1996). The virtual absence of these species (one each seen in only one of the three years) may have been a factor in the high productivity, relative to the provincial averages. The low levels of Brown-headed Cowbird nest parasitism (4.6% of nests in 2004 and none in 2003 and 2005), probably also contributed. By contrast, Brown-headed Cowbirds parasitized 11% of Red-winged Blackbird nests in the Okanagan Valley (Cannings *et al.* 1987). In this study, weather was clearly the dominant factor in lower nestling productivity in 2005 compared to 2004.

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