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COSTS OF BROWN-HEADED COWBIRD PARASITISM TO WILLOW FLYCATCHERS

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Abstract. The costs of Brown-headed Cowbird (*Molothrus ater*) brood parasitism to Willow Flycatcher (*Empidonax traillii adastus*) seasonal fecundity and lifetime reproductive success were assessed in a long-term study conducted from 1988–1997 at Malheur National Wildlife Refuge, Oregon. Parasitism rates of Willow Flycatcher pairs (N = 882) among three study areas averaged 23.4%, ranging from 10.9–40.7% over 10 years (all study areas combined) and from 15.4–41.5% across the three study areas (all years combined). The lowest (0.0%, Dredger South, 1997) and highest (87.1%, Bridge Creek, 1991) parasitism rates underline the high variability of cowbird parasitism across time and space. Nest success (pairs fledging ≥ 1 young) of parasitized pairs was 50.3% less than that of unparasitized pairs; parasitized pairs had fewer eggs survive to fledging (17.3 vs. 51.4%), lost more eggs (3.08 vs.1.28) and nestlings (1.18 vs. 0.79), and reared fewer offspring (0.80 vs. 2.11) in a season compared to unparasitized pairs. Parasitized females also incurred higher costs by spending more time attending nests (2–4.5 days), building more nests (1.83 vs. 1.38), laying more eggs (4.72 vs. 4.12), and fledging young later (4 days) within a season compared to unparasitized females. Return rates and survival varied by age and sex; although there was no difference in the overall return rates or survival of parasitized vs. unparasitized females or of their young, males of parasitized pairs tended to survive longer than unparasitized males (1.29 vs. 1.01 years). Among successful pairs, the return rate of females parasitized in their initial year of capture was greater than that of unparasitized females, but survival did not differ between these groups. There were no differences in return rates and survival between parasitized and unparasitized successful males. Lifetime reproductive success of females depended on their parasitism and first-year success status; parasitized females reared significantly fewer young over their lifespans than unparasitized females (2.25 vs. 4.09 young), but there was no difference in lifetime output between these groups in years subsequent to their first breeding season (2.84 vs. 3.49 young). Whether females were successful or not, or parasitized or not, did not significantly affect reproductive success in subsequent years. Seasonal fecundity losses due to predation (0.74 young/pair) were greater than losses to parasitism (0.30 young/pair); lifetime reproductive losses displayed similar trends (predation vs. parasitism losses: 0.70 young/pair vs. 0.37 young/pair). Our results suggest that: (1) robustness of Willow Flycatcher reproductive strategies in response to cowbird parasitism is evident; (2) cowbird parasitism appears to exact the greatest toll on first-year birds; (3) similarities across parasitism and success classes for lifetime reproductive success in years subsequent to their first breeding year suggest that older Willow Flycatchers may learn improved anti-parasite strategies over time; and (4) similar return rates, survival, and lifetime reproductive success (subsequent to first-year) of parasitized vs. unparasitized pairs suggest that female cowbirds may be selecting for superior host parents.

Key Words: brood parasitism, Brown-headed Cowbird, *Empidonax traillii adastus*, lifetime reproductive success, *Molothrus ater*, seasonal fecundity, spatial and temporal variability, Willow Flycatcher.

Brown-headed Cowbirds (*Molothrus ater*) are known to parasitize over 200 species of birds (Friedmann et al. 1977) and have dramatically increased in distribution and abundance over the last 100 years (Rothstein 1994). Historically thought to occupy primarily the short-grass prairie regions of central North America, cowbird populations have spread both eastward and westward at a rapid rate (DeSante and George 1994). Most host species and populations are believed to be able to withstand some level of brood parasitism, but if parasitism rates are high and defense mechanisms poorly developed, parasitism could threaten population viability. Recent contact with this brood parasite poses a serious problem for a number of species, including the Willow Flycatcher (*Empidonax traillii*) (Rothstein 1994).

In the western United States, the Willow Flycatcher is composed of a mosaic of healthy and threatened populations. Many appear to be reproductively stable, but in some parts of the West, Willow Flycatchers have shown significant declines, including Washington, Oregon, California, and Arizona (DeSante and George 1994, Sauer et al. 1997). The high levels of reported cowbird parasitism of Willow Flycatchers (Trautman 1940, Sedgwick and Knopf 1988), especially of the endangered subspecies, *E. t. extimus* (Brown 1988, 1994, Rothstein 1994), have made parasitism a topic of concern regarding the conservation of both the endangered subspecies and other subspecies of Willow Flycatchers in North America (Robinson et al. 1995a).

Small passerine hosts such as the Willow Flycatcher often incur a variety of costs as a result of brood parasitism. These costs are usually expressed in terms of information collected on individual nests, such as reduced nest success, the number of host eggs removed by cowbirds, lower hatching success, and fewer fledglings produced. Primarily because of nest abandonment and renesting following some instances of parasitism, and variation in the length of the breeding season, brood reduction per nest and lower nest success are only indirect measures of the costs of parasitism (Pease and Grzybowski 1995, Payne 1997). The decrease in seasonal fecundity per pair (or female) is a more direct measure of the consequences of brood parasitism and a better measure of fitness of host populations. Because information on seasonal fecundity requires following individual females throughout an entire breeding season, most studies report data from individual nesting attempts. Only a few studies (e.g., Nolan 1978, Smith 1981, Payne 1989) have measured the costs of parasitism in terms of seasonal fecundity.

Even fewer studies have examined the costs of parasitism over the lifespan of a group of marked individuals (Newton 1989). This requires long-term, or longitudinal, studies that track the breeding success of animals throughout their lifespans. Such studies combine survival and the seasonal fecundities of an individual into one measure of performance–lifetime reproductive success. Thus, a comparison of lifetime reproductive success of parasitized and unparasitized animals is a comparison of approximations of biological fitness, and may be a better indicator of the effects of parasitism on the population as a whole (May and Robinson 1985, Newton 1989). Longitudinal studies have the additional advantages of reducing variability due to short-term environmental variation and accounting for annual variation in the distribution of animal samples.

In addition to the costs of parasitism directly associated with reproductive output, hosts may incur a number of other, less obvious costs affecting their long-term survival. Energetic costs may be higher for parasitized females because they may ultimately build more nests, spend a greater portion of the breeding season attending nests, and lay a greater number of eggs than unparasitized females. In turn, adult survival, particularly that of females, may be lower for parasitized birds because of these higher energy demands imposed on them as a consequence of abandoning previously parasitized nests and renesting (Drent and Daan 1980, Gowaty 1996). The potentially high energy costs of feeding a brood parasite that is often three to four times larger than host nestlings may reduce adult survival and return rates as well (Rosa and Murphy 1994). Finally, direct costs to fitness may arise due to phenology shifts. Because of multiple nest abandonment of parasitized nests and subsequent renesting, fledging of host young may be set back, resulting in lower return rates and increased mortality of late-born young (Perrins 1965, Morton 1992).

Whereas most field biologists would agree that parasitism can have negative consequences for a host population, the way in which such information is presented often overstates the costs of parasitism. Most studies report comparisons between parasitized and unparasitized classes, and the differences between these two classes are often quite dramatic, with unparasitized nests, for example, often fledging many more young than parasitized nests. This comparison can be somewhat misleading, however, if only a small portion of the population is parasitized (Payne 1997). In such cases, the overall costs of parasitism to the population will be smaller than the parasitized-unparasitized comparison suggests, and may even be relatively minor, especially in comparison to other factors, such as predation (Davies and Brooke 1988). Comparisons of the entire population to an unparasitized subgroup provide a more realistic view of the consequences of parasitism to a population (Nolan 1978:390). This latter comparison asks the question: How well did the entire population actually do compared to how well the population would have done if unparasitized?

To assess the consequences of cowbird parasitism on Willow Flycatcher populations, we established a long-term study at Malheur National Wildlife Refuge in southeastern Oregon. Our objectives were to examine the effects of cowbird parasitism on a large and stable host population to provide insights for evaluating ecological limiting factors at locations where the species is declining. In this paper, we focus on the costs of parasitism in terms of seasonal fecundity, lifetime reproductive success, energetic demands, and survival. In addition, we evaluate the population-level effects of parasitism by comparing the entire population to an unparasitized subgroup.

STUDY AREA AND METHODS

STUDY AREA

Our study was conducted at Malheur NWR, which lies at the northern extremity of the Great Basin in Harney County, southeastern Oregon (42°52′N, 118°53′W). It is one of the largest wildlife refuges in the lower 48 states (73,250 ha) and comprises one of the largest wetland complexes in North America. Dominant features of the refuge include rimrocks, freshwater marshes, lakes, meadows, alkali flats, shrub uplands, and shrub-willow riparian areas. We selected three riparian reaches (spanning 5 km) of the Blitzen River at the southern end of the refuge based on habitat suitability and presence of Willow Flycatchers. The three study areas, Bridge Creek (BC), Dredger South (DS), and Dredger North (DN) were 1.5 km, 1.5 km, and 2.0 km in length and were interrupted by gaps of 1.5 km and 2.0 km between study sites.

Stringer shrub willow (*Salix exigua* and *S. lutea*) occurs along a channelized portion of the Blitzen River in approximately linear arrangements. Willow stringers along the Blitzen River in these areas range from 5–10 m in width, but often extend laterally for short distances (5–100 m) into adjacent management units (i.e., fields, meadows, and wetlands). Other common riparian shrubs include currant (*Ribes* sp.), wild rose (*Rosa* sp.), and chokecherry (*Prunus* sp.).

FIELD METHODS

Productivity of Willow Flycatchers was evaluated by locating and monitoring nests to determine clutch size, hatching success, fledging success, incidence of cowbird parasitism, and mortality patterns occurring during the breeding season. Nearly all nests and renests of approximately 100 pairs per year breeding on the three study sites were located and monitored from 1988 to 1997 (N = 1,168 total nests). The majority of nests were found before the first egg was laid and were checked every other day, which enabled more precise estimates of laying patterns and egg removal by cowbirds.

Willow Flycatcher adults, and nestlings near fledging (8–10 d of age), were banded to evaluate survival, differential productivity, and fecundity per pair. Adults were captured using mist nets placed near nests and young were captured on the nest prior to fledging (8–10 d after hatching). Adult flycatchers were banded with both a US Fish and Wildlife Service (USFWS) band and either one or two color bands; thus each adult carried up to three bands (two on one leg and one on the other). Nestlings were banded with a USFWS band, and in the first 2 years of the study (1988 and 1989) were also color-banded. Birds returning to the study areas as adults but originally banded as nestlings or hatching-year birds (USFWS band only), were then banded with color bands as well. Adults were sexed by cloacal protuberance (males) and brood patch (females), and in a few instances by a combination of wing length, tail length (longer in males), and the above characters (Pyle et al. 1987). Locals and hatching-year birds could not be sexed. There is no known method of aging adults; all adults were categorized as after-hatching-year birds.

Each year, identities of adults were determined by initial capture (and banding, if necessary) of territorial occupants. We subsequently verified the identity of territory holders by visual determination of color band combinations through binoculars or spotting scopes. Not all birds could be captured, nor could the identities of all adults associated with particular territories be determined with certainty (i.e., of 882 pairs, we positively identified 76.8% of the males and 85.6% of the females). But because most of the population was marked and positively associated with a territory, we were able to assess seasonal fecundity for most pairs.

DATA ANALYSIS

Because one of our primary objectives was an examination of the impacts of parasitism on seasonal fecundity and lifetime reproductive success, we restricted our analysis of return rates and survival to birds returning to the study areas and occupying a territory. Thus, individuals that may have been captured in one or more years subsequent to the year of initial capture, but that were not positively associated with a nest, were not considered to have returned or to have survived for the purposes of the analyses in this paper. Only a small proportion of adults recaptured in subsequent years were not associated with nests, and thus our somewhat restrictive analysis reflects a reasonable estimate of actual return rates and survival for adults. Restricting our analysis to birds returning and nesting for birds originally banded in their first year of life (as nestlings or hatching-year birds) reduced our sample by about one half. About 15% of nestlings ultimately returned, but only about half that many returned and nested on our study areas. We define a return as a bird returning to one of the study areas and nesting at least once after its initial year of capture. Survival data consider the age of individuals and take into account how many times a bird returned to the study areas and how many years it survived.

To assess the effects of parasitism, we compared reproductive output and effort between pairs that had and had not been parasitized. This comparison generated estimates of difference in reproductive effort between these two groups. Another way to characterize the impact of cowbirds on a population would be to compare reproductive effort of females from unparasitized nests to that of all females in the population (Nolan 1978). The average reproductive effort of the unparasitized subgroup gives a baseline estimate of how the population would do (under the environmental conditions within that given breeding season) if no parasitism were occurring. However, statistical analyses of these comparisons are limited due to the non-independence of the data sets being compared. We report comparisons between unparasitized pairs vs. all (unparasitized and parasitized combined) pairs in an effort to demonstrate a more direct and simple measure of the effects of parasitism on Willow Flycatchers, and to contrast with the more conventional comparison.

We estimated reproductive success in a number of ways. Basic measures of the consequences of parasitism are comparisons between parasitized and unparasitized pairs of the number of eggs surviving to the nestling stage and the number of eggs and nestlings surviving to fledging. Another measure of the cost of parasitism is clutch and brood reduction. We include seasonal egg and nestling losses as well as any reductions in seasonal fecundity or reproductive output in this category. We further incorporated into our analysis fecundity losses that occurred within the following six success and parasitism classes to determine the effects of parasitism on each of these sub-groups: (1) successful, unparasitized pairs; (2) successful, parasitized pairs that reared one cowbird and at least one flycatcher young; (3) successful, parasitized pairs that reared only flycatcher young; (4) unsuccessful, parasitized pairs that reared only cowbird young; (5) unsuccessful, unparasitized pairs with no young; and (6) unsuccessful, parasitized pairs with no young.

Parasitism may have less obvious costs to the reproductive success of the host female in the additional time and energetic costs spent building more nests, laying additional numbers of eggs, increased nest attentiveness, and phenology shifts caused by these delays in the breeding cycle. In turn, adult survival (particularly that of females) and survival of their young may be lower. We estimated these increased time and energetic costs by estimating parental investment in days occupied attending active nests (from egg 1 of the first nest to fledging or failure of last nests of the season), total number of nests built per season, and total number of eggs laid per season. We also compared the return rates and survival of young by three fledging classes: early fledges (1–15 July), mid-season fledges (16–31 July), and late fledges (after 1 August). Finally, we compared return rates and survival across the parasitism classes for adults by categorizing adults as either parasitized or unparasitized in their initial year of capture.

We analyzed lifetime reproductive success of Willow Flycatcher females (the number of flycatcher young fledged in their lifetime) in several different ways. First, we compared lifetime output based on parasitism class (parasitized vs. unparasitized) in the initial year of capture. That is, we compared lifetime reproductive success of females that were, or were not, parasitized in their first year. We subdivided these groups further by comparing the number of offspring produced in the six success and parasitism classes simultaneously. We then calculated the reproductive success of parasitized and unparasitized females for the years following their first breeding season to test whether or not parasitism in a bird's first year had an effect on subsequent lifetime output.

To evaluate the relative costs of parasitism versus predation, we compare the seasonal fecundity and lifetime reproductive success of three different success classes: (1) unparasitized, successful pairs; (2) all unparasitized pairs; and (3) all pairs. When comparing between all pairs and all unparasitized pairs, differences in fecundity, for example, are due to the effects of parasitism. The comparison is of fecundity of the entire population to a subgroup not under the constraints of parasitism and so is a population-level estimate of the consequences of parasitism. Comparisons between all unparasitized pairs and successful, unparasitized pairs account for the effects of predation. The difference in fecundity, for example, between these two classes is largely a measure of predation on fecundity (but may also include losses due to infertile eggs and weather), as all instances of parasitism are excluded from each class.

Statistical procedures were conducted using the Statistical Analysis System (SAS Institute 1985). We used the Chi-square test of homogeneity to test simple measures of nest success, egg success, and return rates between classes of flycatchers. We used the General Linear Models Procedure (SAS Institute 1985) to test means of continuous variables (e.g., egg and nestling losses/pair, brood reduction, survival) across classes. Statistical tests were not possible for some comparisons (e.g., all pairs vs. unparasitized pairs) because of a lack of independence between classes (i.e., the class "all pairs" includes the class "unparasitized pairs"). Null hypotheses were rejected at $\alpha \leq 0.05$.

RESULTS

PARASITISM RATES

Parasitism of Willow Flycatcher pairs (N = 876) averaged 23.4% and ranged from 10.9–40.7% over 10 years (all study areas combined) and from 15.4–41.5% across three study areas (all years combined; Table 1). A prescribed fire in the early spring of 1991 resulted in the accidental burning of approximately 50% of the ri-

TABLE I. SPATIAL AND TEMPORAL VARIABILITY OF COWBIRD PARASITISM OF WILLOW FLYCATCHER PAIRS, MALHEUR NATIONAL WILDLIFE REFUGE, OREGON (1988–1997)

	Study area							
	Bridge Creek		Dredger South		Dredger North		Total	
Year	%	(N)	%	(N)	%	(N)	%	(N)
1988	11.1	(9)	25.0	(16)	8.8	(34)	13.6	(59)
1989	55.0	(20)	53.1	(32)	13.5	(37)	37.1	(89)
1990	51.6	(31)	17.7	(34)	19.6	(56)	27.3	(121)
1991	87.1	(31)	15.4	(26)	25.5	(51)	40.7	(108)
1992	34.6	(26)	15.6	(32)	6.4	(47)	16.2	(105)
1993	34.6	(26)	20.0	(30)	22.2	(36)	25.0	(92)
1994	40.0	(30)	14.7	(34)	14.6	(41)	21.7	(105)
1995	12.0	(25)	13.5	(37)	9.5	(42)	11.5	(104)
1996	13.3	(15)	15.6	(32)	—[a]		14.9	(47)
1997	31.3	(16)	0.0	(30)	—[a]		10.9	(46)
Total	41.5	(229)	18.8	(303)	15.4	(344)	23.4	(876)

[a] No data.

parian stringers in the BC study area and may have been the apparent cause of an explosive increase in parasitism there in 1991 (51.6% in 1990 vs. 87.1% in 1991 and 34.6% in 1992). The lowest (0.0%, DS, 1997) and highest (87.1%, BC, 1991) rates of parasitism underline the high variability in parasitism rates across both time and space.

EGG SUCCESS AND PAIR SUCCESS

The percentage of eggs surviving to the nestling stage for parasitized pairs (34.6%) was significantly less than that for eggs of unparasitized pairs (69.1%; $\chi^2_{1df} = 334.5$, $P < 0.001$; Table 2). The number of eggs surviving to fledging was also lower for parasitized pairs (17.3%) than for unparasitized pairs (51.4%; $\chi^2_{1df} = 321.2$, $P < 0.001$) as was the number of nestlings surviving to fledging (parasitized: 50.0%; unparasitized: 74.4%; $\chi^2_{1df} = 77.6$, $P < 0.001$).

Flycatcher success (pairs fledging ≥ 1 young) of unparasitized pairs (74.1%) was more than twice that of parasitized pairs (36.8%; $\chi^2_{1df} = 96.2$, $P < 0.001$) yielding a 50.3% reduction in pair success. However, when comparing pair success of unparasitized pairs (74.1%) to all (parasitized and unparasitized) pairs (65.4%) in the population, the cost of parasitism was a reduction of 11.7% in pair success ($\chi^2_{1df} = 13.5$, $P < 0.001$). This is a more direct estimate of the consequences of parasitism to the population as it compares the nest success of a subgroup not under the constraints of parasitism to that of the entire population. This comparison effectively accounts for the fact that only 23.4% of all pairs were parasitized (Table 1).

Of the 204 parasitized pairs, 81 (39.7%) failed to produce any fledglings. The remaining 123 parasitized pairs produced either a cowbird (48 pairs, 23.5%), Willow Flycatcher(s) (57 pairs, 27.9%), or both (18 pairs, 8.8%). Thus, although only 36.8% of parasitized pairs produced flycatchers, more parasitized pairs fledged flycatchers (N = 75) than cowbirds (N = 66), with Willow Flycatchers raising 0.32 cowbirds/parasitized pair.

TABLE 2. EGGS LAID, EGGS SURVIVING TO THE NESTLING STAGE, EGGS SURVIVING TO FLEDGING, AND NESTLINGS SURVIVING TO FLEDGING IN PARASITIZED AND UNPARASITIZED WILLOW FLYCATCHER PAIRS, MALHEUR NWR, OREGON (1988–1997)

	No. eggs laid	Eggs surviving to nestling stage		Δ related to parasitism	Eggs surviving to fledging		Δ related to parasitism	Nestlings surviving to fledging		Δ related to parasitism
	N	%	N	(%)[a]	%	N	(%)[a]	%	N	(%)[a]
Parasitized	907	34.6	314		17.3	157		50.0	157	
				−50.0[b]			−66.3[b]			−32.8[b]
Unparasitized	2630	69.1	1817		51.4	1353		74.4	1353	
				−8.9[c]			−16.9[c]			−4.7[c]
All	3537	60.2	2131		42.7	1510		70.9	1510	

[a] Comparison of parasitized and unparasitized pairs, and unparasitized and all (parasitized + unparasitized) pairs.

[b] Significant difference at $P < 0.001$.

[c] No statistical tests possible (see Methods).

TABLE 3. SEASONAL CLUTCH AND BROOD REDUCTION, AND FECUNDITY OF PARASITIZED AND UNPARASITIZED WILLOW FLYCATCHER PAIRS (N), MALHEUR NWR, OREGON (1988–1997)

	Eggs lost			Δ related to parasitism	Nestlings lost			Δ related to parasitism	Young fledged			Δ related to parasitism
	N	$\bar{x}$	SE	(eggs)[a]	N	$\bar{x}$	SE	(nestlings)[a]	N	$\bar{x}$	SE	(young)[a]
Parasitized	194	3.08	0.16		122	1.18	0.12		204	0.80	0.08	
				+1.80[b]				+0.39[c]				−1.31[b]
Unparasitized	642	1.28	0.06		579	0.79	0.05		670	2.11	0.06	
				+0.41[d]				+0.07[d]				−0.30[d]
All	836	1.69	0.07		701	0.86	0.05		874	1.81	0.05	

[a] Comparison of parasitized and unparasitized pairs, and unparasitized and all (parasitized + unparasitized) pairs.

[b] Significant difference at $P < 0.001$.

[c] Significant difference at $P = 0.003$.

[d] No statistical tests possible (see Methods).

SEASONAL CLUTCH AND BROOD REDUCTION

Parasitized pairs lost 3.08 ± 0.16 eggs over the course of a season compared to only 1.28 ± 0.06 eggs lost for unparasitized females ($P < 0.001$; Table 3). Parasitized females lost more nestlings (1.18 ± 0.12) as well, compared to unparasitized females (0.79 ± 0.05; $P = 0.003$). Seasonal fecundity was reduced by 1.31 young/pair, with parasitized pairs fledging only 0.80 ± 0.08 young and unparasitized pairs fledging 2.11 ± 0.06 young ($P < 0.001$).

As in the case of pair success, brood reduction was much less severe (0.30 young/pair) when comparing seasonal fecundity of unparasitized pairs (2.11 ± 0.06) with that of the entire population (1.81 ± 0.05, parasitized and unparasitized pairs combined; Table 3). Similarly, unparasitized pairs lost fewer eggs (0.41 egg/pair; 1.28 ± 0.06 vs. 1.69 ± 0.07) and fewer nestlings (0.07 nestlings/pair; 0.79 ± 0.05 vs. 0.86 ± 0.05) in comparison with the entire population.

In comparison of success-by-parasitism classes, successful, unparasitized pairs reared more flycatchers annually than either parasitized pairs raising only flycatchers or parasitized pairs rearing both cowbirds and flycatchers ($P < 0.001$; Table 4). Seasonal egg losses were least for successful, unparasitized pairs (0.88 ± 0.04) and greatest for unsuccessful pairs rearing only cowbird(s) (3.14 ± 0.33) and unsuccessful, parasitized pairs rearing neither flycatchers nor cowbirds (3.77 ± 0.24; $P < 0.001$). Seasonal nestling losses were least for successful flycatcher pairs (0.41–0.75) and greatest for unsuccessful pairs (1.81–2.58).

TIME AND ENERGETIC COSTS

Successful, parasitized females spent more time attending nests (35.12 ± 0.90 d) than successful, unparasitized females (33.03 ± 0.35 d, $P = 0.012$; Table 5). This trend was also the case for unsuccessful, parasitized females (25.92 ± 1.31 d) compared to unsuccessful, unparasitized females (21.25 ± 0.79; $P = 0.002$). Parasitized females built more nests (1.83 ± 0.06) in a season than unparasitized females (1.38 ± 0.02; $P < 0.001$) and also laid more eggs (4.72 ± 0.15) in a season than unparasitized females (4.12 ± 0.05; $P < 0.001$). This difference in the number of eggs laid understates the actual difference between parasitized and unparasitized females because of presumed undetected egg removal by cowbirds. We estimated undetected egg removal as the difference between the number of eggs laid by unparasitized females who had only one nest in a season (3.66 ± 0.03) and the number laid by parasitized females that had only one nest (3.31 ± 0.12; $P = 0.001$). We assumed that an undetected 0.35 eggs (3.66–3.31) were removed by cowbirds between nest checks, and so 0.35 could be added to the 4.72 eggs laid in a season by parasitized females.

Direct costs (comparing unparasitized pairs to all pairs) were as follows: (1) time invested attending active nests by successful females: 33.03 ± 0.35 d (unparasitized) vs. 33.44 ± 0.33 d (all); (2) time invested by unsuccessful females: 21.25 ± 0.79 d (unparasitized) vs. 22.73 ± 0.69 d (all); (3) nests built: 1.38 ± 0.02 (unparasitized) vs. 1.49 ± 0.02 (all); and (4) total eggs laid: 4.12 ± 0.05 (unparasitized) vs. 4.26 ± 0.05 (all). As with our earlier comparisons, the effects of brood parasitism on measures of seasonal fecundity are diminished when compared to the entire population as a whole.

PHENOLOGY SHIFTS

The mean (julian) fledging date of young from nests of successful parasitized pairs (211.4 ± 1.0) differed from that of young from nests of successful unparasitized pairs (207.5 ± 0.4, $P < 0.001$; Table 6). Thus, young of parasitized pairs fledged nearly 4 d later than young produced by unparasitized pairs. Initiation dates of first nests were nearly identical by parasitism class, and so the investment of parasitized fe-

TABLE 4. SEASONAL CLUTCH AND BROOD REDUCTION AND FECUNDITY OF WILLOW FLYCATCHER PAIRS (N), BY SUCCESS-BY-PARASITISM CLASSES, MALHEUR NWR, OREGON (1988–1997)

	Seasonal fecundity			Duncan's multiple range test[c]	Eggs lost			Duncan's multiple range test[d]	Young lost			Duncan's multiple range test[e]
	N	x̄	SE		N	x̄	SE		N	x̄	SE	
Successful, unparasitized, flycatcher only	497	2.85	0.04	A[f]	472	0.88	0.06	C[f]	474	0.41	0.04	C[f]
Successful, parasitized, rearing both[a]	18	1.39	0.14	B	15	2.20	0.55	B	16	0.75	0.23	C
Successful, parasitized, flycatcher only	58	2.40	0.12	C	57	2.32	0.25	B	56	0.41	0.12	C
Unsuccessful, parasitized, cowbird only	48	1.06[b]	0.04[b]	—	43	3.14	0.33	A	26	1.81	0.24	B
Unsuccessful, unparasitized, no young	173	—	—	—	170	2.37	0.15	B	105	2.51	0.12	A
Unsuccessful, parasitized, no young	80	—	—	—	79	3.77	0.24	A	24	2.58	0.22	A

[a] Females that successfully reared one cowbird and at least one Willow Flycatcher young.
[b] Number of cowbirds reared per pair that successfully fledged cowbirds.
[c] $F = 525.58$, $P < 0.001$.
[d] $F = 62.37$, $P < 0.001$.
[e] $F = 97.79$, $P < 0.001$.
[f] Values sharing the same letter are not significantly different ($P > 0.05$).

males was also about 4 d longer than that of unparasitized females. The later mean fledging date can be attributed to the greater number of nests built by successful, parasitized females (1.81 ± 0.09) compared to successful, unparasitized females (1.30 ± 0.02; $P < 0.001$) and more eggs laid (5.01 ± 0.23 parasitized vs. 4.17 ± 0.06 unparasitized; $P < 0.001$), because of renesting and further egg laying following abandonment of some parasitized nests.

RETURN RATES, SURVIVAL, AND PARASITISM

Return rates of parasitized adult females (48.9%) and unparasitized adult females (55.3%) were similar ($\chi^2_{1df} = 1.11$, $P = 0.29$); there was no significant difference in female survival rates (parasitized: 0.967 ± 0.07 yr; unparasitized: 0.969 ± 0.14 yr; $P = 0.99$; Table 7). Return rates of parasitized males (55.6%) and unparasitized males (51.2%) were also similar ($\chi^2_{1df} = 0.36$, $P = 0.55$). Parasitized males tended to survive longer (1.29 ± 0.23 yr) than unparasitized males (1.01 ± 0.09 yr), but the difference was not significant ($P = 0.18$).

Successful, parasitized adult females were more likely to return to the study area in subsequent years than successful, unparasitized females (Table 7). The return rate of successful, parasitized (in their initial year of capture) females (72%) was greater than that of successful, unparasitized females (56.5%; $\chi^2_{1df} = 3.92$, $P = 0.048$) but survival did not differ (successful, parasitized: 1.20 ± 0.16 yr; successful, unparasitized: 0.99 ± 0.09 yr; $P = 0.271$). Return rates for successful, parasitized males (60.0%) were similar to those of successful, unparasitized males (50.7%; $\chi^2_{1df} = 0.75$, $P = 0.385$) as was survival (successful, parasitized: 1.08 ± 0.24 yr; successful, unparasitized: 1.08 ± 0.12 yr; $P = 0.99$).

There was no difference in the return rates of young produced by parasitized (5.4%) vs. unparasitized (7.7%) pairs ($\chi^2_{1df} = 0.81$, $P = 0.367$) nor was there a difference in survival of young produced by parasitized (0.116 ± 0.05 yr) vs. unparasitized (0.169 ± 0.02 yr) pairs ($P = 0.42$; Table 7). The return rate of early fledges (29.1%) was much greater than that of mid-season fledges (4.8%) and late fledges (5.4%; $\chi^2_{2df} = 97.46$, $P < 0.001$; Table 8). Survival also differed across these three classes (early: 0.70 ± 0.13 yr; mid-season: 0.10 ± 0.02 yr; late: 0.10 ± 0.10 yr; $P < 0.001$). However, survival of birds returning to the study area at least one time was not significantly different (early: 2.41 ± 0.29 yr; mid-season: 2.15 ± 0.23 yr; late: 1.94 ± 0.33 yr; $P = 0.55$).

TABLE 5. Annual energetic costs to parasitized and unparasitized Willow Flycatcher females (N) in terms of time investment, number of nests built and eggs laid, Malheur NWR, Oregon (1988–1997)

	Investment (days), successful females			Δ related to parasitism (days)[a]	Investment (days), unsuccessful females			Δ related to parasitism (days)[a]	Nests built			Δ related to parasitism (nests)[a]	Eggs laid			Δ related to parasitism (eggs)[a]
	N	x̄	SE		N	x̄	SE		N	x̄	SE		N	x̄	SE	
Parasitized	121	35.12	0.90		78	25.92	1.31		188	1.83	0.06		192	4.72	0.15	
				+2.09[b]				+4.67[c]				+0.45[d]				+0.60[d]
Unparasitized	489	33.03	0.35		168	21.25	0.79		594	1.38	0.02		639	4.12	0.05	
				+0.41[e]				+1.48[e]				+0.11[e]				+0.14[e]
All	610	33.44	0.33		246	22.73	0.69		782	1.49	0.02		831	4.26	0.05	

[a] Comparison of parasitized and unparasitized pairs, and unparasitized and all (parasitized + unparasitized) pairs.

[b] Significant difference at P = 0.001.

[c] Significant difference at P = 0.002.

[d] Significant difference at P < 0.001.

[e] No statistical tests possible (see Methods).

LIFETIME REPRODUCTIVE SUCCESS

Females parasitized in their first year reared significantly fewer flycatcher young (2.25 ± 0.28) over their lifespans compared to unparasitized females (4.09 ± 0.20 young, $P < 0.001$; Table 9). Unparasitized, successful females had the highest lifetime output (4.79 ± 0.21 young), followed by parasitized females that raised both flycatchers and a cowbird in their first year (3.89 ± 0.84 young), and parasitized females that successfully reared only flycatchers (3.76 ± 0.48 young; Table 9). The other three classes (those raising [1] only a cowbird, [2] unsuccessful, unparasitized females, and [3] unsuccessful, parasitized females) reared significantly fewer flycatchers over their lifespans ($P < 0.001$). Thus, the three classes rearing flycatchers in their first year also had the highest lifetime output, whereas the three classes raising only a cowbird, or neither flycatchers nor cowbirds, had the lowest lifetime reproductive success. Females unparasitized in their first year did not rear significantly more young over the remainder of their lifespans (3.49 ± 0.26) compared to females parasitized in their first year (2.84 ± 0.43) ($P = 0.214$; Table 10). A comparison of overall and after-first-year lifetime reproductive success (compare Tables 9 and 10) suggests that females that were parasitized in their first year and returned closed the gap with females that were unparasitized in their first year by increasing lifetime output. Combining parasitism and success classes as above, reproductive outputs were similar across all six success-by-parasitism classes ($F = 0.64$, $P = 0.67$; Table 10). Previously unparasitized females tended to rear more young in subsequent years than parasitized females, but those females rearing a cowbird in their first year subsequently reared about as many flycatchers (3.56 ± 1.14) as unsuccessful (4.04 ± 0.74) and successful (3.38 ± 0.27) unparasitized females. But whether birds were successful or not, or parasitized or not, did not significantly affect reproductive success in years subsequent to their first breeding effort (Table 10).

RELATIVE COSTS OF PARASITISM AND PREDATION

For Willow Flycatchers, the costs of parasitism were relatively minor compared to the costs of predation. Losses in seasonal fecundity due to predation were 0.74 young/pair when comparing fecundity of unparasitized, successful pairs (2.85 ± 0.04 young) to all unparasitized pairs (2.11 ± 0.06 young). Fecundity losses due to parasitism were only 0.30 young/pair, or less than half the cost of predation, when comparing reproductive output of unparasitized (2.11 ± 0.06) vs. all (1.81 ± 0.05) pairs. Comparisons

TABLE 6. PHENOLGY SHIFT IN FLEDGING DATE AND ASSOCIATED VARIABLES FOR SUCCESSFUL PARASITIZED AND UNPARASITIZED WILLOW FLYCATCHER PAIRS, MALHEUR NWR, OREGON (1988–1997)

	Successful parasitized			Successful unparasitized			
	N	$\bar{x}$	SE	N	$\bar{x}$	SE	P[a]
Fledging Date (Julian Date)	76	211.43	1.01	496	207.47	0.42	0.001
Nest Initiation Date (Julian Date)	76	174.28	0.67	489	174.33	0.30	0.943
Investment (days)	76	37.16	1.00	489	32.97	0.35	0.001
No. of Nests	75	1.81	0.09	457	1.30	0.02	0.001
Eggs laid	72	5.01	0.23	471	4.17	0.06	0.001

[a] One-way analysis of variance (ANOVA).

of the lifetime reproductive success of females yielded similar results. The estimate of the cost of parasitism to lifetime output was 0.37 young/female (lifetime reproductive output of all unparasitized pairs: 3.96 ± 0.20 young/female vs. lifetime reproductive output of all pairs: 3.59 ± 0.17 young/female). The cost of predation to lifetime reproductive output (0.70 young/female) was nearly twice that of parasitism (lifetime reproductive output of successful unparasitized pairs: 4.66 ± 0.20 young/female vs. lifetime reproductive output of all unparasitized pairs: 3.96 ± 0.20 young/female).

DISCUSSION

PARASITISM RATES

The overall parasitism rate (23.4%) on the three study areas during the 10 years of this study was somewhat lower than that reported for most other populations of Willow Flycatchers. Prior to cowbird trapping in California, parasitism of *E. t. extimus* averaged 66% (Whitfield and Sogge *this volume*). Brown (1994) reported a 50% rate in the Grand Canyon of Arizona for *E. t. extimus,* and Sedgwick and Knopf (1988) reported a rate of 40.7% for *E. t. adastus* in Colorado. Lower rates (<25%) are reported for most sites in Arizona (*E. t. extimus*) but range from 3% to 48%; parasitism rates in New Mexico ranged from 18% to 40% (Whitfield and Sogge *this volume*). For the eastern subspecies (*E. t. traillii*; 6 studies) rates were <17% (Friedmann 1963), although one eastern study reported a higher rate of parasitism (56.3%; Trautman 1940). Variability at the local scale was high (15.4–41.5%) in this study, and this pattern repeats itself at broader geographical scales in other regions of the country.

Temporal variability of parasitism rates was equally dramatic at Malheur NWR (10.9–40.7% from 1988 to 1997, all study areas combined) and is typical of patterns at broader geographic scales throughout the West. Whitfield and Sogge (*this volume*) summarized annual variability in parasitism rates of *E. t. extimus* in three states: Arizona, 8–40%; California, 50–80%; and New Mexico, 14.7–27%. Variability in parasitism rates across time is not difficult to understand, and is almost to be expected, because of large annual fluctuations in densities of both parasites and hosts (Trail and Baptista 1993). Long-term, longitudinal studies address this problem by including both average years and extreme years of environmental variation and the distribution of animal samples.

Variability in parasitism rates across space, especially at the local scale, is more difficult to explain. At Malheur NWR, our three study areas were all in the same drainage, vegetation types were similar, and the three areas were each sep-

TABLE 7. RETURN RATES (%) AND SURVIVAL (YR) OF PARASITIZED AND UNPARASITIZED WILLOW FLYCATCHERS, MALHEUR NWR, OREGON (1988–1997)

	Parasitized				Unparasitized			
		No. birds returned	Survival			No. birds returned	Survival	
	N	%	Yr	SE	N	%	Yr	SE
Juveniles	129	5.4	0.116	0.05	1142	7.7[a]	0.169	0.02[a]
All females	92	48.9	0.967	0.14	255	55.3[a]	0.969	0.07[a]
All males	63	55.6	1.29	0.23	201	51.2[a]	1.01	0.09[b]
Successful females	50	72.0	1.20	0.16	184	56.5[c]	0.99	0.09[a]
Successful males	25	60.0	1.08	0.24	154	50.7[a]	1.08	0.12[a]

[a] No significant difference ($P > 0.05$).

[b] Significance between survival of parasitized and unparasitized males: $P = 0.18$.

[c] Significance between return rates of parasitized and unparasitized successful females: $P = 0.048$.

TABLE 8. RETURN RATES AND SURVIVAL OF WILLOW FLYCATCHER YOUNG BY FLEDGING DATE CATEGORIES, MALHEUR NWR, OREGON (1988–1997)

		Returning young[a]	Overall survival (yr)[b]			Survival of returning birds (yr)[c]		
	N	%	N	$\bar{x}$	SE	N	$\bar{x}$	SE
Early (1–15 July)	127	29.1	127	0.70	0.13	37	2.41	0.29
Middle (16–31 July)	828	4.8	828	0.10	0.02	40	2.15	0.23
Late (1–26 Aug)	316	5.4	316	0.10	0.03	7	1.94	0.33

[a] Difference among return rates: $P < 0.001$.

[b] Difference among overall survival: $P < 0.001$.

[c] Difference among survival of returning birds: $P = 0.55$.

arated from one another by ≤2 km. Other researchers have also reported a patchy distribution of parasitism rates, even at the local level. These differences in rates are sometimes explained by habitat variability, such as the availability of tall perches, which may enhance the ability of cowbirds to locate and parasitize nests (Anderson and Storer 1976, Freeman et al. 1990). The availability of nearby foraging areas for cowbirds has also been linked to differences in parasitism rates, but at geographic scales broader than those considered at Malheur NWR (Verner and Ritter 1983). Because of the proximity of our three study areas and their similar vegetation structures, we believe that any differences in parasite densities, flycatcher densities, or densities of alternate hosts (sensu Barber and Martin 1997) are insignificant and are not causal factors in differences in parasitism rates among areas at Malheur NWR. Thus, the large differences in rates of parasitism across the three study areas at Malheur NWR remain an enigma, but may not be unusual as others have also reported pockets of parasitism in areas of uniform vegetation (Marvil and Cruz 1989). Variability in rates of parasitism, both locally and regionally, demonstrates that a direct estimate of the number of nests parasitized may not be adequate in assessing the true impact of parasitism. More intensive studies from a number of locations may be required to get an averaging for regional, and local, parasitism rates. Variability in cowbird parasitism at the broad, and especially at the local, geographic scale suggests the need for carefully designed, long-term studies to fully assess parasitism rates across time and space.

EGG AND PAIR SUCCESS AND SEASONAL FECUNDITY

Fewer eggs and nestlings survived to fledging, and nest success of parasitized pairs was far less than that of unparasitized pairs at Malheur NWR. Generalized costs such as these have been reported for a number of host species throughout North America (May and Robinson 1985). Parasitized Willow Flycatcher pairs also lost significantly more eggs and nestlings over the course of a season and fledged an average of 1.31 fewer young (61.6% fewer) than unparasitized pairs. Seasonal fecundity of successful, unparasitized pairs was greater, and seasonal egg losses fewer than for pairs of either of two parasitized classes: those raising both flycatchers and cowbirds, or those rearing only flycatchers.

TABLE 9. LIFETIME REPRODUCTIVE SUCCESS OF FEMALE WILLOW FLYCATCHERS (N), BY PARASITISM AND SUCCESS-BY-PARASITISM CLASSES, MALHEUR NWR, OREGON (1988–1997)

	Flycatcher young fledged			Duncan's multiple range test[a]	
	N	$\bar{x}$	SE		
Overall					
Parasitized	92	2.25	0.28	A	$F = 23.63$, $P < 0.001$
Unparasitized	257	4.09	0.20	B	
Success-By-Parasitism Class					
Successful, Unparasitized, Flycatcher Only	200	4.79	0.21	A	$F = 20.76$, $P < 0.001$
Successful, Parasitized, Rearing Both[b]	9	3.89	0.84	A	
Successful, Parasitized, Flycatcher Only	29	3.76	0.48	A	
Unsuccessful, Parasitized, Cowbird Only	18	1.78	0.70	B	
Unsuccessful, Unparasitized, No Young	57	1.63	0.40	B	
Unsuccessful, Parasitized, No Young	36	0.86	0.32	B	

[a] Values sharing the same letter are not significantly different ($P > 0.05$).

[b] Females that successfully reared one Cowbird and at least one Willow Flycatcher young.

TABLE 10. LIFETIME REPRODUCTIVE SUCCESS OF FEMALE WILLOW FLYCATCHERS (N), BY PARASITISM AND SUCCESS-BY-PARASITISM CLASSES, SUBSEQUENT TO THEIR FIRST YEAR, MALHEUR NWR, OREGON (1988–1997)

	Flycatcher young fledged			Duncan's multiple range test[a]	
	N	$\bar{x}$	SE		
Overall					
Parasitized	44	2.84	0.43	A	F = 1.55, P = 0.214
Unparasitized	141	3.49	0.26	A	
Success-By-Parasitism Class					
Successful, Unparasitized, Flycatcher Only	118	3.38	0.27	A	F = 0.64, P = 0.67
Successful, Parasitized, Rearing Both[b]	7	3.00	0.72	A	
Successful, Parasitized, Flycatcher Only	16	2.56	0.82	A	
Unsuccessful, Parasitized, Cowbird Only	9	3.56	1.14	A	
Unsuccessful, Unparasitized, No Young	23	4.04	0.74	A	
Unsuccessful, Parasitized, No Young	12	2.58	0.74	A	

[a] Values sharing the same letter are not significantly different (P > 0.05).

[b] Females that successfully reared one cowbird and at least one Willow Flycatcher young.

Seasonal nestling losses were similar for the above three successful groups indicating that most of the consequences of parasitism to seasonal fecundity were due to egg, and not nestling, losses.

Only a few studies have examined seasonal reductions in fecundity: Nolan (1978) reported only a 13.3% reduction in seasonal fecundity for Prairie Warblers (*Dendroica discolor*); Trail and Baptista (1993) presented data from Petrinovich and Patterson (1978, 1983) from which we calculated a reduction of 44.3% in seasonal fecundity for Nuttall's White-crowned Sparrows (*Zonotrichia leucophrys nuttalli*); and Smith (1981) found that parasitized female Song Sparrows (*Melospiza melodia*) raised as many young to independence as unparasitized female Song Sparrows.

There are numerous studies that report reductions in the average number of young produced on a per nest basis, with reductions typically most pronounced for hosts that have longer incubation periods and are smaller than cowbirds (Friedmann 1963, Rothstein 1975a). For example, Marvil and Cruz (1989) reported a significant reduction in per nest fledgling production between unparasitized (2.35) and parasitized (0.50) nests for Plumbeous Vireos (*Vireo plumbeus*); 1.2–1.9 fewer Dickcissels (*Spiza americana*) fledged in parasitized than unparasitized nests in a Kansas study (Zimmerman 1983); Yellow Warblers (*Dendroica petechia*) with unparasitized nests fledged significantly more young (2.28) than those with parasitized (1.64–1.90) nests (Weatherhead 1989); and parasitism by Shiny Cowbirds (*Molothrus bonariensis*) reduced by 84% the number of young fledged per active Puerto Rican Vireo (*Vireo latimeri*) nest (Woodworth 1997). Brood reductions on a per nest basis, however, are only indirect measures of the consequences of brood parasitism on seasonal fecundity because of multiple nesting (due to abandonment of parasitized nests and subsequent renesting) and some nesting of hosts before or after the egg-laying period of cowbirds (Pease and Grzybowski 1995, Robinson et al. 1995a).

From the above examples, it seems clear that at least on a per nest basis, parasitism can dramatically reduce the fecundity of small hosts. And seasonal fecundity reductions (parasitized pairs vs. unparasitized pairs) for Willow Flycatchers (1.31 young/pair, our study) also suggest significant costs as a consequence of parasitism. The population-level cost of seasonal fecundity (comparing seasonal fecundity of unparasitized pairs [2.11] to that of all pairs [1.81]) is not as severe (0.30 young/pair) because only 23.4% of all flycatcher pairs were parasitized. But no matter how the cost of parasitism is expressed, it still begs the question: Can Willow Flycatcher populations persist in the face of this level of reduction in seasonal fecundity?

ENERGETIC COSTS

Parasitism may increase adult mortality if parasitized females expend more energy during the breeding season than unparasitized females (Robinson et al. 1995a). We found that parasitized females spent more time attending nests, built more nests, and laid more eggs than unparasitized females. Return and survival rates of parasitized and unparasitized females were similar, however, suggesting that increased energetic costs as a consequence of parasitism do not increase female mortality in Willow Flycatchers. Smith (1981) also found no differences in survival of parasitized and unparasitized female Song Sparrows. However, energetic costs, or other factors associated with parasitism, may be linked to return rates for some species. Return rates of Black-capped Vireos (*Vireo atricapillus*), for example, were low following years of high rates of parasitism and were higher following years of low rates of parasitism (Gryzbowski 1991).

PHENOLOGY SHIFTS

Phenology shifts in fledging date may diminish reproductive output and be an additional, hidden cost of parasitism. Lowered reproductive output as a result of phenology shifts has been shown for a number of species, and is often corroborated by lower return rates and increased mortality in late-born young (Perrins 1965, Morton 1992). In our study, young produced by parasitized pairs fledged only 4 d later than young produced by unparasitized pairs. It seems clear that there is a direct link between this phenology shift and cowbird parasitism: fledging is delayed because of the greater number of eggs laid and nests built by parasitized female Willow Flycatchers. The delay in fledging is less than one might expect and, indeed, is less than the phenology shift (11 d) due to parasitism found by Whitfield and Sogge (*this volume*) for *E. t. extimus* in California. Neither shift (4 d or 11 d) would seem great enough to diminish seasonal fecundity; it is unlikely that females feeding nestlings only 4–11 d later in the season would be far enough out of phase with the foraging resource to affect reproductive success (Immelmann 1971). Because Willow Flycatchers rarely attempt to raise two broods in a season (J. Sedgwick, unpubl. data), phenology shifts cannot result in lost opportunities for fecundity enhancements from second broods. Greater phenology shifts, such as those for Common Flickers (*Colaptes auratus*) (21 d; Ingold 1996; D. Ingold, pers. comm.) and for Great Tits (*Parus major*) (49 d; Perrins 1965), have been shown to lower reproductive success, however.

The phenology shift at Malheur NWR was apparently not enough to affect return rates or survival. Larger differences in fledging dates do affect return rates in Willow Flycatchers, however, as the earliest fledging young (1–15 July) had return rates (29.1%) more than 5 times greater than for later fledging young (4.8–5.4%). Similarly, Whitfield and Sogge (*this volume*) reported significantly higher return rates for early-fledged compared to late-fledged *E. t. extimus*, and Morton (1992) and Drilling and Thompson (1988) documented higher return rates for early-fledged White-crowned Sparrows and House Wrens (*Troglodytes aedon*), respectively. Under certain circumstances, phenology shifts as a result of parasitism could conceivably be large enough to diminish return rates.

RETURN RATES, SURVIVAL, AND PARASITISM

Return rates and survival were low for juvenile Willow Flycatchers, due presumably to high juvenile mortality and/or dispersal, common in passerines (Horn and Rubenstein 1984, Plissner and Gowaty 1996). There were no significant differences in return rates or survival between juveniles from parasitized and unparasitized pairs in our study, even though juveniles from parasitized nests fledged on average four days later than offspring from unparasitized nests. Because later fledging potentially reduces the ability of young produced by parasitized pairs to survive to the following breeding season (Sullivan 1988), we expected a lower return rate among flycatcher young from parasitized nests. The greatest costs of parasitism incurred by juveniles probably occur during the post-fledging period. Several studies have found that late-fledging birds have increased mortality rates, especially in species where foraging skills and attainment of pre-migratory condition are essential for over-winter survival (Heinsohn 1987, 1991). However, our data indicated that once juveniles from parasitized nests pass through the bottleneck of post-fledging, their chances of overwinter survival and return to their natal areas were as good as offspring from unparasitized nests.

The return rates and survival of all parasitized and all unparasitized females did not differ. Among successful females, parasitized birds returned to the study area at a significantly higher rate than unparasitized females, but survival did not differ. Parasitized females incur a number of costs, including lower pair success, increased time investment, construction of more nests and laying more eggs, as well as feeding large parasite young (Payne 1977). Despite these costs, parasitized females still returned and survived at roughly the same rates as females from unparasitized nests. We offer these possible interpretations: (1) increased time and energy costs, while statistically significant, are simply of no biological consequence; or (2) parasitized Willow Flycatcher females may be superior in some way compared to average flycatchers and may return at the same (or better) rate as unparasitized females because they are better host parents and are able to bear the added energetic costs incurred as a result of parasitism (sensu Smith 1981). If cowbirds are selecting superior females to parasitize, then we might reasonably expect them to have higher return rates.

Neither return rates nor survival of parasitized and unparasitized male Willow Flycatchers differed; in fact, survival of parasitized males tended to be higher (Table 7). This was counter to what we anticipated, given that parasitized males probably invest more time defending territories (because their females attend nests longer) than unparasitized males, and are ultimately less successful because of parasitism. As with female flycatchers, cowbirds may be parasitizing those males that are deemed better host parents. Both the slightly higher survival of parasitized males and similar survival and return rates for females intimate that parasitized pairs may be superior individuals (Smith 1981, Smith and Arcese 1994). Hahn et al. (*this volume*) found that female cowbirds have home range fidelity over successive breeding seasons and concluded that cowbirds know their hosts and the quality of care their hosts provide. This seems to lend support to the argument that female cowbirds may select flycatcher pairs that are outstanding candidates to raise young under the burden of parasitism.

The differences we observed in the effects of parasitism on return and survival rates of female vs. male Willow Flycatchers may be related to the differences in energetic costs of breeding for females and males (Nur 1988). Despite the energetic expense of territorial defense and parasite-predator detection, males do not incur the same level of energetic costs as females, because they are only occasional participants in feeding offspring (J. Sedgwick, pers. obs.). This may explain their slightly higher survival rates. Parasitized females may have likewise returned more frequently than unparasitized females (as the parasitized males do), but do not do so because of their higher energetic costs (relative to males) imposed by parasitism.

LIFETIME REPRODUCTIVE SUCCESS

The consequences of parasitism to lifetime reproductive success of females supported our prediction: parasitized females fledged fewer young than unparasitized females, with an expected gradient of reproductive success from high (successful, unparasitized females) to low (unsuccessful, parasitized females). Notably, females that were parasitized and successfully reared a cowbird and at least one flycatcher had a lifetime output similar to those females that were parasitized and successfully raised only flycatchers. Given the increased energetic burden of rearing a large cowbird young (Payne 1977) and the associated loss a parasitic offspring represents to Willow Flycatcher fecundity, this is contrary to expectation. But if these females tend to be better host parents because cowbirds are selecting superior pairs, then the increased energetic costs of rearing a cowbird may be inconsequential. If parasitized females rearing both a cowbird and flycatcher(s) do not recognize that they have been parasitized, they may return in subsequent years based on past reproductive success, regardless of whether the offspring were their own or cowbirds. So the combination of (1) being superior parents and (2) past reproductive success based on number of offspring fledged, not species, may explain the high lifetime reproductive success of parasitized Willow Flycatcher females raising both cowbirds and flycatchers. Similarly, Smith (1981) presented evidence that female Song Sparrows, despite being parasitized, were able to rear as many young to fledging as unparasitized females and suggested that female cowbirds may be actively selecting host individuals with the greatest chance of successfully rearing cowbird young.

If host selection is occurring, what criteria do female cowbirds use to select superior parents? For the parasitic female, these criteria may be relatively simple, e.g., the intensity of anti-parasite behavior displayed by the host territorial male (Robertson and Norman 1977, Uyehara and Narins 1995); the foraging behavior of host males within their territories, especially during courtship (Payne 1977); host density (Verner and Ritter 1983, Rothstein et al. 1986a); or the characteristics of the individual host birds nesting in the cowbird's home range (D. C. Hahn, pers. comm.).

Given the similar return rates and survival of parasitized pairs, we asked if the overall lifetime reproductive success that we observed for females may be affected by parasitism incurred during their first breeding attempt. The greatest impact to the lifetime reproductive success of female Willow Flycatchers may occur during their first year of reproduction, when inexperienced breeders may be most susceptible to cowbird parasitism (Payne 1997). If Willow Flycatcher adults are more naive to cowbird parasitism in their first breeding season but able to learn better evasion techniques in subsequent breeding attempts, we would expect that lifetime reproductive success may increase in the years subsequent to parasitism (Payne 1997). To evaluate this first-year effect, we examined the lifetime reproductive success of female Willow Flycatchers in years subsequent to their first year of reproduction.

Two trends emerge from these data. First, Willow Flycatcher females that are successful in their first year fledged no more young over the remainder of their lifespans than females that were unsuccessful in their first year. Thus, successful females do not appear to improve in subsequent performance as a result of their success. This suggests that successful females may be taking advantage of their unparasitized state in their first year and maximizing chick production when they can, but may pay a cost in diminished lifetime output after this first year. Unparasitized Willow Flycatcher females may be peaking in their reproductive success within their first year in this short-lived species.

Second, subsequent lifetime reproductive success was similar for all classes whether birds were parasitized or not, or successful or not, in their first year. This suggests that unsuccessful females may learn from experience how to become successful, and that parasitized females may learn how to avoid parasitism. Females that were parasitized were certainly not inferior, because they were just as successful in subsequent years as unparasitized females. They may have been more naive to cowbirds in their first year and more easily duped into raising a cowbird, however. Thus, cowbirds may be selecting the most naive host individuals, but not individuals that are reproductively inferior. Similarly, females that were successful and unparasitized in their first year, and had high lifetime reproductive success, may have been more experienced and less naive to cowbirds. Thus, they may have not been parasitized because they did not fit the criteria for cowbird selection of good host parents.

Our data suggest that although parasitism in the first year of breeding is detrimental to the reproductive success of Willow Flycatcher females over their lifespans, other factors, such as learning anti-parasite behaviors (Hobson and Sealy 1989, Payne 1997) or how to become better parents (Drent and Daan 1980), need to be considered in addressing lifetime reproductive success. It may not be just a matter of being parasitized, but also when parasitism occurs and learning from the experience to increase lifetime reproductive success.

RELATIVE COSTS OF PARASITISM AND PREDATION

Predation is thought to be one of the most important selective pressures shaping reproductive and survival strategies of prey species (Wittenberger 1981). The greatest threat from predators occurs during nesting and shortly after fledging when progeny are most vulnerable. At Malheur NWR, predation accounted for a greater proportion of the loss of potential progeny (0.74 young/season; 0.70 young/lifetime) than parasitism (0.30 young/season; 0.37 young/lifetime); therefore, we conclude that local predators must exert greater selective pressure on Willow Flycatchers at Malheur NWR than do cowbirds. The greater influence of predation has been reported for numerous species, such as California Gnatcatcher (*Polioptila californica*; Braden et al. 1997b), Prairie Warbler (Nolan 1978), Indigo Bunting (*Passerina cyanea*; Best and Stauffer 1980), Kirtland's Warbler (*Dendroica kirtlandii*; Mayfield 1960), and Yellow-breasted Chat (*Icteria virens*; Thompson and Nolan 1973). Fewer studies have found that parasitism accounted for higher proportions of nest losses, for example, Plumbeous Vireo (Marvil and Cruz 1989), Red-eyed Vireo (*Vireo olivaceus*; Southern 1958), Black-capped Vireo (Graber 1961), and Yellow Warbler (Burgham and Picman 1989). If parasitism proves to be relatively less important than predation for a given species, then the selective pressures to evolve anti-parasite strategies may be lower than those to reduce predation. But regardless of the level of parasitism, if a heretofore unparasitized species is in equilibrium with historic levels of predation, then the additional reproductive costs of parasitism may lower productivity below that needed to replace adult mortality.

IMPLICATIONS FOR PERSISTENCE OF THE WILLOW FLYCATCHER

Of the small hosts with incubation periods longer than that of the cowbird, Willow Flycatchers appear to be fairly typical in terms of the costs of parasitism. Parasitized pairs hatch fewer eggs, fledge fewer young, have far fewer successful nests, and suffer reductions in seasonal fecundity and lifetime reproductive success. In addition, parasitized females expend more energy, and nestlings of parasitized females fledge slightly later than those of unparasitized females. Thus, in spite of nest abandonment, cowbird egg burial, and aggressive attempts to thwart cowbirds at the nest (Sedgwick and Knopf 1988), parasitized pairs have substantially lower fecundity than unparasitized pairs. However, a relatively small percentage of the population we studied was parasitized, and the population level consequences of parasitism do not appear to be severe. Furthermore, return rates of both sexes of parasitized adults and young of parasitized pairs are at least as high as those of unparasitized birds. Similar return rates for females suggest that the energetic costs they incur are not pivotal and similar return rates for young suggest that the slight delay in fledging is of no consequence. Compared to parasitism, predation would appear to be a much more significant selective force. In situations where there are pockets of parasitism, and especially where populations are small and fragmented, as is the case for most populations of *E. t. extimus*, parasitism may have more of a negative impact and reproductive success may not be sufficient to balance mortality. We believe we have reasonable estimates for most of the demographic parameters (seasonal fecundity, parasitism rates, and female mortality) for Willow Flycatchers at Malheur, all of which are necessary to assess effects of parasites on host populations (May and Robinson 1985). However, we lack a credible estimate of annual juvenile mortality. We again ask the question: Can Willow Flycatcher populations persist in the face of the levels of reduction in seasonal fecundity due to cowbird parasitism at Malheur? Using the equation for the critical probability of parasitism (p_c) in May and Robinson (1985),

$$p_c = \{\lambda - [2\mu/(1 - \mu_0)]\}/(\lambda - \lambda')$$

and using values from our study for the Malheur population (the probability of parasitism [$p_c = 0.234$], female mortality [$\mu = 0.464$; J. Sedgwick, unpubl. data], and seasonal fecundity of unparasitized [$\lambda = 2.11$] and parasitized [$\lambda' = 0.80$] females), and solving for the annual mortality of juveniles (μ_0, the only unknown), we calculate that $\mu_0 = 0.49$. This means that juvenile survival from fledging to breeding in the next year must be 0.51. Because of presumed low site fidelity and dispersal of juveniles, our return rates (5.4–7.7%; Table 7) are far below the calculated μ_0, but the latter is what they must be if the population is to persist. Therefore, the implication may be that the Malheur Willow Flycatcher population is in decline or is a sink population maintained only by immigration from other areas. However, given unknown rates of overwinter juvenile mortality and unknown rates of juvenile dispersal to and from respective natal areas, no reliable conclusions can be drawn. Information is lacking, as it is for virtually all other passerines, on juvenile survival rates, and until we have a better grasp of juvenile survival to first year of breeding, our estimates of the demographic consequences of parasitism are severely limited.

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