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Chapter 9:

The Ecology of Brown-Headed Cowbirds and Their Effects on Southwestern Willow Flycatchers

Brown-headed cowbirds (*Molothrus ater*) are obligate brood-parasites, that is, female cowbirds lay their eggs in nests of other species. If the cowbird eggs are accepted, the host pair may raise the young cowbird, often at a reduction of the hosts' reproductive success. Cowbird females are also known to remove host eggs and nestlings from nests, which may also affect the reproductive success of the hosts (Smith 1981, Scott et al. 1992, Sealy 1992). It is difficult to assess the impact of parasitism both because reproductive success operates at many levels and because the hosts have defenses against parasitism or cowbird intrusion. In this chapter, we review the data on the effects of brood parasitism on reproductive success of the southwestern willow flycatchers (WIFL). We estimate the effects of brood parasitism on populations of WIFLs and the degree to which parasitism is a factor in their recovery. For most of the analyses, we use data from one population along the South Fork Kern River, Kern County, California.

Cowbird Ecology

In this section, we review the ecology of cowbirds and point out how the ecological and life history considerations may affect various management decisions regarding WIFLs. Because cowbirds are a wide-ranging species, we have focussed our literature review on studies conducted in the southwest, within the historic range of the Southwestern Willow Flycatcher.

Breeding Biology

The breeding season of cowbirds overlaps with the initial period of breeding for southwestern willow flycatchers. In mid-April to early May, female cowbirds arrive on their breeding grounds (Fleischer et al. 1987, Braden et al. 1997), although in some years, females may arrive earlier (Darley 1983). Cowbirds begin laying eggs at the end of April and end in mid-July throughout much of the cowbirds' range (e.g., Payne 1976, Yokel 1987, Brown 1994, Braden et al. 1997, Schweitzer et al. 1998). In some areas, cowbirds may lay in late July (Whitfield, unpub. data). The length of the breeding season for an individual female may depend on weather conditions (e.g., Scott and Ankney 1979), age of the female (Fleischer et al. 1987) or location. Typically, however, most female cowbirds are laying eggs in May and June. As the breeding season progresses, fewer cowbirds are laying eggs

(Scott and Ankney 1979, Yokel 1987, Holford and Roby 1993). Because WIFLs generally begin nesting at the end of May, with the highest number of nests initiated in June, and with some nesting into August (Sogge et al. 1997), the early nests of WIFLs are at a higher risk of parasitism than later nests.

During the breeding season, female cowbirds are egg-laying machines with the maximum number of eggs laid dependent on the laying rate and breeding season length. The laying rate of cowbirds may vary by age and region, but studies show that cowbirds lay eggs at rates of 0.5 to 0.8 eggs per day (Scott and Ankney 1979 and 1980; Fleischer et al. 1987, Jackson and Roby 1992, Holford and Roby 1993).

Female cowbirds are extreme generalists, having been documented to parasitize over 200 species in North America (Friedmann and Kiff 1985). Variability in host preference by cowbirds is observed in individual females and between regions. Individual females lay eggs in nests of many hosts (Fleischer 1985 and 1986). Between regions of North America, the primary hosts of cowbirds differ, i.e., hosts that are parasitized heavily in one region may not be the preferred host in another region (Hoover and Brittingham 1993). Thus, the relationship of cowbird parasitism to an endangered host is not a simple relationship of cowbird abundance to endangered host number . So, although cowbirds may be present in an area with WIFLs or endangered populations of hosts, the actual parasitism levels of the endangered species depend on other factors as well.

During the breeding season, cowbird females likely have two limiting resources: forage and host nests to parasitize. Because cowbirds are not confined by parental care duties, cowbirds can use one area for breeding and another for feeding. Throughout the southwest, host-rich areas tend to be riparian habitat (cf. Knopf and Samson 1994) and this may be where female cowbirds concentrate their nest searching activities. In some areas with apparently high densities of both hosts and food, individual females stay in a relatively compact home range for a few days or throughout the season (Table 9-1). Examples of use of small home ranges are found in prairie habitats in the Midwest (Elliott 1980), with ephemeral abundant food along a riparian strip in desert (Yokel 1987), and alpine meadows with cattle (Verner, cited in Rothstein et al. 1987).

When the two resources of host and forage are spatially separated, female cowbirds split their time between host-rich areas and concentrated food sources. Females generally stay in their breeding areas or host-rich areas in the morning before 1100 hrs and then commute to feeding areas (Raim 1978, Smith 1981, Dufty 1982a, Rothstein et al. 1984, Yokel 1987, Thompson 1994, Gates and Evans 1998, Farmer 1999). Depending on the landscape, the feeding areas may be adjacent to the breeding areas or disjunct from the breeding areas. Feeding areas favored by cowbirds have short-grass and high invertebrate densities or grain seeds. Feeding areas are often associated with anthropogenic factors, e.g., livestock-grazed pastures, feedlots, dairy farming, golf courses, bird feeders, and camping grounds (Rothstein et al. 1984, Rothstein et al. 1987, Thompson 1994, Morris and Thompson 1998, Goguen and Matthews 1999, Farmer 1999) but generally, cowbirds feed near livestock (Morris and Thompson 1998).

The distances that cowbirds commute vary across landscapes (Table 9-1). Feeding sites tend to attract cowbirds from a great distance, but will tend to have proportionately lower numbers of female cowbirds (Rothstein et al. 1984, Rothstein et al. 1987). Recent research indicates a gradient of cowbird abundance and parasitism rates from feeding sites. In studies where cowbirds were feeding near cattle and the cattle were subsequently moved further from breeding areas, cowbird density or parasitism rates of hosts decreased (Goguen and Matthews 1997, Cook et al. 1997). Therefore, if potential feeding sites are distant from breeding areas, parasitism rates of riparian-nesting species may be lowered.

Later in the day, female cowbirds either roost with other blackbirds and cowbirds in the evening (e.g., Thompson 1994) or return to their breeding areas (Rothstein et al. 1984) by dusk. Shortly before sunrise, female cowbirds generally fly straight to a host's nest to lay their egg (Scott 1991) and presumably begin the cycle again. Rarely do females lay an egg later than 30 minutes past sunrise (Scott 1991).

Female Cowbird Range and Densities

In historic times, cowbirds were found in Arizona, New Mexico, and California (Perriman and Kelly, this vol.). By the 1920s, cowbirds were considered abundant along the Colorado and Gila River valleys and the rivers' tributaries in Arizona (Wyman and Burnell 1925). In New Mexico in the same time period, cowbirds were considered "fairly common" in the southern parts of New Mexico (Bailey 1928, cited in Schweitzer et al. 1998). In southern California, cowbirds expanded their range from the southeastern areas to the northwest throughout the early 1900s (Laymon 1987, Rothstein 1994).

In more recent decades, cowbird abundance throughout the southwest has shown no consistent trend, based on Breeding Bird Survey data (Wiedenfeld, in press). During 1966-1996, the mean abundances range from the lowest density category of 0.01-1 birds/survey to intermediate density category, 4-10 birds/survey (Sauer et al. 1997).

Table 9-1. The habitats which female cowbirds used for breeding and feeding sometimes differred. The area which female cowbirds used primarily for breeding or feeding is listed in parentheses along with the sample size of banded or radiotracked females. The mean or range of distances that female cowbirds commuted between the breeding and feeding areas are listed, when given.

Breeding (ha, sample size)	Feeding	Distance between breeding/feeding	Reference
		(km)	
riparian in desert (2.64 ha, n=25)	corrals, bird feeders, grazed pastures	0.6-3.3	from Yokel, 1987
woodland, open woodland, shrub, swamp (9.6 ha, n=7)	bird feeders, lawns cattle pastures, woodland, swamp		Teather and Robertson, 1985
campus/creek (4.5 ha, n=39)	open lawn areas		Darley 1983
montane forest, riparian (78 ha, n=5)	bird feeders, corrals	2.1-6.7	Rothstein et al., 1984
campus, New York (21.2 ha, n =13)		ca. 0.4	Dufty 1982a
riparian	pastures, golf course urban, dairy	2.8-13.6	Farmer, in press
forest/shrub sapling (*, n=84)	short-grass, crops, feedlots	mean=1.3	Thompson 1994
grassy meadows, shrubs/trees	not on island	1.3-7 km	Smith 1981
prairie pastures	cattle-grazed pastures	0	Elliott 1980
deciduous forest with brush (ca 8.8, n=19)	mainly grazed pastures	mean = 2.27 (0.3-6.14)	Gates and Evans, 1998
oak/juniper oak/savannah (99 ha,n=28)	cattle-grazed pastures, (0-18.1)	mean=1.7	Koloszar, in prep

Cowbirds tend to concentrate in specific habitats within a landscape, in the 'edges' of forest or in larger open areas within forests (Gates and Gysel 1978, Brittingham and Temple 1983 and 1996, Coker and Capen 1995, Annand and Thompson 1997, Niemuth and Boyce 1997, Evan and Gates 1997, Miller et al. 1998). The size of the opening within forests or the distance to feeding sites may affect cowbird abundance (Germaine et al. 1997), but the relationship of cowbird abundance with 'edge' transitions in landscapes is not always found throughout North America (Hahn and Hatfield 1995, Suarez et al. 1997, Bielefeldt and Rosenfield 1997, Miller et al. 1998). Generally, cowbirds are found in the highest densities near riparian zones and agricultural-use fields (Anderson et al. 1984, Chase 1997, Cook et al. 1997, Evan and Gates 1997, Farmer 1998). Cowbirds are found in low densities in desert (Sauer et al. 1997), coastal sage scrub (Farmer 1999 a,b, Braden et al. 1997), and in the interior of forests with small openings and low anthropogenic influences (Verner and Ritter 1983, Germaine et al. 1997 but see Hahn and Hatfield 1995). Cowbird densities in riparian areas traversing deserts can have low abundances, e.g., Lower San Pedro, Hunter, unpub data), although if there are anthropogenic factors nearby then densities can be high, e.g., Owens River near Bishop, California (Yokel 1987; pers obs). Because southwestern willow flycatchers nest in riparian habitats (e.g., Miller 1951), and because riparian habitat tends to be fragmented or linear

throughout the southwest (Johnson and Haight 1984), cowbirds tend to occupy the same breeding habitat as do WIFLs.

Parasitism rates and effects are hypothesized to be correlated with abundance of cowbirds. This correlation is the rationale for many cowbird trapping programs. Obviously, with no cowbirds present, there is no parasitism. With varying densities of cowbirds, however, the effects on specific hosts depends on many factors, such as the relative abundance of cowbirds to hosts (e.g., May and Robinson 1985), the host preferences of cowbirds between areas (Hahn and Hatfield 1995, Hoover and Brittingham 1993), proximity of other nests near nests of an endangered species (Barber and Martin 1997), overall nest availability (e.g., Sedgwick and Knopf 1988), surrounding landscape use and bird community (e.g., Strausberger and Ashley 1997) and the efficacy of host responses (e.g., Uyehara and Narins 1995). The regional host preferences of cowbirds and the parasitism levels of WIFLs within different host assemblages needs to be researched.

Factors Affecting Cowbird Surveys

Given the sex-specific and temporal aspects of cowbird movements, surveying both breeding areas and (potential) feeding sites yields different information. Cowbirds are opportunistic feeders and use ephemeral sources of food, e.g., outbreaks of cicadas (Yokel 1987) within the breeding areas. But if insect or seed availability is low within a breeding area, cowbirds commute to feeding sites by afternoon (Yokel 1987; Thompson 1994). Therefore, censusing cowbirds in breeding areas before 1100 hrs will yield a more accurate number of breeding females in an area. Because females spend part of the morning concealed within the vegetation or under the canopy, (Norman and Robertson 1975, Payne 1973, Lowther 1979, Uyehara 1996), detection of female cowbirds is enhanced with playbacks of the female 'chatter' call (e.g., Dufty 1982b, Rothstein et al., in press).

Throughout its range, male cowbirds tend to outnumber females. This sex bias could be due to the higher mortality rate of females (Darley 1971), although in one California study, female cowbirds did not have higher mortality rates than males (Yokel 1987). In the western US, female cowbirds are actively monogamous (Yokel 1986) and breeding males tend to be older (Yokel and Rothstein 1991). The breeding males have consistent morning ranges within which copulations occur (Yokel 1989). Younger, presumably unmated, males tend to visit more feeding sites and travel further than females (Darley 1983, Rothstein et al. 1987). This difference suggests that trapping males at feeding sites is not as effective at controlling parasitism as trapping on the breeding grounds (Rothstein et al. 1987), although more studies are needed.

Cowbird Management Practices

The effect of parasitism or cowbird management practices on particular hosts has been difficult to assess. If parasitism is affecting a species, then high parasitism rates and low nesting success would be correlated with declining populations (e.g., Trail and Baptista 1993). However, high parasitism rates and low nesting success have been reported for species with relatively stable populations (e.g., Robinson 1992) and low parasitism rates have been reported for fluctuating populations (McCabe 1991). Thus, the effect of cowbirds on hosts needs to be assessed for each species or assemblage of species (e.g., Barber and Martin 1997), host density (e.g., Spautz 1999), and site-specific vegetation characteristics.

For long-term benefits to hosts, increasing suitable habitat has been advocated (Laymon 1987). Decreased parasitism levels have been associated with dense vegetative cover around the nesting heights (e.g., Spautz 1999, Farmer 1999b, Uyehara and Whitfield *in press*). Decreased parasitism has also been associated with fewer perch sites from which presumably, female cowbirds use to scan the adjacent area (e.g., Uyehara 1996, Brittingham and Temple 1996, Averill-Murray et al. 1999).

To control parasitism in specific host populations, cowbirds have often been removed, either selectively (Stutchbury 1997) or through intensive trapping efforts using decoy traps. Selective removal is likely most effective at low densities of cowbirds (e.g., Stutchbury 1997). Intensive trapping can be highly effective at decreasing cowbird numbers at sites with a concomitant increase in host numbers (Griffith and Griffith, in press). However, cowbird removal programs have not always led to increases in nesting success or host numbers (e.g., Kelly and DeCapita 1982, Braden et al. 1997, Whitfield et al. 1999, Winter and McKelvey 1999). For WIFL, cowbird trapping programs have not resulted in an increase in populations at two sites in California (Whitfield et al. 1999, Winter and McKelvey 1999) In addition, cowbird traps can cause mortality of nontarget species (Terpening 1999).

To minimize the effects of parasitism, cowbird eggs in nests have been addled or removed. Because cowbirds also remove host eggs from nests, this strategy does not eliminate the effects of parasitism.

We present information on parasitism rates at different sites and reproductive success with different management regimes. In one population in Kern County, CA, cowbirds were not removed from 1989-1990. Selective removal of 23 female cowbirds was used in 1991. Cowbird trapping was instituted in 1993 with increasing number of traps in subsequent years. In addition, cowbird eggs found in WIFL nests were shaken to prevent hatching from 1992.

Effects of Parasitism on WIFL _____

Cowbird Abundance and Parasitism Rates

McCabe (1991) hypothesized that, in the case of linear habitats with low availability of hosts, the parasitism rates of WIFLs may be higher than in areas with less fragmentation and higher densities of other hosts. This hypothesis is supported by two studies of WIFLs. Of nine parasitized hosts in a coastal central Californian community, WIFLs are parasitized more often than expected given the overall parasitism rate found within the community (Farmer 1999b).

WIFLs occupy territories with structural heterogeneity (Sedgwick and Knopf 1992, Uyehara and Whitfield in press). Pairs of WIFLs which occupied territories with more open canopy and less dense vegetation at the horizontal level around the nest were more likely to be parasitized than were pairs with more continuous canopy and dense vegetation around the nest (Uyehara and Whitfield, *in press*). The association of parasitism with nests located in more open areas has been found with other species (Brittingham and Temple 1996, Burhans 1997, Larison et al. 1998).

The parasitism rates of southwestern willow flycatchers tends to be high throughout their range (cf. Whitfield and Sogge 1999). Of nine sites where 10 or more nests were checked, the annual parasitism rates ranged from 3% at the San Pedro River in Arizona to a high of 66% at the South Fork Kern River in California. In other parts of the west, high parasitism rates occur (Sedgwick and Knopf 1988). Also, at Kern, the relative abundance of cowbirds surveyed in June is significantly correlated with the parasitism rates of the population among years (Fig. 9-1), indicating that a positive relationship exists for this population.

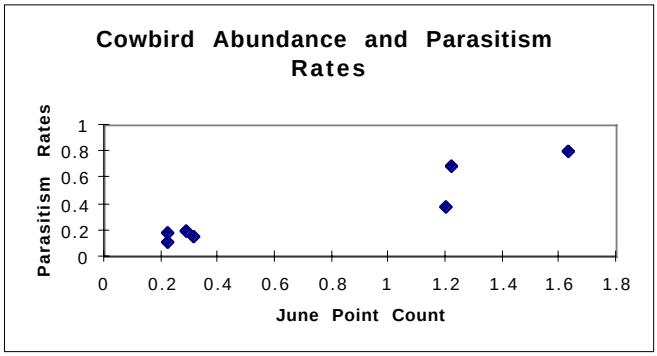

Figure 9-1. Parasitism rates of southwestern willow flycatchers in a central California population are correlated with female cowbird abundance (r=0.94, p=0.002). Sites for point counts (n=60-75 pts/yr) were located 200 m apart along the edge of riparian habitat near the South Fork Kern River.

Nest Level

The effects of parasitism at a WIFL nest depend on the response and subsequent events at that nest (e.g., Whitfield 1990). Even in areas with high densities of cowbirds and relatively low numbers of willow flycatchers, some nests are not parasitized. The WIFLs at unparasitized nests may present fewer cues near the nest, or aggressively distract female cowbirds when cowbirds are further from the nest (Uyehara and Narins 1995).

Female cowbirds sometimes remove host eggs before 1230 hrs or after 1700 hrs (Scott et al. 1991, Sealy 1992), usually before parasitizing a nest. For first clutches of flycatchers from Kern County, CA (Table 9-2), 52 parasitized nests had a significantly

Table 9-2. Possible effects of parasitism at the nest level are listed and tested with data from Kern County, CA. A parasitized nest contained at least one cowbird egg.

Effect	Data from Kern County, CA, 1989-1991
a) Reduced clutch size	Mean number of eggs/clutch: parasitized nests = 3.17 unparasitized nests = 3.60 eggs,
b) Reduced hatching success	% Flycatcher eggs hatched parasitized nests = 22% unparasitized nests = 63%
c) Reduced fledging rates	28/73 parasitized nests hatched cowbirds, 3/73 parasitized nests fledged flycatchers
d) Overall nesting success	% nests fledged one flycatcher For unparasitized nests only = 54.8%. All nests, par and unpar = 28.9%.

lower mean number of eggs than did 97 unparasitized nests (t-test, t = -2.94, p = 0.004).

The presence of a cowbird egg in the nest is associated with decreased hatchability of flycatcher eggs (Table 9-2). The reduced hatchability of flycatcher eggs in parasitized nests may be due to insufficient incubation by the host if there is a larger egg in the nest, due to cracking of the flycatcher egg, or due to desertion of the nest. We have documented the effect of reduced hatchability at Kern but have no data on the mechanism leading to the reduced hatching rate.

If a cowbird hatches in a flycatcher nest, WIFLs rarely are able to successfully raise both their own young with the cowbird. There is also some evidence that cowbirds eat or remove all eggs or nestlings from a nest (e.g., Scott et al. 1992, Sealy 1992, Scott and McKinney 1994, Arcese et al. 1996, Sheppard 1996), perhaps to initiate renesting by the host. To our knowledge, there are no observations of nestling predation by cowbirds in WIFL nests.

The low success at fledging WIFLs in parasitized nests does not mean that the WIFLs are necessarily fledging cowbirds successfully. The actual proportion of cowbird eggs that hatch and subsequently fledge young in flycatcher nests is low (Fig. 9-2 and Table 9-2). This low success rate is due partially to the responses of flycatchers, which can reject the cowbird egg by burying the cowbird egg (which prevents hatching) or abandoning the nest. At Kern, of a total of 73 parasitized nests in 1989-1991, 11 eggs were buried within the nest floor. In 47 parasitized nests, WIFLs initially accepted the cowbird egg, but of those, 26 nests were eventually abandoned, probably as a response to some aspect of parasitism. Overall, for about half of the parasitized nests, the flycatchers responded so that the cowbird egg never hatched. Of 28 nests in which cowbirds hatched, three successfully fledged flycatchers. These nests were likely successful because the cowbird egg was laid late during incubation.

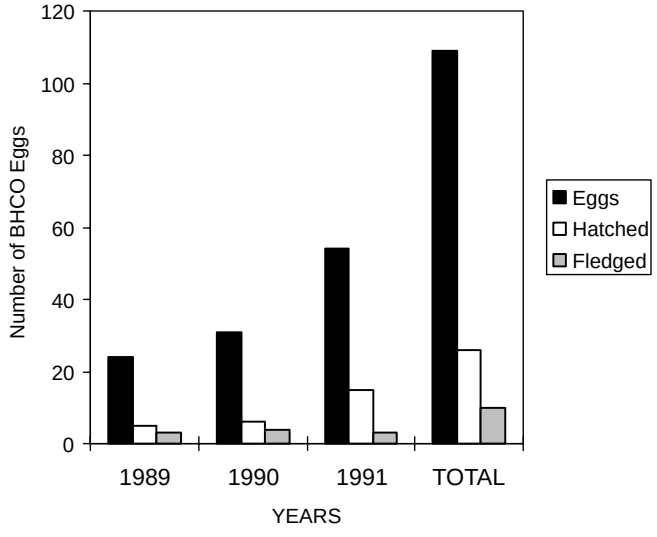

Figure 9-2. Of the cowbird eggs laid in southwestern willow flycatcher nests, only a small proportion hatched or fledged.

Nesting success is defined as the percentage of nests that fledge at least one flycatcher young. Parasitized nests rarely fledge flycatcher young. Of 28 nests in which cowbirds hatched, two nests fledged the flycatcher and the cowbird nestling died. One nest fledged one flycatcher and cowbird each.

Parasitism can reduce reproductive success at all nesting stages for flycatchers. For other populations of WIFLs, (not the southwestern willow flycatcher), the composite nest success is 83% across five studies (summarized in McCabe 1991, p 114). Thus, the nesting success at Kern is low relative to that of other subspecies (McCabe 1991, Stoleson et al., this vol).

Paradoxically, if a parasitized nest is subsequently depredated the flycatcher may renest, which may increase the flycatchers' nesting success. Thus, to better assess the effects of parasitism, we examined parasitism effects at the level of female reproductive success per season.

Annual Reproductive Success Per Female

Sedgwick and Knopf (1988) noted that parasitism rates of nests may not be the best measure of the effects of parasitism. Willow flycatchers can still nest after the cowbirds stop laying eggs in mid-July, or a parasitized female may exhibit rejection behavior and produce flycatcher fledglings during a season. Rejection behaviors by the flycatchers have the effect of delaying nesting. At the Kern River Preserve in central California, parasitism followed by rejection of cowbird eggs caused a delay of about 13 days in the first egg dates at parasitized nests relative to unparasitized nests (Whitfield and Sogge 1999).

We tested whether the number of fledglings in a season differed between parasitized and unparasitized females in the Kern population. Over all years, parasitized females raised about 1.05 yg annually whereas unparasitized females fledged 1.93 yg annually. There was considerable variation in the annual reproductive success per female among years (Fig. 9-3), so we also examined the differences for individual seasons. In 1989, parasitized females fledged significantly fewer young than did unparasitized females, (Mann-Whitney U test, U=16.50, p=0.007). However, in 1990, there was no difference in the number of fledglings produced by 18 parasitized and 6 unparasitized females (Mann-Whitney U test, U=55.0, p=0.94). For 1991, there were only 2 unparasitized females, so the data are not amenable to statistical testing. Starting in

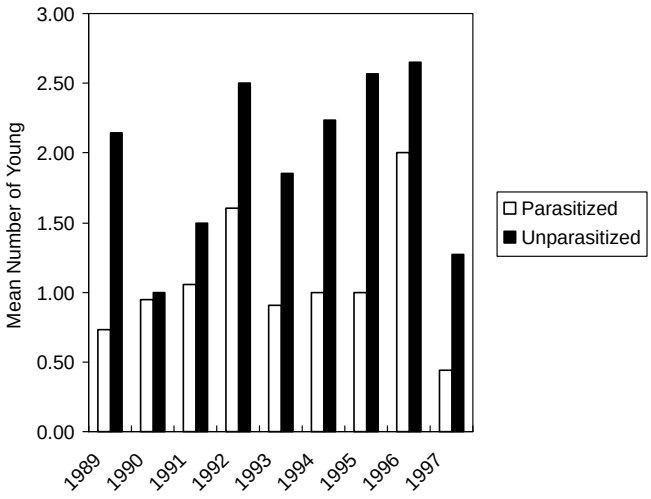

Figure 9-3. The mean number of flycatcher young fledged in parasitized and unparasitized nests. The numbers represent the number of females in the population that were parasitized or unparasitized. Beginning in 1993, management practices designed to minimize parasitism effects were instituted. (See text for additional details.)

1993, we hypothesized that more active management of cowbirds would increase productivity of WIFL females. Despite increased cowbird trapping efforts, the number of fledglings per female were not significantly different between parasitized and unparasitized females for any year between 1993-1997 (Fig. 9-3). To a certain extent, cowbird management practices increased the reproductive success per individual female, although the main effect may have been to reduce parasitism rates so that a smaller proportion of females in the total population were affected by parasitism.

The difference in significance levels between years with and without cowbird management (1989-1991) suggests that other factors besides parasitism are important in determining annual reproductive success per female. This hypothesis is further supported by the variation in reproductive success for unparasitized females over all years (Fig. 9-3) and by studies on other species (Braden et al. 1997). Logically, to assess the effect of parasitism, one has to combine the information of parasitism rates with its subsequent effect on productivity. The productivity of females is the sum of the number of young fledged in a season multiplied by the number of seasons that they reproduce. We do not have the data to assess the impact of parasitism on the survival of females and their lifetime reproductive success. On the other hand, we do have data to examine the effects of parasitism on changes in population size and the year-to-year variation in population growth.

Population Level

We have presented summaries and data that indicate parasitism reduces productivity when measured on the level of the nest and on a per-female basis. Arguably, the most important analysis of the effects of brood parasitism should be conducted at the population level (e.g., Trail and Baptista 1993, Rogers et al. 1997). If brood parasitism is significantly decreasing the population growth rate (λ) below the level of a self-sustaining population, then active management may increase its probability of persistence.

We can test whether the effects of parasitism have been mitigated by management practices at Kern County. We analyzed the correlation between parasitism rates and the annual population growth rates for the Kern population of WIFLs. If parasitism is reducing population growth, we would predict a significant negative relationship between parasitism rates and population growth rates.

We used a standard demographic model to calculate population growth rates. The model makes the following assumptions:

1. Female reproduction is not limited by the availability of males, so it suffices to count only females (Caswell 1989).
2. There is no immigration or emigration of birds outside of the study area.
3. Mortality rates can be calculated as the return rates of banded birds.

We chose a pre-breeding model to include any possible effects of parasitism on (winter) adult survivorship within the same time step as the (summer) parasitism events. Heuristically, the model starts with the survey of adults at the end of May. In reality, some adult females do not arrive until mid-June (Whitfield, unpub data), but for the purposes of the model, all adults are treated as arriving by 1 June. Adults are categorized into two age groups: yearlings (Second-Year or SY) and older adults (After Second-Year or ASY). Both groups nest and raise young. At the end of the breeding season, the juveniles, yearlings, and adults migrate to their wintering sites. Those individuals that survive return as yearlings (SY) and older adults (ASY). The yearlings are those birds hatched the previous year at Kern. The older adults are now the returning SYs and ASYs of the previous year.

In this standard demographic model, there are four parameters that contribute to the population growth rates (Table 9-3):

(a) the reproductive rate of SY adults, or equivalently, the number of fledglings produced by SY adults multiplied by the return rate of the fledglings the next spring;

(b) the reproductive rate of ASY adults, or equivalently, the number of fledglings produced by ASY adults multiplied by the return rate of the fledglings the next spring;
(c) the survival rate of SY adults
(d) the survival rate of ASY adults

Banding data from 1990 to 1997 indicated that the average number of young fledged did not differ by parental age: SY fledged 1.65 yg (n=20) and ASY fledged 1.66 yg (n=29). We also assumed that the survivorship of fledglings to yearlings was the same regardless of parental age, thus simplifying the model so that a = b. We also did not distinguish between the survival rates of SY and ASY adults, so that c = d.

Note that our prebreeding model differs from postbreeding models (e.g., Stoleson et al., this vol). In our calculation of reproductive rates, the fledglings produced by adults must survive to the following June. In a postbreeding model, the reproductive rate of hatching-year birds (HY) is calculated. This reproductive rate is the product of two factors: a) fledgling survival to SY and (b) the mean number of fledglings produced during the following breeding season. In our prebreeding model, we never calculate a reproductive rate for hatching year birds because they do not reproduce until the time step in which they are adults. Instead, a reproductive rate is calculated for all adults (Table 9-3).

The overwinter survival of juveniles and adults were estimated from the data on banded birds, which yields minimum estimates of survival. The numbers of banded birds varied across years as did the field effort to resight birds. In general, the numbers and proportions of banded adults were higher for more recent years than at the beginning of the study. There was an increased field effort to resight and mark adult birds from 1994.

We used the survival and reproductive rates of females to calculate the annual population growth rate, λ. The simplification of a = b and c = d, we were able to calculate the population growth rate, λ, directly as $\lambda = a + c$.

We looked at the relationship between λ for each year (June to June) and the parasitism level of the breeding season (Jun-Aug). We used data from all years, including the six years of cowbird management. Cowbird management practices at Kern may reduce parasitism effects on individual basis, but may not eliminate all effects. A significant negative relationship between λ and the parasitism rate means that parasitism is affecting the population growth rate at Kern.

The growth rates of this WIFL population do tend to decrease with increasing parasitism rates (Fig. 9-4; linear regression analysis, $r^2 = 0.44$, $p=0.073$). Although the p value is slightly above 0.05, parasitism rates explain 44% of the variation in the annual population growth rates. This effect of parasitism rates on λ seems strong, especially considering that cowbird management occurred in 5 of 8 breeding seasons and that the statistical power of our analyses is low due to the small number of years. The slope of the best-fit line gives an indication of the benefit of reducing parasitism rates. For every drop of 0.10 (10%) in parasitism rates, lambda increases by 0.076 for this population.

Table 9-3. Life history parameters of one population of SWFLs in Kern County, California. Banding and nesting biology of SWFLs were used to calculate the population growth rate, Lambda. Rates are calculated for females only. We assumed that half of the banded fledglings were female. This number is parenthetically noted after juvenile survival rates. Rates for adult survival are calculated as the number of banded female adults which were resighted or recaught the following year. The means for all years and for years with cowbird trapping (1993-1996) are calculated separately.

Breeding Year	Female Fledglings per adult	Juvenile Survival Rate (banded female nestlings)	Female Adult Survival (banded adult females)	Reproductive Rate	λ
1989	0.57	0.38(8)	0.00(2)*	0.25	0.63
1990	0.48	0.09(11.5)	0.43(7)	0.05	0.47
1991	0.60	0.00 (4.5)	0.63(8)	0.00	0.63
1992	0.89	0.20 (10)	0.38(8)	0.17	0.55
1993	0.56	0.36(14)	0.54(13)	0.24	0.74
1994	1.00	0.27(17.5)	0.35(20)	0.25	0.62
1995	1.00	0.50(14)	0.42(19)	0.50	0.92
1996	1.27	0.59(19.5)	0.63(19)	0.74	1.39
Mean (All yrs)	0.67	0.30	0.42	0.28	0.74
Mean (Trap yrs)	0.96	0.43	0.49	0.41	0.90

*Neither of the two adult females banded in 1989 returned in 1990. Because of the low number of banded birds for 1989, we used the overall mean of 0.42 for adult survival rate to calculate lambda for 1989-1990.

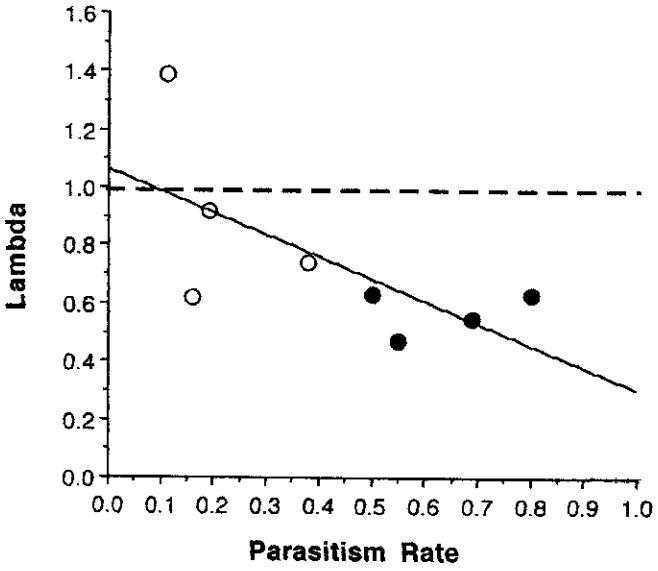

Figure 9-4. The population growth rates of the Kern population is significantly associated with parasitism rates. Solid circles represent years with no cowbird management (1989-1991) and open circles represent years with cowbird management (1993-1996).

The regression analysis suggests that the recovery of the Kern population ($\lambda \geq 1$) necessitates a very low parasitism level. The best-fit line for the data reaches a self-sustaining population ($\lambda = 1$) at the low parasitism rate of 8.4%, with population growth likely only to increase if parasitism levels are maintained below 8.4%. Note that the 8.4% parasitism rate is only a guideline, as it is based on data from a relatively small number of years.

Using this regression analysis, we produced guidelines for parasitism levels for a self-sustaining or recovering Kern population, assuming that the range of rates remain within the parameters for 1989-1997. For the years without cowbird management (1989-1991), the high levels of parasitism and subsequent low λ values indicate that the Kern population was not a self-sustaining population for those years.

The guidelines we have produced are applicable to the Kern population or a population with similar rates for survival and nesting success. Populations with different parameters of nesting success and overwinter survival will have different population growth rates for the same parasitism levels. We cannot compare survival rates because we are unaware of any data on survival rates in other WIFL populations. However, the range of nesting success of the Kern population appears comparable to other populations (cf. Stoleson et al., this volume). The nesting success for the Kern population from 1989-1997 ranges from 0.48 to 1.27 female fledglings per female (Table 9-3) or 0.96 to 2.5 fledglings per female. Stoleson et al. (this vol) report comparable values of 1.25-2.45 fledglings per female for other WIFL populations. One final analysis may indicate how responsive the Kern population would be to continued cowbird management.

Elasticity Analyses and Cowbird Management

The biology and data for rates of survival, reproduction, and parasitism show a pattern that warrants further analysis in planning the recovery of an endangered species. At Kern, parasitism rates have been lowered with cowbird management. Is continued management of cowbirds likely to contribute significantly to population recovery? An indirect answer to this question can be obtained using elasticity analysis of the data (e.g., Stoleson et al., this vol.). Elasticity values predict how a change in each parameter of our prebreeding model would affect the population growth rate.

Cowbird management may directly affect reproductive rates (along with other factors), but have less or no effect on the survival rates of adults. If survival rates are predicted to have a major effect on the population growth then continued cowbird management will have small effects on population growth. Conversely, if changes in reproductive rates of SY or ASY adults have large effects on population growth, then cowbird management as a means of enhancing reproductive success is an efficient option for recovery.

The results of the elasticity analyses support the findings by Stoleson et al. (this vol.) and the efficacy of cowbird management practices (Table 9-4). With no cowbird management, the reproductive rates were low (Table 9-3), and the strongest effect to a change in population growth rate was survival of adults. For example, from Jun 1989-Jun 1990, a 0.01 increase in population growth rates could be accomplished if ASY survival rates increased by 0.025. The elasticity measurements for 1991 show that with poor reproductive success, the population growth rate is most responsive to an increase in adult survivorship. In 1996, the elasticities were more evenly divided. An increase in any one parameter will have about the same effect on the population growth rate, although increasing reproductive success of SY adults will have the most beneficial effect on population growth.

However, cowbird management practices will likely affect reproductive rates of both age-classes simultaneously. When reproductive success is equivalent for females of both age-classes, then we can calculate the reproductive success necessary to produce a self-sustaining population using the mean values during active cowbird management (1993-1996). The overall lambda is 0.90 for the years with active cowbird

Table 9-4. Elasticities of the demographic parameters. From 1989-1991, no cowbird management was attempted. In 1992, selective cowbird shooting at the nest eliminated 21 female cowbirds. From 1993, cowbird traps were placed throughout the breeding and feeding areas.

Year	Parasitism Rate	Lambda	E(a)	E(b)	E(c)	E(d)
1989	0.50	0.67	0.11	0.22	0.22	0.44
1990	0.55	0.48	0.01	0.09	0.09	0.80
1991	0.80	0.63	0.00	0.00	0.00	1.00
1992	0.69	0.55	0.10	0.22	0.22	0.47
1993	0.38	0.78	0.09	0.21	0.21	0.48
1994	0.16	0.59	0.17	0.24	0.24	0.35
1995	0.19	0.92	0.30	0.25	0.25	0.21
1996	0.11	1.37	0.29	0.25	0.25	0.21

management (Table 9-3). This indicates that even with the high survival and reproductive rates recorded for these years, this population needs to increase either productivity or overwinter survival to persist over the long term. A self-sustaining population with cowbird trapping requires a 10% increase in λ or assuming adult survival rates remain constant, then the overall reproductive rate of 0.51 will allow this population to become self-sustaining. Because reproductive rates are the product of nesting success and return rates of fledglings of the previous season and assuming that return rates of fledglings are not amenable to cowbird management, then, on average, a self-sustaining population at Kern requires 1.18 female fledglings per female or an average nest success of 2.36 yg per female. On average, any increase over 2.36 yg per female will contribute to population recovery.

Summary

The brown-headed cowbird parasitizes nests of the southwestern willow flycatcher (*Empidonax traillii extimus*). The main breeding season of cowbirds (May to mid-July) overlaps with the initial nesting period of southwestern willow flycatchers (Jun-Aug). Parasitism rates of willow flycatchers tends to be high, possibly because of the forest structure and landscape influences in current nesting areas. Parasitism rates vary with cowbird abundance, across years, and at different sites. The effect of parasitism on willow flycatchers can depend on many factors: cowbird abundance, the overall parasitism rate of nests, the timing of cowbird parasitism, and the events subsequent to parasitism, e.g., cowbird egg burial, nest desertion, renesting, and predation.

For one central California population of southwestern willow flycatchers, we have documented the effects of cowbird parasitism on a per nest, per female, and population basis. About 1/3 of parasitized nests reached the stage where cowbirds hatched, the stage which is considered to lead to the highest reproductive loss for flycatchers. Of the nests in which cowbirds hatched, 41% fledged cowbirds. Flycatcher response to parasitism, however, ameliorated the effects of parasitism in about half of all parasitized nests.

Per individual female, the major effects of parasitism were to delay nesting, decrease hatchability of flycatcher eggs in parasitized nests and decrease clutch size either because of removal by cowbirds or later clutches tend to be smaller. Except for decreased hatchability, these effects have been documented throughout the range of willow flycatchers. Due to the small but cumulative effects of parasitism, the annual reproductive success of females is influenced by parasitism, if parasitism is the major cause of nest failure for that year.

For one population in Kern County, California, increasing parasitism rates decreases population growth rates. Parasitism can explain 44% of the variation in population growth rates. Our analysis shows that parasitism rates must be low for this population to persist or increase. Given the life history parameters at Kern, population growth may be dependent on active cowbird management to decrease the effects of parasitism. In order for this population to become self-sustaining or increase, females need to fledge an average of 2.4 young. We provide evidence of the detrimental effects of parasitism on southwestern willow flycatcher recovery and document the extent of the benefits of cowbird management. Although our conclusions are based mainly on one population of WIFL, this population appears to be similar enough to others that our conclusions may apply to other populations as well.

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