IMPORTANCE OF PREDATION AND BROOD PARASITISM ON
NEST SUCCESS IN FOUR SPARROW SPECIES IN SOUTHERN
CALIFORNIAN COASTAL SAGE SCRUB

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Abstract. Current knowledge of Brown-headed Cowbird (Molothrus ater) parasitism rates in nests
of resident southern Californian Coastal Sage Scrub (CSS) birds has been limited to studies of the
California Gnatcatcher (Polioptila californica), a frequent cowbird host. Therefore, I located nests of
the four most abundant potential host species to determine the occurrence and impact of parasitism
on CSS species other than the gnatcatcher. I then explored the potential impact of parasitism on CSS
hosts using a seasonal-fecundity model that accounts for both predation and parasitism. The effects
of parasitism were minimal: only 3 of 217 nests were parasitized. However, host breeding phenology
was shown to differ significantly from cowbird breeding activity, suggesting that the potential for
parasitism in CSS birds is often low. In addition, high nest predation rates appear to minimize the
effects of what parasitism does occur. Thus management activities for CSS species may be better
focused at processes other than cowbird control.

Key Words: Aimophila ruficeps, Amphispiza belli, California Towhee, coastal sage scrub, Molothrus
ater, nest predation, phenology, Pipilo crissalis, Pipilo maculatus, Rufous-crowned Sparrow, Sage
Sparrow, Spotted Towhee.

Nest predation and brood parasitism are two
principal determinants of reproductive success
in many passerine birds (Ricklefs 1969, Martin
1987). Both processes have been shown to affect
host reproductive success and population dy-
namics (Martin 1987, Trail and Baptista 1993),
and population declines in many North Ameri-
can songbirds have been attributed to these pro-
cesses (Terborgh 1989). However, rates of nest
predation and parasitism are frequently intercor-
related, and the identification of their relative ef-
fects on nesting success is important both in an
evolutionary context, to identify principal selec-
tion pressures, and in practical application, to
appropriately direct management activities
aimed at conserving avian populations that may
be adversely impacted by these processes.

Coastal Sage Scrub (CSS) is a vegetation type
dominated by drought deciduous shrubs that oc-
curs along the California coast from the San
Francisco Bay area, south to Baja California,
Mexico (Westman 1983). CSS in southern Califor-
nia is bordered by the Coast and Pen-
insular ranges. Historically CSS occurred in
large contiguous patches. Today, however, CSS
is highly fragmented by agriculture and urban-
ization, with few intact patches greater than 500
ha remaining (Westman 1981, 1983; O’Leary
1990). Such fragmentation may alter predator
population dynamics (Soulé et al. 1992) as well
as facilitate access by the brood parasitic Brown-
headed Cowbird (Molothrus ater) (Rothstein et
al. 1980).

Fragmentation is thought to result in height-
ened nest predation rates by increasing edge-to-
to-area ratios. A majority of studies (14 of 21 re-
viewed) have shown positive associations be-
tween edge and higher nest predation rates (Pa-
ton 1994). Because fragmentation may provide
less area of adequate habitat for large-bodied
predators (Soulé et al. 1992), a reduction in the
abundance of large predators may result in the
proliferation of medium-sized nest predators,
thereby resulting in elevated nest predation (Wil-

Brown-headed Cowbirds first began breeding
in southern California sometime in the 1900s
(Laymon 1987), and cowbird populations have
since steadily increased within portions of this
region as indicated by 1966–1996 Breeding Bird
Survey data (Sauer et al. 1997). In addition,
cowbird parasitism has been shown to have re-
duced some host populations within the region
(Laymon 1987). Brood parasitism, therefore,
represents a novel source of reproductive loss
for the host species in this region.

I conducted a two-year study on the relative
effects of brood parasitism and nest predation in
four resident sparrow species in southern Cali-
fornia CSS. Moderate cowbird parasitism has
been documented in nests of the California
Gnatcatcher (Polioptila californica), a resident
of CSS. Therefore, to determine the impact of
cowbird parasitism on other resident CSS spe-
cies, I studied nests of the four most abundant
potential host species in southern Californian
CSS. A study of cowbird host-use in CSS was
desirable as cowbirds are known to acquire and
frequently parasitize new host species, and be-
cause parasitism levels on common species are
known to vary geographically (Friedmann and
Kiff 1985). Recent records of parasitism in sage-
brush vegetation have been attributed to fragmentation and thus, increased cowbird access to an environment previously rarely used (Friedmann and Kiff 1985). Specifically, I wished to determine whether Brown-headed Cowbirds impact host nest success in this vegetation type beyond the effects of nest predation on hosts. In addition to comparing the relative impact of each process to nest success, I also explore the potential effect of each process on population dynamics, under measured and hypothetical conditions, using a model of seasonal fecundity (Pease and Grzybowski 1995).

METHODS

My study was conducted during the breeding seasons of 1996–1997 at the University of California Motte Rimrock Reserve, a typical remnant 250-ha CSS patch located near Perris, Riverside County, California. The areas surrounding the reserve consisted largely of small ranchette homesteads, lightly grazed grassland, and agricultural fields. To assess nest predation and parasitism I followed nest fates of the four most abundant species on the site known to be parasitized by cowbirds.

I conducted 7-min, 50-m fixed-radius point counts during both years to determine the relative abundance of cowbirds and potential host species. Counts were conducted at 15 points located along two transects at 140-m intervals. In addition, I recorded observations of any cowbirds detected outside of point count periods. Female cowbird detections in CSS were assumed to be correlated with breeding activity as all detections occurred prior to noon, females were observed to be actively searching for nests, and because of the absence of cowbird feeding areas limited by the time remaining for nesting prior to the end of the breeding season. Renesting is accomplished through continuous-time equations, modified by renesting parameters, which are accounted for by mathematically tracking the number of females at different stages of the breeding season and nesting cycle. This is accomplished through continuous-time equations, which are used to compute a daily fraction of females that are at a given day of the nesting cycle, and the daily probabilistic fates of each nest. The rate at which females fledge young from nests of both fates (parasitized and unparasitized) is combined with fate-dependent productivity parameters for all nests. This information is then incorporated with the onset and length of the breeding season to produce an estimate of seasonal fecundity. To assess their relative effects on host productivity, I entered observed brood parasitism and predation rates, and
the observed duration of each nest stage for each species into the model.

To measure the impact of parasitism on seasonal fecundity, I generated seasonal fecundity estimates for both species I found to be parasitized at my site (California Towhee and Sage Sparrow) under observed conditions and compared them to estimates generated without parasitism. To determine the hypothetical effects of significantly higher parasitism levels than observed, I estimated seasonal fecundity assuming a 50% rate of nests parasitized.

**PARAMETER ESTIMATION**

**Predation**

Active nests are continuously exposed to nest predation throughout a nest cycle; therefore, the susceptible period to predation is equivalent to the length of each species nest cycle. Since intervals between nest checks were often as much as 4 and 5 days, I obtained daily nest predation rates using the maximum-likelihood estimation program developed by Pease and Grzybowski (1995). The maximum-likelihood method avoids potential biases associated with the assumption that nest fate changes occur at the midpoint of nest-check intervals. Daily predation rates obtained were then used to calculate overall probability of nest survival.

**Parasitism**

Since many resident birds typically breed earlier than Brown-headed Cowbirds in southern California (Bent 1968, Finch 1983, Lowther 1993, Braden et al. 1997b), it was necessary to calculate parasitism rates based on host nest availability coincident with cowbird presence. Thus, brood parasitism rates were obtained by dividing the number of parasitized nests by the total number of observed nest-days available to laying cowbirds. To define this period, I used the criteria that cowbirds in CSS do not lay until mid-April (Braden et al. 1997b), and that normally parasitism occurs within the first 6 days of the host nesting cycle (Pease and Grzybowski 1995). The six-day window of opportunity for brood parasitism was thus set to encompass the day before a first egg was laid and the following five days. Therefore, nest-days available to cowbirds represent the sum of days during the six-day window of susceptibility to parasitism for each nest initiated after 15 April.

**Time windows**

Each species' breeding season length was measured as the difference between the earliest and latest first egg dates. Nest stage durations were estimated from nest check observations, back-dating based on clutch size (assuming one egg was laid per day), and age estimation of young (based on multiple observations of young of different known ages). Limited data on re-nesting after successfully fledging young suggested a refractory period of 7–21 days; therefore I used the 10-day period suggested by Pease and Grzybowski (1995).

The model also requires an estimate of number of young fledged per nest; this was problematic for 1996 data due to the small number of successful nests. Therefore, to estimate the 1996 productivity per nest values, 1996 clutch sizes were compared with 1997 clutches and any significant differences were adjusted by reducing 1997 productivity estimates by the ratio of eggs laid. Productivity of parasitized nests was set at one young, based on the value used in Pease and Grzybowski (1995), as I have no information on the number of host young fledged in parasitized nests of these species.

**RESULTS**

**EMPIRICAL RESULTS**

**Breeding phenology**

Annual rainfall in inland CSS is highly seasonal, with virtually all precipitation occurring from September through April. Although total precipitation was essentially the same in both seasons of the study, the cumulative precipitation curve for 1996–1997 was shifted about one month earlier compared to that for 1995–1996 (Fig. 1). Onset and duration of host breeding season were likewise shifted and differed significantly between years (Table 1). The 1996 season was shortened by intense heat and drought, resulting in season lengths ranging from 30 to 61 days across the species studied. In contrast, 1997 temperatures were milder and periods of rainfall were more evenly dispersed (E. Konno, unpubl. data), and thus individual species season lengths were prolonged to 46–81 days (Figs. 1, 2). The 1997 breeding season was initiated an average of 36 days earlier than in 1996; 1996 nesting began in late March, whereas 1997 nesting started in mid-February (Table 1). 1997 breeding duration was an average of 26 days longer per species than the 1996 season.

**Nest predation**

Nest predation rates were relatively high in CSS. Nest predation accounted for 91% of 140 failed nests across all species. In 1996 (the shorter season), nest success rates ranged from 17% to 36% across the four species studied; in 1997 (the longer season), nest success was between 28% and 44% (Table 2).

Depredated nest conditions ranged from
clutch reduction of one egg to complete nest destruction. A total of 84 nests was empty with cup intact, 33 were empty and disturbed, four had damaged eggs, three were directly observed to be depredated by snakes, and three exhibited a loss of one egg.

Nests were initiated throughout the duration of each breeding season (Fig. 2). Multiple nests (associated with banded birds or birds whose territory was known) were found each season. Two California Towhees were observed constructing subsequent nests while still feeding young at prior nests. Several Rufous-crowned Sparrows were observed to attempt three nests and some pairs successfully fledged two broods. In two cases, Sage Sparrows attempted second nests after fledging young. Multiple nest attempts by Spotted Towhees were detected in response to predation; however, no nest attempts were observed after a successful nest (although they are known to raise multiple broods; Greenlaw 1996).

**Cowbird detection**

Female cowbird detection rates varied from 0.24 females/day in 1996 to 0.88 females/day in 1997. Female cowbirds were detected early to mid-mornings throughout each breeding season. Cowbird breeding activity dates were similar between years, although median activity dates differed significantly (Wilcoxon's Z = 2.23, P = 0.026). However, the cumulative cowbird detec-

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**TABLE 1. 1996 AND 1997 BREEDING SEASON INITIATION DATES (AND DURATION IN DAYS) BASED ON FIRST EGG DATES OF NESTS LOCATED FOR FOUR SPECIES OF COASTAL SAGE SCRUB SPARRWS IN WESTERN RIVERSIDE COUNTY, CALIFORNIA**

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<td>California Towhee</td>
<td>16 April to 17 May</td>
<td>19 Feb to 27 Apr</td>
<td>36</td>
<td>57</td>
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<td>Rufous-crowned Sparrow</td>
<td>25 Mar to 25 May</td>
<td>24 Feb to 4 May</td>
<td>20</td>
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<td>Sage Sparrow</td>
<td>14 Apr to 18 May</td>
<td>10 Mar to 18 May</td>
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<td>Spotted Towhee</td>
<td>17 Apr to 16 May</td>
<td>24 Mar to 10 May</td>
<td>16</td>
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<td>Average duration</td>
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FIGURE 2. 1996 (top) and 1997 (bottom) sparrow species breeding phenology by first egg dates and female cowbird detections in coastal sage scrub in western Riverside County, California. The mid-point in cumulative frequency represents the peak in sparrow breeding/female cowbird detections.

Parasitism

Of nests located in 1996, 374 nest-days distributed among 62 nests were susceptible to cowbird parasitization (i.e., their vulnerable stage overlapped the presence of cowbirds at the site). Since two parasite eggs were found in two host nests, the parasitism rate for nests of that period was 3.2%. In 1997, host nest availability after 15 April was 188 nest-days (31 nests); with one nest parasitized, the 1997 parasitism rate was also 3.2% of available nests.

Three of the total of 217 nests discovered were parasitized; one of 14 California Towhee nests and one of 30 Sage Sparrow nests were parasitized in 1996, and one of 50 California Towhee nests was parasitized in 1997. Of the three nests parasitized, the two California Towhee nests were subsequently depredated, and
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the Sage Sparrow nest was abandoned (0.7% of all nest failure). No clutch reduction by cowbirds was detected. Additionally, no cowbird fledglings were detected in either year.

SEASONAL FECUNDITY ESTIMATES

I used the season length, productivity per nest, and clutch size data obtained on each species (Table 2) to estimate seasonal fecundity. The time window for susceptibility to predation ranged from 24 to 27 days. Abandonment was detected in 13 nests, and accounted for 9.3% of nest failure. Abandoned unparasitized nests were treated as depredated, as nests abandoned represent a similar detriment to productivity and result in renesting. Only the one aforementioned parasitized Sage Sparrow nest appeared to have been abandoned in response to cowbird activity. Spotted Towhee 1996 clutch sizes were significantly smaller than those in 1997 (one-tailed t-test, P < 0.02). As a result, the 1996 productivity estimate was calculated by reducing 1997 productivity per nest by the ratio of clutch sizes (Table 2).

All 1997 seasonal fecundity estimates were greater than those based on 1996 rates (Table 2). In 1996, California Towhee and Sage Sparrow estimates were below the productivity levels required to maintain replacement level reproduction (≥ 2.0 young/pair/season). In contrast, all species seasonal fecundity estimates were above 2.0 young/pair/season in 1997.

Varying only the parasitism rate, with all other 1996 California Towhee parameters held constant, seasonal fecundities were 1.46 young/pair/season with no parasitism, 1.35 young/pair/season at the observed parasitism rate, and 1.02 young/pair/season with a 50% parasitism rate. Therefore, observed reproductive loss to parasitism was a 7.5% decrease in seasonal fecundity. If 50% of nests had been parasitized, a 24.4% decrease in seasonal fecundity would have resulted. Repeating the process with 1997 California Towhee parameter values resulted in estimates of 4.22 young/pair/season with no parasitism, a 4.0% decrease at observed parasitism rates, and a 27.4% reduction at 50% parasitism.

Sage Sparrow fecundity modeled at the predation levels measured in 1996 resulted in seasonal fecundity estimates of 1.85 young/pair/season with no parasitism, 1.60 young/pair/season at observed level of parasitism (−13.5%), and 1.29 young/pair/season at 50% parasitism (−19.4%). At 1997 predation levels, seasonal fecundity in the absence of parasitism was 3.22 young/pair/season, and if 50% of nests were parasitized, 2.25 young/pair/season (−30.1%). For both towhees and sparrows, observed levels of parasitism did not result in fecundity estimate
differences in excess of $-0.25$ young/pair/season.

The sensitivity analysis revealed daily predation rate is the dominant and more sensitive parameter in the calculation of seasonal fecundity values (Fig. 3). The predation axis slope is greatest and the effect is across the resultant surface generated by the matrix of parameters.

DISCUSSION

SEASONAL FECUNDITY ESTIMATION

Comparison of estimates of seasonal fecundity based on observed parasitization rates for California Towhee and Sage Sparrow to estimates generated with parasitism set to zero demonstrated a minimal loss of seasonal fecundity due to parasitism. It appears that parasitism did not occur at levels of biological significance. The potential impact of parasitism on seasonal fecundity was minimized by high nest predation and extended season length. Seasonal fecundity was more sensitive to predation over the range of parasitism levels I observed (Table 2, Fig. 3), yet this relationship was most likely a factor of the amount of breeding season overlap with cowbirds, season length, and, to a lesser degree, the level of brood reduction associated with rearing parasite young.

Increased season length raises average seasonal fecundity by improving an individual's likelihood of successfully nesting. As season length increases, the interaction between parasitism and predation weakens (Grzybowski and Pease, in press). This occurs due to the increased number of nesting attempts, which reduce the chance nests will be both parasitized and depredated. Therefore, season length directly affects seasonal fecundity as it affects the number of renesting attempts possible.

Between-year fecundity varied greatest in the California Towhee, ranging from $1.49$ to $4.05$ young/pair. This variation was associated with varied season length and quite different levels of predation. Clearly, seasonal fecundity is lowest when season length is short, yet factors of food abundance and quality of vegetation for cover must also play a role in this system. Such variation in avian productivity appears to be common in arid environments as suggested by several studies (Grant and Boag 1980, Rotenberry and Wiens 1980, Carter 1986, Newton and Newton 1997).

CLIMATE AND PHENOLOGY

CSS plants are drought-adapted and sensitive to climatic variation (Minnich 1985), with a corresponding variation in avian breeding season initiation and length. During my study, both
peak rainfall and sparrow breeding exhibited a corresponding five-week shift between 1996 and 1997 (Figs. 1, 2). A similar relationship has been found in the California Gnatcatcher (which also nests on the site), in which males began pre-nuptial molt six to seven weeks after the first significant winter rain (K. Preston, pers. comm.). In addition to variation in the time available for nesting, the variation in nest initiation dates most likely induces variation in both nest predation and parasitism levels. For instance, snakes, a major nest predator, were not as active in February 1997 when many birds were initiating nests (K. Ellison, pers. obs.). Whatever the mechanism, nest predation was 22% higher on nests initiated during the first month of the 1996 breeding period than on nests of the first month of 1997 (the early season).

Although the consequences of a 21–57 day shift in breeding season initiation date may include subtle differences in predation, one can easily envision changes in predator impact during more dramatic changes. Five weeks following Hurricane Nora, which passed through northern Baja California, Mexico, in September 1997, several CSS passerine bird species nest were observed in breeding condition (with brood patches and enlarged testes) and an active California Towhee was discovered outside of normal reported nest season dates (P. Unitt, pers. comm.). Although such events are likely infrequent, these observations support the hypothesis that CSS birds will breed opportunistically. Such variation presumably results in exposure to quite different predator abundances and/or predation levels.

Predation rates measured in CSS (Braden et al. 1997a,b; K. Preston and S. Morrison, pers. comm.; this study) are relatively high compared to those commonly reported for passerine birds in other habitat types (Ricklefs 1969, Martin 1992). The levels of predation and variation in depredated nest appearance likely reflect the high diversity of potential nest predators present in CSS.

**Parasite-Host Asynchrony**

The parasitism rates I recorded ranged between 1.8% and 6.9% of susceptible nests during the six-day window to parasitism among nests of the four most abundant potential host species at the site. There are several reasons for the apparent low levels of parasitism detected at the Motte Reserve. Foremost is the seasonal variation in dates of host breeding initiation and duration. As cowbirds do not appear in CSS until mid-March, and as the first cowbird eggs do not appear until mid-April, host species often are free from exposure to parasitism for at least one complete nesting cycle. It is apparent that cowbirds lag behind the peak in host nest availability on my site (Fig. 2). This lag was especially apparent in 1997, presumably due to the earlier season initiation by sparrows and towhees in that year (Fig. 2). The midpoint of female cowbird detection lagged 3 to 4 weeks after the peak in host nesting, and nest availability after 15 April was 188 nest-days. In 1996, cowbird detections more closely tracked host nest availability and of the nests located in 1996, 374 nest-days were available during cowbird laying. Despite greater nest availability in 1996, at the midpoint of cowbird breeding, as measured by cumulative number of detections, cowbirds were left with around two weeks to deposit their eggs (Fig. 2).

My data suggest that cowbirds are not able to track the initiation of host nesting in CSS. The lack of synchrony in host and cowbird breeding seasons appears to be due to the variation in host breeding dates (presumably in response to variation in rainfall), combined with apparently less flexible cowbird breeding dates. In this case, cowbirds may simply not be able to synchronize their breeding season with a majority of hosts in CSS.

In southern California resident cowbird flocks spend the non-breeding season in agricultural areas largely associated with dairy cattle and feedlots, which may lie at considerable distance from breeding areas. Presumably cowbirds utilize a mixture of cues, such as day length, host song, and/or migration of hosts or congeners to initiate breeding season movements. Several such cues may be advantageous throughout historic cowbird breeding range, yet not as adaptive in southern California, where cowbirds may be relatively isolated from hosts, which, in turn, respond to different cues that may vary in timing between years. However, resident bird breeding seasons tend to be extended in this region, thus reducing selection on cowbirds to initiate breeding coincident with the onset of host nesting.

Nest success in the resident sparrows studied was largely determined by nest predation levels; parasitism rates were relatively low, around 3.2%. However, a higher incidence of parasitism (48.1% of 27 nests) has been observed for California Gnatcatchers breeding at this site (Braden et al. 1997b). This is likely due to several factors: (1) gnatcatchers are small-bodied hosts, as preferred by Brown-headed Cowbirds (King 1979, Peck and James 1987); (2) their nests are easily located; and (3) they have a prolonged breeding season (February–July) (Braden et al. 1997b).
CONCLUSIONS

Whether the observed predation levels reflect impacts of fragmentation is unknown due to the lack of nest predation data from larger, more contiguous areas of CSS. Further questions have been raised as fragmentation studies in the West have found parasitism and predation rates to be higher in unfragmented habitat (Langen et al. 1991, Tewksbury et al. 1998), whereas many studies primarily in the Mid-West have demonstrated both processes to increase in habitat fragments (Robinson 1992; reviewed by Paton 1994). Nonetheless, several studies have found that fragmentation of southern Californian chaparral is associated with a rapid disappearance of bird and rodent species (Soulé et al. 1988), suggesting that processes associated with the negative effect of fragmentation cannot be generalized across broad geographic areas.

Cowbird trapping is not nearly as complex as attempting to restore predator populations to more natural levels. However, I think it is apparent that cowbird control at my site would have had a minimal impact on host seasonal fecundity. Before initiating a cowbird trapping program, my recommendation to CSS land managers would be to monitor host nesting initiation dates and cowbird numbers. This could be achieved simply through point counts, for a fraction of cowbird trap maintenance costs. If sparrow nesting seasons were retarded due to weather conditions, cowbird trapping might then be deemed necessary. Thus, knowledge of winter rainfall patterns (a predictor of avian breeding initiation dates) and its associated potential for a temporal refuge from reproductive loss to parasitism could enable managers to appropriately focus trapping funds and efforts to better conserve avian populations on a year-to-year basis.

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