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 bellii, 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 dynamics (Martin 1987, Trail and Baptista 1993), and population declines in many North American songbirds have been attributed to these processes (Terborgh 1989). However, rates of nest predation and parasitism are frequently intercorrelated, and the identification of their relative effects on nesting success is important both in an evolutionary context, to identify principal selection 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 occurs along the California coast from the San Francisco Bay area, south to Baja California, Mexico (Westman 1983). CSS in southern California is bordered inland by the Coast and Peninsular ranges. Historically CSS occurred in large contiguous patches. Today, however, CSS is highly fragmented by agriculture and urbanization, 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 heightened nest predation rates by increasing edge-to-area ratios. A majority of studies (14 of 21 reviewed) have shown positive associations between edge and higher nest predation rates (Paton 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 (Wilcove 1985, Soulé et al. 1988).

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 reduced 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 California 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 species, 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 because 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 acces⁻ to an environment previously rarely used (Fi..·dmann and Kiff 1985). Specifically, I wisheu to determine whether Brown-headed Cowbirds im.act host nest success in this vegetation type be·ond 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 within the CSS at my site.

The site had a known history of cowbird parasi ⁻m on the California Gnatcatcher, and trapping efforts in 1994 resulted in the capture and rei·⁻val of 42 cowbirds (19 of which were females) (Braden et al. 1997b; R. L. McKernan, pers. comm.). No trapping was conducted in any other year at the Motte Reserve (Braden et al. 1997b).

I studied the California Towhee (*Pipilo crissalis*), Spotted Towhee (*Pipilo maculatus*), Sage Sparrow (*Amphispiza bellii*), and Rufouscrowned Sparrow (*Aimophila ruficeps*). The four host species were found to be the four most abundant species detected during 34 point counts at my site. These species are also among the most common potential hosts in CSS regionally; California Towhee, Spotted Towhee, Rufous-crowned Sparrow, and Sage Sparrow were detected at 94%, 90%, 57%, and 24% of 155 CSS point counts throughout Southern Califor-

nia (M. K. Chase et al., unpubl. data). All four species are known cowbird hosts (Friedmann and Kiff 1985). However, there are few recent nest records for these species in southern Californian CSS, where current studies have documented fairly frequent parasitism in nests of other species (Braden et al. 1997b).

I located nests of the four potential host species through repeated visits to territories, following individuals, and opportunistic discovery. Emphasis was placed on locating nests while under construction to ensure the detection of any cowbird eggs before host abandonment occurred. Nest contents were checked every 1 to 5 days. To minimize observer-impact on nest predation, nest contents were checked using a 1.5-m pole with a mirror attached. The condition of each depredated nest was recorded in an attempt to identify broad categories of nest predators. Depredated nest categories included tilted or disturbed nest, undisturbed and empty nest and nestcup, and damaged eggs, which may represent predation by medium-sized mammals, snakes, and birds or small mammals, respectively (Bergin et al. 1997).

Each species' seasonal onset and duration of breeding was compared between years using a Wilcoxon rank sum test. Similarly, I compared the dates of female cowbird detection and host breeding dates.

SEASONAL FECUNDITY MODEL

The Pease and Grzybowski (1995) model estimates seasonal fecundity based on rates of nest predation, parasitism, host response to parasitism, period of susceptibility to both predation and parasitism, and number of young fledged. Nest fate probabilities are fit into time windows of the nesting cycle during which they may occur. The cumulative probability is then further modified by renesting parameters, which are limited by the time remaining for nesting prior to the end of the breeding season. Renesting is 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 fat s of each nest. The rate at which females flecge young from nests of t ₀th 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 renesting 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).

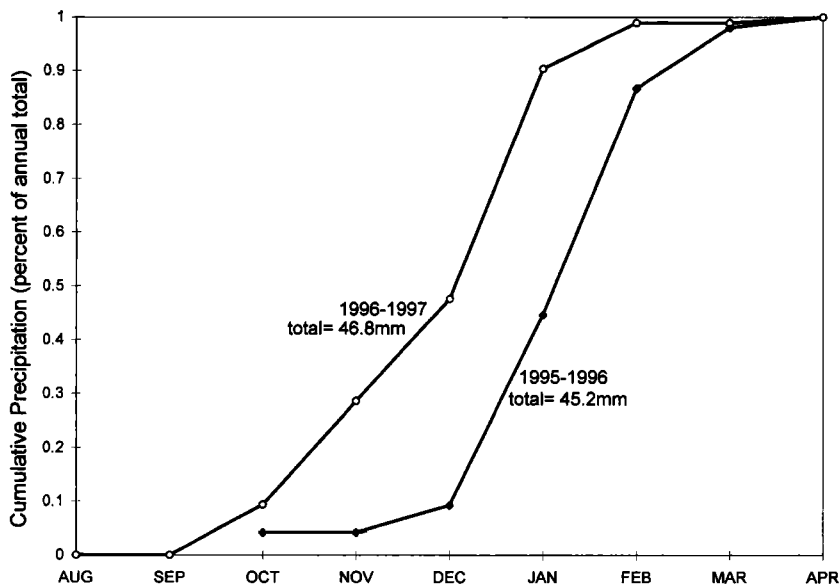Depredated nest conditions ranged from

FIGURE 1.   Proportional monthly cumulative rainfall at the University of California Motte Rimrock Reserve (1995–1997).

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-

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 SPARROWS IN WESTERN RIVERSIDE COUNTY, CALIFORNIA

|	First egg dates		Season length difference (1997–1996)	Initiation date difference (1997–1996)	Wilcoxon 2-sample Z P > |Z|
	1996	1997			
California Towhee	16 April to 17 May (32)	19 Feb to 27 Apr (68)	36	57	<0.001
Rufous-crowned Sparrow	25 Mar to 25 May (61)	24 Feb to 4 May (81)	20	30	0.018
Sage Sparrow	14 Apr to 18 May (34)	10 Mar to 18 May (68)	34	34	<0.001
Spotted Towhee	17 Apr to 16 May (30)	24 Mar to 10 May (46)	16	21	<0.001
Average duration	39	66	27	36	—
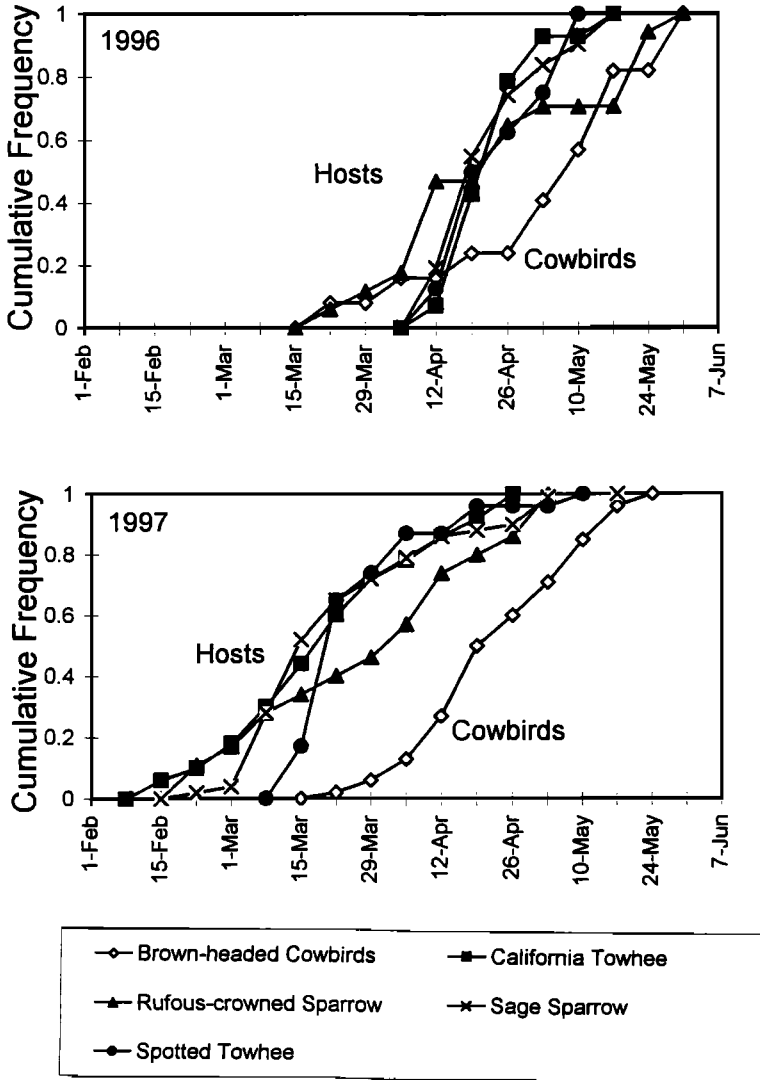
FIGURE 2. 1996 (top) and 1997 (bottom) sparrow species breeding phenology by first egg dates and female cowbird detections in coastal sage scrub in western Riverside County, California. The mid-point in cumulative frequency represents the peak in sparrow breeding/female cowbird detections.

tion frequency differed from host laying seasons in duration and onset (Fig. 2) and median female cowbird detection dates differed significantly from the median first egg date of all hosts combined in each year (1996: Wilcoxon's $Z = 2.71$, $P = 0.007$; 1997: Wilcoxon's $Z = 7.99$, $P < 0.001$).

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

TABLE 2. LIFE-HISTORY PARAMETERS (N = 217 NESTS) USED IN SEASONAL FECUNDITY ESTIMATION FOR SPARROWS IN COASTAL SAGE SCRUB IN WESTERN RIVERSIDE CO., CALIFORNIA (1996–1997)

	California Towhee		Rufous-crowned Sparrow		Sage Sparrow		Spotted Towhee	
	1996	1997	1996	1997	1996	1997	1996	1997
Season length (days)	32	68	61	81	34	68	30	46
Fledglings/successful nest	—[a]	2.65	—[a]	3	—[a]	2.7	2.6[b]	3.4
Daily parasitism	0.012	0.003	0	0	0.005	0	0	0
Maximum likelihood estimated daily predation	0.068	0.032	0.040	0.044	0.053	0.048	0.048	0.046
Nest success (%)	16.9	44.0	36.3	34.0	23.1	27.8	30.6	32.3
Average clutch size (N)	3.00 (14)	3.12 (49)	3.18 (17)	3.18 (16)	3.07 (14)	3.22 (23)	2.88 (8)	3.74 (23)
Estimated seasonal fecundity # of young/pair/season	1.35	4.05	3.98	4.86	1.60	3.22	2.28	3.23

[a] Sample too small; 1997 estimates used as no significant difference was found between 1996–97 clutch sizes (two-tailed t-test: California Towhee $P > 0.55$; Rufous-crowned Sparrow $P > 0.97$; Sage Sparrow $P > 0.42$).
[b] Estimate generated by reducing 1997 value by ratio of 1996: 1997 clutch size.

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
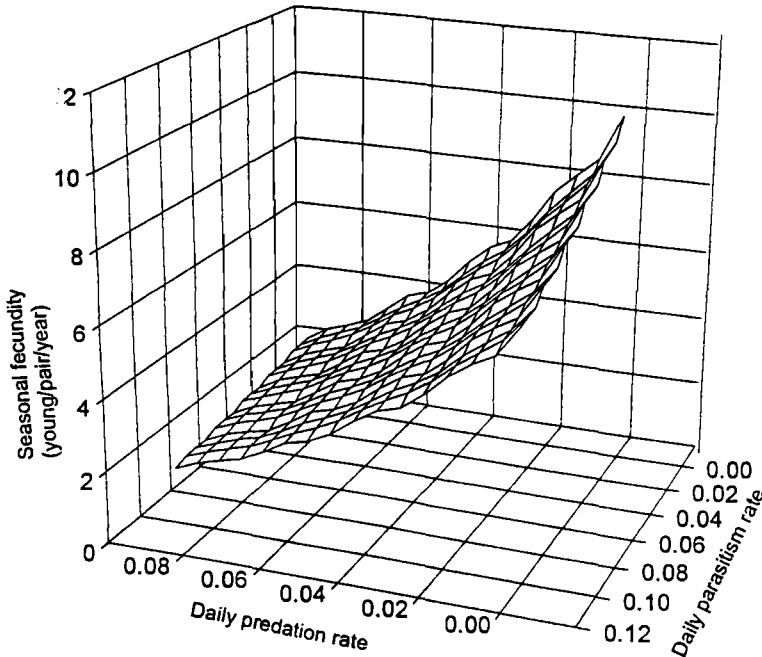
FIGURE 3. Sensitivity of seasonal fecundity estimates to variation in parasitism and predation rates. A 50% parasitism rate is comparable to a daily rate of 0.11.

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 effects 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 pre-dation and parasitism levels. For instance, snakes, a major nest predator, were not as active in February 1997 when many birds were initi-ating 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 in-clude subtle differences in predation, one can easily envision changes in predator impact dur-ing more dramatic changes. Five weeks follow-ing 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 Cal-ifornia Towhee was discovered outside of nor-mal reported nest season dates (P. Unitt, pers. comm.). Although such events are likely infre-quent, 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 be-tween 1.8% and 6.9% of susceptible nests dur-ing 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 un-til 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 cow-birds lag behind the peak in host nest availability on my site (Fig. 2). This lag was especially ap-parent in 1997, presumably due to the earlier season initiation by sparrows and towhees in that year (Fig. 2). The midpoint of female cow-bird 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 de-tections more closely tracked host nest avail-ability 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 vari-ation 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 ar-eas largely associated with dairy cattle and feed-lots, 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 cow-bird breeding range, yet not as adaptive in south-ern California, where cowbirds may be relative-ly isolated from hosts, which, in turn, respond to different cues that may vary in timing be-tween years. However, resident bird breeding seasons tend to be extended in this region, thus reducing selection on cowbirds to initiate breed-ing 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 Cal-ifornia Gnatcatchers breeding at this site (Bra-den 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.