species then incubates the cowbird eggs, which typically hatch prior to the host's own eggs. Cowbird eggs require a relatively short incubation period of 10 to 12 days. Thus, the young cowbirds have several advantages over the host's young; they hatch earlier, they are larger, and they are also more aggressive than the host's young. Cowbird nestlings typically outcompete those of the host species for parental care, and, as a result, the host species' own reproduction is reduced or eliminated (Bent 1965, McGeen 1972, Mayfield 1977a, Harrison 1979, Brittingham and Temple 1983).

The brown-headed cowbird commonly preys on insects stirred up by grazing ungulates, and was originally restricted to the Great Plains, where it was strongly associated with American bison (Bison bison). As North America was settled, cowbirds became associated with livestock and human agriculture because of the food sources they provided (Bent 1965, Flett and Sanders 1987, Valentine et al. 1988). The expansion of agriculture, livestock grazing, and wide scale human activities in general caused opening and fragmenting of forest and woodland habitats. Habitat fragmentation and agriculture are strongly correlated with increased rates of brood parasitism by brown-headed cowbirds (Rothstein et al. 1980, Brittingham and Temple 1983, Airola 1986, Robinson et al. 1993). Some species are likely to have adapted to parasitism over time, particularly prairie nesters in the original range of the cowbird. However, the cowbird's rapid expansion now brings it into contact with forest and woodland species not adapted to deal with brood parasitism, significantly impacting those species (Hill 1976, Mayfield 1977a, Robinson et al. 1993).

The brown-headed cowbird was apparently an uncommon bird within the range of *E. t. extimus,* until the late 1800's. Since then, the species has greatly expanded in numbers and distribution throughout the region (Laymon 1987, Rothstein in prep.). Increases in cowbirds in the San Bernardino Valley between 1918 and 1928 caused Hanna (1928) "considerable alarm." Although Friedmann *et al.* (1977) reported relatively low rates of parasitism of willow flycatchers in the western United States, this was apparently owing to their data (egg sets) being collected prior to the major incursions of cowbirds into Pacific coast riparian habitats (L. Kiff, Western Foundation for Vertebrate Zoology, in litt. 1993). Brood parasitism of several subspecies of the willow flycatcher, including E. t.

extimus, by brown-headed cowbirds is well documented (Hanna 1928, Rowley 1930, Willett 1933, Hicks 1934, King 1954, Holcomb 1972, Friedmann *et al.* 1977, Garret and Dunn 1981, Harris *et al.* 1987, Brown 1988, 1991, Sedgewick and Knopf 1988, Whitfield 1990, Harris 1991, Sogge *et al.* 1993, Muiznieks *et al.* 1994).

The increases in cowbirds in the Southwest and parasitism of E. t. extimus and other birds are generally attributed to the following scenario: The introduction of modern human settlements, livestock grazing, and other agricultural developments resulted in habitat fragmentation. Simultaneously, livestock grazing and other agricultural developments served as vectors for cowbirds by providing feeding areas near host species' nesting habitats (Hanna 1928, Gaines 1974, Mayfield 1977a). Cowbirds may travel almost 7 kilometers (4.2 miles) from feeding sites where livestock congregate to areas where host species are parasitized (Rothstein et al. 1984). These factors increased both the vulnerability of *E. t.* extimus and the likelihood of encounters with cowbirds. Finally, the high edge-to-interior ratio of linear riparian habitats like those used by E. t. extimus renders birds nesting there particularly vulnerable to parasitism (Airola 1986, Laymon 1987, Harris 1991). Linear riparian habitats are also especially vulnerable to fragmentation by grazing, which further increases both the edge-to-interior ratio and the threat of parasitism.

The effects of parasitism by brownheaded cowbirds on willow flycatchers include reducing nest success rate and egg-to-fledging rate, and delaying successful fledging (because of renesting attempts) (Harris 1991). A common response to parasitism is abandonment of the nest (Holcomb 1972). Willow flycatchers may also respond to parasitism by ejecting cowbird eggs, by burying them with nesting material and renesting on top of them, or by renesting in another nest (Harris et al. 1991). However, the success rate of renesting is often reduced, because these attempts produce fledglings several weeks later than normal, which may not allow them adequate time to prepare for migration (Harris 1991). Renesting also usually consists of smaller clutches, further reducing overall reproductive potential (Holcomb 1974).

McCabe (1991) downplayed the significance of cowbird parasitism as a threat to any species except Kirtland's warbler (*Dendroica kirtlandii*). McCabe's monograph focussed on the combined "Traill's flycatcher" superspecies, comprised of *E. t. traillii*

and E. alnorum in marshy habitats in the upper Midwest, where parasitism rates ranged from 3 percent to 19 percent. However, perhaps reflecting his regional perspective, he characterized the high parasitism rates on willow flycatchers reported by Trautman (1940, cited in McCabe 1991) and Sedgwick and Knopf (1988) as aberrant (56 percent and 41 percent, respectively). McCabe considered the high rates the result of the "* * * linear configuration of the habitat * * * [c]owbirds lay eggs in songbird nests closest to cover edge.' The vast majority of southwestern willow flycatcher habitat is very linear and may experience higher rates of parasitism than other willow flycatcher subspecies.

Brittingham and Temple (1983) considered "high" parasitism rates (percent of nests parasitized) to be 24 percent, with some as high as 72 percent. Mayfield (1977a) thought a species (or population) might be able to survive a 24 percent parasitism rate, but that losses much higher than that "would be alarming." Parasitism rates of 72 percent to 83 percent on Kirtland's warbler (Mayfield 1977b) resulted in a precipitous population decline. Where parasitism rates are known for E. t. *extimus*, they are comparable to rates for Kirtland's warbler and are capable of causing similar declines. In California, parasitism rates ranged from 50 percent to 80 percent between 1987 and 1992. when an estimated population size decreased from 44 to 28 nesting pairs (Whitfield 1990, Harris et al. 1991, Whitfield and Laymon, unpubl. data). These parasitism rates were considered minimum measures, because several nests were abandoned each year due to unknown causes, which could have been parasitism. Brown (1988) reported an average 50 percent parasitism rate in the Grand Canyon between 1982 and 1987. Although his estimated population increased from two pairs to 11 during that period, it has since decreased back as low as two nesting pairs (Brown 1991, Sogge and Tibbitts 1992). In 1993, parasitism reached 100 percent in the Grand Canyon, and no E. t. extimus were fledged (Sogge et al. 1993). Harris et al. (1991) believed that the parasitism rates observed on the Kern River in 1987 (68 percent of all nests, 88 percent of all nest territories) were high enough to prevent *E. t.* extimus from recolonizing lowland riparian habitat, even if it were restored.

Rothstein *et al.* (1980), Stafford and Valentine (1985), and Harris (1991) believed parasitism may be correlated with elevation, being more severe at lower elevations. Coupled with greater loss of lowland (desert) riparian habitat,