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## AVIAN NEST SUCCESS, BROOD PARASITISM AND EDGE-INDEPENDENT REPRODUCTION IN AN ALASKAN WETLAND

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**Abstract.**—Nest predation, brood parasitism, and edge-dependent fledgling output were measured in four passerine species inhabiting Sheep Creek Valley, a large riparian shrub wetland near Juneau, southeastern Alaska. Frequency of Brown-headed Cowbird (*Molothrus ater*) fledglings in passerine broods and abundance of adult cowbirds were also measured in the valley and in nearby upland forest. The Yellow Warbler (*Dendroica petechia*) and Swainson's Thrush (*Catharus swainsoni*) were single-brooded, while the Fox Sparrow (*Passerella iliaca*) and American Robin (*Turdus migratorius*) were double-brooded. The Yellow Warbler had high (>90%), and the sparrow and robin intermediate (45–65%) nest success with both the apparent and Mayfield methods. Nest predation was a major cause of nest failure in all four species. No cowbirds (eggs, young, or adults) were found. Fledglings/nest was edge-independent in the Yellow Warbler and the sparrow and robin (latter two species pooled); the breeding bird community of Sheep Creek Valley is apparently not suffering edge-dependent nest predation and brood parasitism observed in other anthropogenic landscapes. One possible explanation of these results is that southeastern Alaska is still geographically isolated from the burgeoning populations of nest predators and brood parasites in the lower 48 states and southern Canada.

## ÉXITO EN EL ANIDAJE, PARASITISMO DE CAMADAS Y REPRODUCCIÓN INDEPENDIENTE DE LOS LINDEROS EN UNA ZONA ANEGADA DE ALASKA

**Sinopsis.**—Se midió la depredación de nidos, parasitismo de camadas y la producción de volantones dependiente de los linderos en cuatro especies paserinas habitantes del Valle de Sheep Creek, una gran zona riparia anegada con arbustos cerca de Juneau, al sudeste de Alaska. También se midieron las frecuencias de volantones de *Molothrus ater* en el valle y en un bosque de altura cercano. Las aves *Dendroica petechia* y *Catharus swainsoni* tuvieron una sola camada, mientras que *Passerella iliaca* y *Turdus migratorius* tuvieron dos camadas. Usando los métodos aparentes y Mayfield, *Dendroica petechia* tuvo un alto (>90%) éxito de anidamiento, y *Passerella iliaca* y *Turdus migratorius* tuvieron éxitos intermedios (45–65%). La

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depredación de nidos fue una causa principal del fracaso de nidos en las cuatro especies. No se hallaron huevos, jóvenes o adultos de *Molothrus*. El número de volantones/nido fue independiente de los linderos en *Dendroica petechia* y en nidos combinados de *Passerella iliaca* y *Turdus migratorius*. La comunidad de aves que anidan en el valle de Sheep Creek aparentemente no sufre de depredación de nidos ni de parasitismo de camadas asociadas a los linderos que se observan en otros paisajes antropogénicos. Una posible explicación es que el sudeste de Alaska todavía está geográficamente aislado de las poblaciones crecientes de depredadores de nidos y de parásitos de camadas en los 48 estados del sur continental y en Canadá.

Many species of North American songbirds have suffered long-term population declines in the fragmented habitats of the eastern and central United States (Aldrich and Robbins 1970, Askins et al. 1990, James et al. 1992, Robbins et al. 1989, Sauer and Droege 1992, Whitcomb et al. 1981). The habitat fragmentation model explains these declines by suggesting that increased habitat edge exposes breeding populations to nest predators and brood parasites. In spite of recent interest in the viability of North American songbird populations, at least three gaps in knowledge remain.

First, almost no information exists concerning the population status of songbirds in western North America, although this region supports diverse avian communities (Terborgh 1992) but some areas are undergoing rapid habitat fragmentation (Harris 1984). Especially little is known about the status of the brood-parasitic Brown-headed Cowbird (*Molothrus ater*) in western North America, although they may be increasing in some western regions, e.g., California. Second, most studies are of Neotropical migrants, and other groups, e.g., short-distance migrants, have been largely ignored. This is surprising, because even short-distance migrants have declined in eastern North America, including Canada (Canadian Wildlife Service 1993, Hagan et al. 1992, Witham and Hunter 1992). Third, only a few studies in any geographic region (Gates and Gysel 1978, Temple and Cary 1988, Vickery et al. 1992, Wilcove 1985) have tested the critical prediction of the habitat fragmentation hypothesis that nest predation and reproductive success are edge-dependent. The purpose of the present study was to begin to fill these gaps by measuring rates of nest success, nest predation, brood parasitism, and edge-dependent nest success in both Neotropical-migratory and short-distance migratory species breeding in a large shrub wetland in southeastern Alaska. Studies of nest success in Alaska are especially needed, as they appear to be absent from the ornithological literature, at least on Neotropical migrants (Martin 1992), and landscape alteration appears inexorable in this region.

#### STUDY AREA AND METHODS

*Sheep Creek Valley.*—The study area is the Sheep Creek Valley (58°17'N, 134°18'W), a large (300 ha) riparian floodplain in coastal mountains 6 km southeast of Juneau, Alaska. The floodplain is dominated by dense, shrubby growth (4–6 m in height) of sitka alder (*Alnus sinuata*) and willow (*Salix* spp.). Also common are the shrubs elderberry (*Sambucus racemosa*), devil's club (*Echinopanax horridum*) and salmonberry (*Rubus*

*spectabilis*). Black cottonwood (*Populus trichocarpa*) occurs densely along the stream margin and in small patches throughout the shrub growth. The herbaceous vegetation includes horsetails (*Equisetum*) and lady's slipper (*Cypripedium*).

*Nesting biology and nest success.*—Nesting data were gathered on two species of Neotropical migrants (Yellow Warbler [*Dendroica petechia*], Swainson's Thrush [*Catharus ustulatus*]) and two species of short-distance migrants (Fox Sparrow [*Passerella iliaca*], American Robin [*Turdus migratorius*]) in a 60-ha portion of the floodplain. The high frequency of song, territorial skirmishes and sighting of individuals indicated that these four species (and the Wilson's Warbler [*Wilsonia pusilla*]) are very common breeders in Sheep Creek Valley. Between early May and late July 1992, active nests were located during systematic walks, and all nests found were checked every 3–5 d for changes in contents. Nest success was measured with the apparent and Mayfield methods (Mayfield 1961, 1975). A successful nest was defined as a nest that fledged one or more young; failed nests fledged no young.

Nest height (m) was measured when the nest was first found. The distance to the nearest habitat edge (m) was measured by pacing (calibrated at 1 m/pace). Edge was defined as a border of any discontinuity in the alder-willow growth, including a clearing for a powerline and several small buildings, natural wet meadows, and stream courses.

The number of fledglings per nest was used as the dependent variable in multiple regression analyses that assessed the effects of distance from habitat edge, nest height, and their two-way interactions on reproductive success (SAS Institute 1985, general linear models; type III sums of squares, resulting in conservative tests, were used). I included (distance to edge)<sup>2</sup> as a fourth independent variable in a search for a non-linear edge effect (Gates and Gysel 1978). Two regressions were carried out, one on the Yellow Warbler ( $n = 20$  nests) and one on the Fox Sparrow and American Robin ( $n = 31$  nests). The latter two species showed similar nesting biology in Sheep Creek Valley (below), so data were pooled to increase sample size. Use of the number of fledglings per nest as the dependent variable accounted for possible effects of both complete and partial nest predation, and is therefore more informative than the binomial variable of nest success (0 young or  $\geq 1$  young fledged).

*Level of brood parasitism.*—The level of brood parasitism was determined at Sheep Creek Valley and in the vicinity of Juneau in three complementary ways. (1) The presence of cowbird eggs and nestlings was determined for all nests monitored at Sheep Creek. Yellow Warbler nests were inspected after fledging for cowbird eggs buried in the nest foundation. (2) In May–July 1992 cowbirds at 24 upland forest/forest edge sites (forest consisted mostly of western hemlock [*Tsuga heterophylla*] and sitka spruce [*Picea sitchensis*]) were censused by walking 0.5–1.0 km along a given edge and then immediately walking the same distance while 110 m inside the forest. The census design included the following forest-edge systems and sample sizes: wet meadows bordering forest,  $n = 5$ ; ocean

TABLE 1. Aspects of breeding biology, nest success (apparent and Mayfield methods), causes of nest failure, and fledgling production of four passerine bird species breeding in a riparian shrub wetland in southeastern Alaska. All other causes of nest failure: abandoned, unknown cause and abandonment after partial predation.

Species	Clutch size ( <i>n</i> )	Date of first egg (last fledg- ling)	Apparent nest success (Mayfield, <i>n</i> )	Proportion nests failing from		Fledglings/ Successful nest	
				Com- plete preda- tion	All other causes	Nest	Suc- cessful nest
Yellow Warbler	5.11 ± 0.57 (20)	24 May (26 Jun.)	0.950 (0.923, 19)	0.050	0.000	4.35	4.58
Swainson's Thrush	4.00 ± 0.63 (7)	3 Jun. (7 Jul.)	0.286 (0.218, 7)	0.429	0.286	1.00	3.50
Fox Sparrow	4.11 ± 0.33 (9)	1 May (2 Jul.)	0.632 (0.573, 19)	0.316	0.052	1.96	3.38
American Robin	4.50 ± 0.71 (13)	27 Apr. (26 Jul.)	0.538 (0.488, 13)	0.462	0.000	1.69	3.20

beach bordering forest,  $n = 5$ ; disturbed openings near houses,  $n = 5$ ; clear-cuts,  $n = 5$ ; riparian edge bordering forest,  $n = 4$ . All sites were at least 0.5 km apart except four of the five forest beach sites, which were consecutive 1.0 km-long censuses along the coast south of Juneau. (3) Sheep Creek Valley was traversed during the entire study period and the presence or absence of cowbird fledglings in fledged broods was noted; similar data were collected for broods observed on the 24 formal census routes. Care was taken not to assess the cowbird status of a fledged brood more than once, and to exclude broods involved in the study of nest success.

#### RESULTS

*General aspects of nests and broods.*—The approximate length of the breeding period was just over 1 mo for the Yellow Warbler and Swainson's Thrush, and 3 mo for the American Robin and Fox Sparrow (Table 1). No nest initiation dates were found for any species in July. Mean clutch size differed significantly among the four species (ANOVA  $P < 0.05$ ) with only warbler clutch size exceeding five eggs (Table 1).

*Nest success and causes of nest failure.*—The Yellow Warbler had nest success of over 90% with both the apparent and Mayfield methods, and fledged almost five young per successful nest (Table 1). After the young fledged in late June, all song and territorial behavior ceased abruptly, and very few birds, adults or young, were observed in the study area through late July. The Fox Sparrow and American Robin both displayed lower nest success than the Yellow Warbler (Table 1); the apparent and Mayfield methods again agreed closely. On the basis of limited data, the Swainson's Thrush displayed very low nest success (Table 1).

*Level of brood parasitism.*—No cowbird eggs or nestlings were found in

the nests of any species studied. No adult cowbirds were detected on the 24 formal censuses of forest interior and edges. Finally, of 81 fledged broods in 15 passerine species studied at Sheep Creek and in upland forest/edge, no fledged brood was found to contain a cowbird fledgling.

*Edge-independent nest success at Sheep Creek.*—In the Yellow Warbler and Fox Sparrow/American Robin data sets, nest height, distance to edge, the height-distance interaction, and (distance to edge)<sup>2</sup> were non-significant predictors of number of fledglings per nest (all  $P > 0.09$  and all  $P > 0.26$  for respective data sets). Distance from edge varied from 0 to 58 m (warbler) and 0 to 40 m (sparrow/robin).

#### DISCUSSION

*General aspects of nests and broods.*—The Yellow Warbler population in Sheep Creek Valley was apparently synchronous and single-brooded, consistent with the earlier account of Yellow Warbler breeding behavior in southeastern Alaska by Gabrielson and Lincoln (1959). These investigators also described an abrupt cessation of song and breeding behavior in midsummer after a single brood was fledged, with adults and young “silently slipping away” and becoming very inconspicuous. Although data were fewer, the Swainson’s Thrush at Sheep Creek also appeared to be synchronous and single-brooded, with a breeding period similar in length to that of the Yellow Warbler.

The relatively long breeding periods of the Fox Sparrow and American Robin suggests that these two species are double-brooded in Sheep Creek Valley. The longer breeding periods of the sparrow and robin may only reflect, however, continued renesting after nests were depredated instead of double-broodedness. Given observed nest predation rates, some re-nesting undoubtedly occurred, yet, the very early initiation of nesting in late April (robin) and 1 May (sparrow) support the conclusion of two broods. Gabrielson and Lincoln (1959) also described two broods per year in the Fox Sparrow in southeastern Alaska, but did not give a brood number for the robin.

*Nest success and causes of nest failure.*—Nest predation was consistently the most frequent cause of nest failure, as concluded earlier for small birds in general (Ricklefs 1969). The high nest success in the Yellow Warbler (>90%) exceeds all values for nest success of Neotropical migrants in the extensive literature review of Martin (1992). Although methodological differences preclude exact comparisons among studies, it may be safely concluded that Yellow Warblers at Sheep Creek Valley showed high nest success compared to many other Neotropical migrants in other regions of North America.

*Level of brood parasitism.*—In contrast to trends in other regions (Hoover and Brittingham 1993), three lines of evidence suggest that the Brown-headed Cowbird is either absent or very rare near Juneau, Alaska. (1) No cowbird eggs or young were observed in nests of four songbird species (although the American Robin is an ejector species). (2) No adult cowbirds were detected on 24 widely scattered censuses of interior forest

and edge habitat of five different types. (3) No cowbird fledglings were seen in a large number of fledged broods of 15 passerine species in shrub, forest, and forest edge habitat. Thus, although the Brown-headed Cowbird is listed as a probable breeder in south-coastal Alaska (American Ornithologist's Union 1983), at present it is of little or no ecological significance in the vicinity of Juneau. Furthermore, it is difficult to imagine that cowbird abundance is very high anywhere in southeastern Alaska, a region almost completely lacking agricultural development, a key factor in the historical range expansion of this species (Ehrlich et al. 1988).

*Edge-independent nest success.*—The number of fledglings per nest was edge-independent in two data sets from Sheep Creek Valley. These results differ from the original study in eastern North America showing edge-dependent fledgling output on the same spatial scale used at Sheep Creek (Gates and Geysel 1978); the present results also differ from a more recent study showing edge-dependency on a much larger spatial scale (Temple and Cary 1988). The edge-independence of the present study is consistent, however, with edge-independence of avian reproduction in a Maine grassland bird community using scale intervals of 50 m (Vickery et al. 1992).

One possible explanation for edge-independent reproduction at Sheep Creek is that the spatial distribution of nest predators was edge-independent. This may have multiple causation. First, Sheep Creek Valley is not surrounded by ecosystems capable of artificially supporting burgeoning, edge-dwelling predator populations (e.g., agricultural fields, suburban developments); it is instead surrounded by the steep, rugged coastal mountains of southeastern Alaska. Second, of the many predators thought to be responsible for edge-dependent nest predation in the eastern deciduous forest are absent from southeastern Alaska (opossum, *Didelphis marsupialis*; raccoon, *Procyon lotor*; striped skunk, *Mephitis mephitis*; gray squirrel, *Sciurus carolinensis*). Three corvid species (Northwestern Crow *Corvus caurinus*; Northern Raven *C. corax*; Steller's Jay *Cyanocitta stelleri*), noted nest predators via visual searching (Bent 1946, Ouellet 1970, Verbeek 1982) are common in this region but were absent from Sheep Creek Valley, at least in the 1992 breeding season. Although only one breeding season was studied, these baseline population data could prove useful to investigators concerned with future landscape alteration and its attendant effects on songbird populations in southeastern Alaska.

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