

LATENT POPULATION RESPONSES OF SUMMER BIRDS TO A CATASTROPHIC, CLIMATOLOGICAL EVENT¹

FRITZ L. KNOPF AND JAMES A. SEDGWICK

National Ecology Center, U.S. Fish and Wildlife Service, 1300 Blue Spruce Drive,
Fort Collins, CO 80524-2098

Abstract. Catastrophic events can create ecological crunches for avian populations. Ornithologists generally assume that such events elicit immediate, dramatic declines in populations followed by rapid recolonization of a site with habitat recovery. Despite total inundation of habitats within the South Platte floodplain of eastern Colorado during the 1983 breeding season, populations of Brown Thrashers (*Toxostoma rufum*) and Rufous-sided Towhees (*Pipilo erythrophthalmus*) did not decline significantly from 1982 densities. However, populations of both species declined significantly in 1984 and towhee populations remained low in 1985. These observations support speculations from recent studies of shrubsteppe bird populations that site tenacity may play a stronger role in determining annual densities of breeding birds than previously realized.

Key words: *Brown Thrasher*; *Toxostoma rufum*; *Rufous-sided Towhee*; *Pipilo erythrophthalmus*; *flooding*; *Colorado*; *site tenacity*; *riparian*.

INTRODUCTION

Water levels of major river systems rise and fall annually, and hydroperiod (amplitude of water level) fluctuations can produce dramatic changes in riparian (streamside) vegetative communities (Ewel 1979). The duration and surface area of flooding varies among years depending upon snowmelt conditions, rainfall patterns, and other climatological events—often at sites hundreds of kilometers distant. In western North America, the onset or duration of flooding is generally not predictable from local climatological conditions, and species of birds in riparian woodlands that forage and nest on or near the ground periodically find their habitats completely inundated for variable periods of time. Field biologists have only been able to speculate about the immediate and subsequent-year impacts of such catastrophic events upon bird populations.

During ongoing studies of the riparian avifauna of the South Platte River floodplain in eastern Colorado, annual spring flooding of the river varied dramatically over a 4-year period. This paper describes changes in the densities of two species of migratory birds before, during, and for 2 years after a year of major flooding of the South Platte River in northeastern Colorado. The two species, both of which forage and nest on or near the ground, were the Brown Thrasher (*Toxostoma*

rufum) and Rufous-sided Towhee (*Pipilo erythrophthalmus*). Because unflooded habitats of these species were not available locally to use as control sites, we interpreted population changes relative to changes in densities of the two most common species that were least likely to be influenced by flooding. Those latter species, which foraged and nested in the tree canopy, were the Northern Oriole (*Icterus galbula*) and Orchard Oriole (*I. spurius*).

We made two predictions relative to densities of the four species on the area. First, we predicted that the two representative species from the ground-shrub guild would respond to the major flood of 1983 by leaving the study area or occurring in drastically reduced numbers, whereas densities of species from the canopy guild would not change dramatically. Second, we predicted that densities of individual species in both guilds would be comparable among the pre-flood year and post-flood nesting seasons.

STUDY AREA

The study area was the South Platte Wildlife Management Area near Crook (Logan County), Colorado. The area varies in elevation from 1,149 m on the west to 1,116 m on the east. The riparian zone of vegetation varies from 500 to 1,000 m wide at this location, and is surrounded by uplands of sand sagebrush (*Artemisia filifolia*)/mixed prairie (Harrington 1954; see Knopf 1986 for photographs of the upland) and agricultural lands. The riparian sites had not been grazed by

¹ Received 21 January 1987. Final acceptance 31 March 1987.

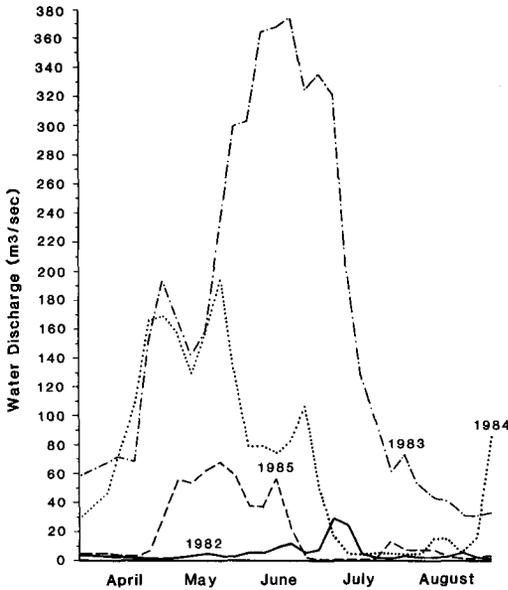


FIGURE 1. Comparative weekly flows (m^3/sec) of the South Platte River during spring runoff, 1982 to 1985. Flow data are from a station at Julesburg, 30 km east of Crook, Colorado.

cattle for approximately 30 years prior to this study (M. Gardner, Colorado Div. Wildl., pers. comm.). Plains cottonwood (*Populus sargentii*) dominates an overstory that also includes peach-leaf willow (*Salix amygdaloides*). The understory is dominated by shrubs such as snowberry (*Symphoricarpos occidentalis*), coyote willow (*Salix exigua*), sandbar willow (*S. interior*), poison ivy (*Toxicodendron radicans*), and woods rose (*Rosa woodsii*). Prairie cordgrass (*Spartina pectinata*), common reed (*Phragmites communis*), and poison hemlock (*Conium maculatum*) dominate the herbaceous community.

METHODS

We designed a study to survey summer resident birds on the study area on 10 mornings during the last 2 weeks of May each year, 1982 to 1985. Surveys were to include four replications at each of 155 permanent stakes (steel posts protruding approximately 150 cm above the ground surface) within 10 16-ha plots scattered along approximately a 14-km stretch of the floodplain. Due to severe overbank flooding in 1983, however, 117 (95%) of 123 stakes were partially or completely submerged and field personnel (using canoes tied to the stakes) were only able to complete two replications of the surveys. The additional 32 stakes were inaccessible or could not be surveyed

during the 10-day interval; data for these latter stakes were discarded for all 4 years.

Birds were counted at each stake using point transect techniques (Burnham et al. 1980:195) with a field methodology following Reynolds et al. (1980). A motionless observer recorded each bird seen during a 10-min interval following a 1-min equilibration period. The daily surveys were conducted from sunrise until about 10:00.

Population densities of the four bird species were calculated using a three-parameter Fourier Series model within program TRANSECT (Burnham et al. 1980) adapted for point data (K. P. Burnham, pers. comm.). This program does not provide sum of squares calculations that are necessary for a one-way analysis of variance test for the influence of time on the species across the 4 years. A series of paired Z calculations for years can be summed within species with $n - 1$ degrees of freedom to provide this comparison, but the approach requires the assumption of asymptotic normality which is likely to be violated (G. C. White, pers. comm.). Thus, we restricted our comparisons to simple, paired t -tests.

RESULTS

DESCRIPTION OF FLOODING

The water volume and flow rates of the South Platte River varied among the 4 years from a maximum mean daily flow of $44 \text{ m}^3/\text{sec}$ in 1982 to $405 \text{ m}^3/\text{sec}$ during the severe flood year of 1983 (Fig. 1). Flow rates $\geq 300 \text{ m}^3/\text{sec}$ corresponded to an average water depth of about 1 m in the plots. No overbank flooding occurred in 1982, whereas overbank flooding was severe in 1983 (Fig. 2) when it commenced in mid-May after migratory birds arrived on the area and continued into early July. Maximum flow rates during the springs of 1984 to 1985 were intermediate compared to the other years, and flooding was minor with waters receding into the river channels by late May. Based on towhee and thrasher nest site selection during nonflood years (unpubl. data), the high water levels in 1983 precluded nesting by these species on the area.

AVIAN RESPONSES TO FLOODING

Densities failed to change as predicted for the ground-shrub guild representatives during the 1983 flood (Table 1). Rufous-sided Towhee densities declined 36%, but not significantly so (one-tailed $t = 1.32$, $P = 0.10$) and Brown Thrasher densities changed significantly (one-tailed $t = 1.94$, $P = 0.03$), but not in the direction pre-

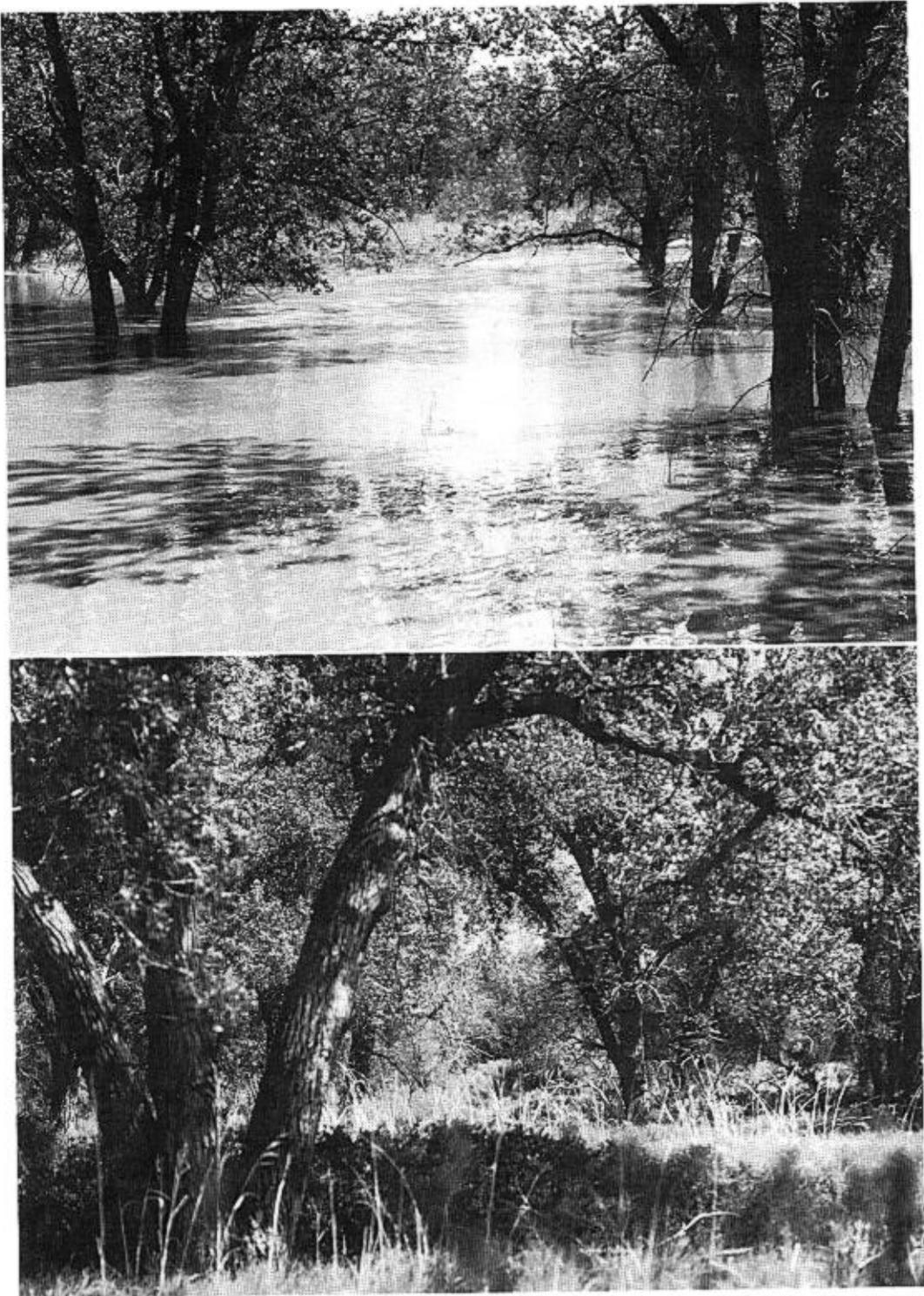


FIGURE 2. Cottonwood floodplain of the South Platte River at Crook, Colorado on 27 May 1983 during period of severe overbank flooding (top), and 1 year later (29 May 1984) during period of normal flows.

TABLE 1. Calculated densities, \hat{D} (birds/hectare) of four species of birds surveyed at 123 permanent points on the South Platte Wildlife Management Area near Crook, Colorado, 1982 to 1985.

Species	Year	<i>n</i>	\hat{D}	SE
Ground species				
Brown Thrasher	1982	55	0.31	0.070
	1983	89	0.55	0.102
	1984	29	0.14	0.054
	1985	30	0.24	0.073
Rufous-sided Towhee	1982	41	0.36	0.077
	1983	22	0.23	0.061
	1984	19	0.05	0.043
	1985	16	0.08	0.025
Canopy species				
Northern Oriole	1982	140	1.29	0.151
	1983	167	1.40	0.197
	1984	116	1.10	0.180
	1985	166	1.82	0.260
Orchard Oriole	1982	77	1.02	0.160
	1983	87	0.79	0.166
	1984	81	0.88	0.167
	1985	72	0.98	0.188

dicted. Populations of the canopy species responded as predicted with densities of both the Orchard Oriole (two-tailed $t = 0.98$, $P = 0.34$) and Northern Oriole (two-tailed $t = 0.44$, $P > 0.50$) being comparable prior to (1982), and during (1983) the flood year. We concluded that the severe flooding of 1983 did not negatively affect population densities of the ground-foraging species on the area in that year.

The 1984 and 1985 surveys supported our second prediction of similar densities for canopy species during the seasons of minimal overbank flooding, but again failed to support the prediction for the ground-shrub species. Densities of Northern Orioles (1982/1984— $t = 0.84$, $P = 0.43$; 1982/1985— $t = 1.76$, $P = 0.08$) and Orchard Orioles (1982/1984— $t = 0.61$, $P > 0.50$; 1982/1985— $t = 0.16$, $P > 0.50$) were comparable among the 3 years. Densities of Brown Thrashers were lower ($t = 1.92$, $P = 0.03$) in 1984 than 1982, and Rufous-sided Towhee densities declined $>80\%$ ($t = 3.52$, $P = 0.00$). Thrasher numbers approximated pre-flood densities in 1985 ($t = 0.69$, $P = 0.25$) the second year post-flood while towhee numbers remained depressed ($t = 3.46$, $P = 0.00$).

DISCUSSION

Riparian vegetation provides habitats for more species of birds than other native vegetative

communities in western states (Hubbard 1971, 1977; Knopf 1985; Knopf et al., in press). A total of 83 species has been recorded in the riparian vegetation of the South Platte River in late May (Knopf 1986). The Brown Thrasher and Rufous-sided Towhee were not the only two species in the ground-shrub guild on the study area. Additional common species that bred on the area included House Wren (*Troglodytes aedon*), American Robin (*Turdus migratorius*), Common Yellowthroat (*Geothlypis trichas*), and Yellow-breasted Chat (*Icteria virens*) (Sedgwick and Knopf 1987). Wrens and robins nested >1 m above the ground and were not as susceptible to flooding disturbance. Yellowthroats and chats occurred in too few numbers in 1983 to estimate densities using program TRANSECT. Many additional canopy species were present. The orioles were the most abundant species within this guild and were chosen to assure the most precise density estimates.

Thrasher and towhee responses to flooding could not be attributed to differences in the vegetative community among the 4 years. Grasses and forbs were inventoried by clipping 0.5-m² plots and areal coverage by woody species was quantified along four 25-m line intercepts oriented in the cardinal directions at each stake annually. Those data (unpubl.) show no significant changes within the grass/forb/shrub association among years. The flood ultimately may have influenced the quality or distribution of thrasher and towhee foods within the floodplain, but we cannot speculate how those changes may have influenced the responses of these birds.

Individuals of many species of birds tend to return to the same site each year to breed (e.g., Nice 1937, Nolan 1978). Such site tenacity is influenced by a variety of factors including age or sex of a bird, local habitat or nest-site stability, and prior breeding experience at a site or with a particular individual (Freer 1979, Harvey et al. 1979, Shields 1984). Previous breeding experience, especially, appears to be a major determinant of whether an individual will return in subsequent years (e.g., Blancher and Robertson 1985). Densities in 1982 were similar to those in 1983 for all four species although habitats of the ground species were inundated completely. The 1983 densities likely reflected the return of 1982 successful breeders to the site in 1983.

Overbank flooding of the South Platte River continued through July in 1983. Brown Thrashers and Rufous-sided Towhees that were on the

study area in 1983 likely did not breed successfully as no suitable alternative habitats were available locally in the adjacent uplands of native grasslands and shrubsteppe vegetation. Densities of these two species declined dramatically the first year after the flood, indicating that the influence of such major habitat perturbations upon a species population (and an avifauna) may neither be immediate nor obvious until a year or more after the disturbance. Supportive conclusions have been reported for forest bird populations in response to drought (Smith 1982), colonial seabird behavior during flooding of nests (Burger 1982), and elsewhere. Avian field studies have generally ignored such time lags in individual and population responses (Wiens 1977), especially those that may be attributed to site tenacity of birds (Wiens et al. 1986).

Rufous-sided Towhee populations remained low the second year postflood. Assuming a constant pattern in winter mortality, towhees may have bred successfully beyond the general vicinity during the first year postflood and did not return to the area the second year after the flood. If such is the case, towhee recolonization of the South Platte floodplain will be slow. Thrasher populations recovered the second year indicating that birds either did not breed successfully elsewhere and came back in 1985, or that thrashers recolonized the site faster than towhees.

ACKNOWLEDGMENTS

We thank T. G. Andrews, J. F. Ellis, S. S. Ellis, T. E. Olson, E. A. Ernst, S. J. Martin, T. R. Ryon, and E. L. Smith for assistance with the avian surveys. K. P. Burnham provided assistance in adapting program TRANSECT to point data. C. E. Bock and F. B. Samson commented on the manuscript. This research is a product of Cooperative Agreement No. 2463-4 between the Colorado Division of Wildlife and U.S. Fish and Wildlife Service.

LITERATURE CITED

- BLANCHER, P. J., AND R. J. ROBERTSON. 1985. Site consistency in kingbird breeding performance: implications for site fidelity. *J. Anim. Ecol.* 54:1017-1027.
- BURGER, J. 1982. The role of reproductive success in colony-site selection and abandonment in Black Skimmers (*Rynchops niger*). *Auk* 99:109-115.
- BURNHAM, K. P., D. R. ANDERSON, AND J. L. LAAKE. 1980. Estimation of density from line transect sampling of biological populations. *Wildl. Monogr.* 72.
- EWEL, K. C. 1979. Riparian ecosystems: conservation of their unique characteristics, p. 56-62. *In* R. R. Johnson and J. F. McCormick [tech. coords.], Strategies for protection and management of floodplain wetlands and other riparian ecosystems. U.S. Dep. Agric. For. Serv. Gen. Tech. Rep. WO-12.
- FREER, V. M. 1979. Factors affecting site tenacity in New York Bank Swallows. *Bird-Banding* 50:349-357.
- HARRINGTON, H. D. 1954. *Manual of the plants of Colorado*. Sage Books, Denver.
- HARVEY, P. H., P. J. GREENWOOD, AND C. M. PERRINS. 1979. Breeding area fidelity of Great Tits (*Parus major*). *J. Anim. Ecol.* 48:305-313.
- HUBBARD, J. P. 1971. The summer birds of the Gila Valley, New Mexico. *Nemouria* No. 2.
- HUBBARD, J. P. 1977. Importance of riparian ecosystems: biotic considerations, p. 14-18. *In* R. R. Johnson and D. A. Jones [tech. coords.], Importance, preservation, and management of riparian habitat: a symposium. U.S. Dep. Agric. For. Serv. Gen. Tech. Rep. RM-43.
- KNOFF, F. L. 1985. Significance of riparian vegetation to breeding birds across an altitudinal cline, p. 105-111. *In* R. R. Johnson, C. D. Ziebell, D. R. Patten, P. F. Ffolliott, and R. H. Hamre [tech. coords.], First North American riparian conference. U.S. Dep. Agric. For. Serv. Gen. Tech. Rep. RM-120.
- KNOFF, F. L. 1986. Changing landscapes and the cosmopolitanism of the eastern Colorado avifauna. *Wildl. Soc. Bull.* 14:132-142.
- KNOFF, F. L., R. R. JOHNSON, T. RICH, F. B. SAMSON, AND R. C. SZARO. *In press*. Conservation of riparian ecosystems in the United States. *Wilson Bull.*
- NICE, M. M. 1937. Studies in the life history of the Song Sparrow, part 1. *Trans. Linn. Soc. N.Y.* 4: 1-247.
- NOLAN, V., JR. 1978. The ecology and behavior of the Prairie Warbler *Dendroica discolor*. *Ornithol. Monogr.* No. 26.
- REYNOLDS, R. T., J. M. SCOTT, AND R. A. NUSSBAUM. 1980. A variable circular-plot method for estimating bird numbers. *Condor* 82:309-313.
- SEDGWICK, J. A., AND F. L. KNOFF. 1987. Breeding bird response to cattle grazing of a cottonwood bottomland. *J. Wildl. Manage.* 51:230-237.
- SHIELDS, W. M. 1984. Factors affecting nest and site fidelity in Adirondack Barn Swallows (*Hirundo rustica*). *Auk* 101:780-789.
- SMITH, K. G. 1982. Drought-induced changes in avian community structure along a montane sere. *Ecology* 63:952-961.
- WIENS, J. A. 1977. On competitive and variable environments. *Am. Sci.* 65:590-597.
- WIENS, J. A., J. T. ROTENBERRY, AND B. VAN HORNE. 1986. A lesson in the limitations of field experiments: shrubsteppe birds and habitat alteration. *Ecology* 67:365-376.