

### An Assessment of Ground-nest Depredation in a Catastrophically Disturbed Region, Mount St. Helens, Washington

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The explosive eruption of the Mount St. Helens volcano on 18 May 1980 severely affected a large array of plant and animal populations (Edwards and Schwartz 1981, MacMahon 1982, Wissmar et al. 1982) over a vast area (>600 km<sup>2</sup>) (Fig. 1). Volcanic eruptions are relatively common agents of large-scale biotic disturbance, yet few studies have addressed either short- or long-term effects on avian populations (see Hayward et al. 1982 for entry on pre-1980 literature). We present data gathered during 1980–1984 on relative abundances of birds in disturbed areas near Mount St. Helens. These data indicate that a ground-nesting species was numerically dominant in the early posteruption avifauna. We also test the null hypothesis that predation rates on ground nests were unaltered by the eruption. We assumed that the breeding abundance of ground-nesting species is affected significantly by nesting success in previous years (Duebbert and Lokemoen 1980) and speculated whether dramatic changes in ground-nest predation rate might have occurred as a result of the eruption.

Details of the eruption are presented in Lipman and Mullineaux (1981) and Franklin et al. (1985). Greatly simplified, the event consisted of a landslide and subsequent north-directed blast of hot (200–300+°C), rapidly moving (100–300 m/s; Kieffer 1981) gas and tephra (an assortment of ash, pumice, and explosion debris). The gas incinerated and carried away much of the aboveground organic material within 10 km of the former summit. Beyond this “blast” zone (Fig. 1), the force wave leveled old-growth forest trees, creating a 350-km<sup>2</sup> area of decumbent dead trees overlying tephra. This is the “blowdown” zone. The ejection of pumice and ash that followed the blast produced downwind deposits that varied in thickness and composition with distance. Tephra depths within this “tephrafall” zone ranged from 15–30 cm 15 km northeast of the mountain to 1–7 cm 400 km east, near the Washington-Idaho border (Hayward et al. 1982). A reduction in plant cover 0–0.5 m tall was evident in all disturbance zones, from nearly complete absence of vegetative or litter cover in the blast zone to a 50% reduction in clearcuts within proximate portions of the tephrafall zone (Andersen and MacMahon 1985a).

We first made observations in the disturbed areas in September 1980 and began systematic surveys of the avifauna in 1981, after restrictions on movements of researchers were relaxed. Birds were surveyed monthly from June through September. Only pertinent July (breeding season) data from open habitats

(described below) are presented here. The complete data set will appear elsewhere.

Three relatively open sites, chosen to represent different forms of disturbance, were surveyed. A blowdown site was established in a broad basin in what was old-growth forest (elevation 1,100 m) near Meta Lake, 13 km northeast of the Mount St. Helens volcano (46°11'N, 122°12'W). A tephrafall site (USDA Forest Serv. designation Snyder Pasture Clearcut #4; elevation 1,300 m) was located 20 km northeast of the volcano. This site, which has a westerly aspect and 10% slope, was clearcut in 1963. It received a deposit of cool, wind-borne tephra that averaged 12 cm thick 4 months after deposition (Andersen 1982). A relatively undisturbed site, a clearcut of approximately the same age as the tephrafall site (USDA Forest Serv. Upper Owens #3; elevation 1,120 m), was established 32 km northeast of the volcano. This site, considered a control, was not affected by the lateral blast and received <0.5 cm of tephra. The site has a southerly aspect and 10% slope. A linear 1,000-m transect was marked permanently on each site with wooden posts set at 50-m intervals. The transect was walked slowly between 0600 and 1000, and all birds seen were identified and counted. The sites were surveyed on successive days. The transect data were augmented with observations made at each site during periodic visits of a few to several hours during the breeding season in conjunction with other research activities. We consider the augmented data to accurately reflect the complete list of breeding species from each site.

Although quantitative data are unavailable, there was little doubt that bird populations were reduced or eliminated within the disturbed areas. All birds present within the blowdown zone at the time of the initial blast probably were killed. However, we noted individuals of several species, presumably colonists or survivors, within each of the disturbance zones in late summer 1980. The observational data indicate that species richness in the blowdown zone was variable between 1981 and 1984, with no apparent trend (Table 1). The number of species observed during the 3–4 h on the blowdown transect was consistently less than that noted at the site over the length of the breeding season. This difference, not observed at the other sites, was likely due to the very low densities of some species. Species numbers in the blowdown zone were usually less than those in the tephrafall zone, while tephrafall zone values matched undisturbed clearcut values in both 1983 and 1984.

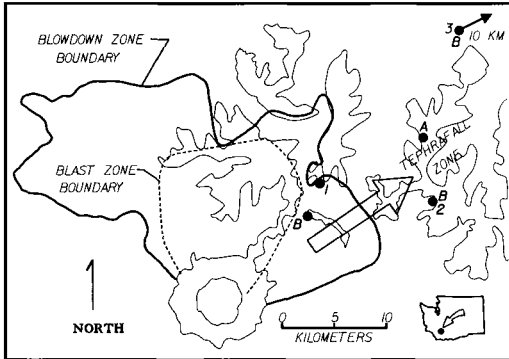


Fig. 1. Mount St. Helens and vicinity, showing the area devastated by the 18 May 1980 explosive eruption. The 1,220-m elevation contour is shown, with the 1,830-m contour shown on the former Mount St. Helens. The large arrow depicts the prevailing wind direction during the eruption. Letters correspond to sites where junco nests were found in 1981 (A) and 1982 (B). Numbers indicate sites at which transect surveys were conducted and artificial nests were arrayed. Site 3, the control, is 10 km northeast of the mapped position.

We found that the Dark-eyed Junco (*Junco hyemalis*) was the most abundant bird within each habitat during all four breeding seasons (Table 1). Breeding activity was not documented in any disturbed area in 1980, although it could have occurred. Both juncos and Mountain Bluebirds (*Sialia currucoides*) bred in the blast and blowdown zones in 1981.

Juncos and other ground-nesting species could face unusual risk of having nests depredated in the volcanically disturbed zones. The net effect of the volcanic

disturbance on ground-nest depredation rates would depend on how the eruption affected landscape features that contribute to concealment cover (e.g. plant diversity, physiognomy, and surface debris) and how it affected populations of predator and prey species. Potential mammalian ground-nest predators survived the May 1980 eruption and persisted or expanded into the various disturbance zones (Andersen and MacMahon 1985b). Both spatial heterogeneity of the habitat, as indexed by ground cover, and the array of potential predators generally decreased in the volcanically disturbed areas used by breeding juncos. Reduction of habitat heterogeneity would tend to reduce survivorship by making nests easier to locate (Bowman and Harris 1980). The increase in large woody debris (blowdown) at ground level, however, may have effectively maintained, or increased, local spatial heterogeneity in some sites. Reduced predator populations should enhance nest survivorship, but a simultaneous decrease in prey populations could lead surviving predators to increase their reliance on eggs or nestlings, thus reducing nest survivorship.

We tested for an effect of the eruption on the frequency or intensity of predation on ground nests in 1983 and 1984 by comparing the fate of artificial nests containing fresh quail eggs placed in blowdown and tephrafall areas with that of nests in a relatively undisturbed "control" site. The use of artificial nests and commercially available eggs is a common technique for assessing aspects of breeding bird ecology (e.g. Janzen 1977, Andersson and Wiklund 1978, Gottfried and Thompson 1978, Boag et al. 1984). However, the ability to extrapolate from such data is more limited than from data based upon natural nests. Our data can furnish only an index to the relative probability of nest depredation for ground-nesting birds along the disturbance gradient. The rates we

TABLE 1. Number of individuals of three species and total for all bird species observed along 1,000 m of transect during July in 1981-1984 at three sites in the vicinity of Mount St. Helens. The lowermost tabulated value is the total number of species observed either on or off the transect during the breeding season.

	No. of individuals or species											
	Blowdown				Tephrafall clearcut				Control clearcut			
	1981 <sup>a</sup>	1982	1983	1984	1981 <sup>a</sup>	1982	1983	1984	1981 <sup>a</sup>	1982	1983	1984
Dark-eyed Junco	5	7	12	15	16	8	28	12	22	18	6 <sup>b</sup>	20
Gray Jay	0	0	0	0	0	2	1	0	9	2	1	2
Common Raven	P <sup>c</sup>	0	0	1	0	0	0	0	0	0	0	0
Total for all species	6	7	17	17	32	17	52	29	58	39	22	37
No. of species observed on transect	2	1	3	2	6	3	7	7	8	7	7	7
No. of species observed on study site	5	3	6	3	6	3	7	9	10	8	7	7

<sup>a</sup> Data from August surveys; no surveys were conducted in July 1981.

<sup>b</sup> Value is probably artificially low due to weather conditions during the survey period; the August 1983 value was 23 individuals.

<sup>c</sup> P = seen at times other than transect sampling.

TABLE 2. Cumulative predation frequency (F, proportion of nests with damage to one or more eggs) and mean intensity (I, proportion of eggs in nest that are damaged) for 4 × 5 arrays of artificial nests in areas differing in intensity of volcanic disturbance. Nests were monitored 3 times in 1983 and 5 times in 1984.

Year	Site	Total exposure time (days)															
		3			6			9			10			12			15
		F	I	F	I	F	I	F	I	F	I	F	I	F	I	F	I
1984	Control	0.05	0.33	0.05	0.33	0.05	0.33	0.05	0.33	0.05	0.33	0.05	0.33	0.05	0.33	0.05	0.33
	High tephrafall	0.10	0.66	0.15	0.78	0.20	0.67	0.20	0.67	0.20	0.67	0.20	0.67	0.20	0.67	0.20	0.67
	Blowdown	0.0	—	0.05	0.33	0.05	0.33	0.05	0.33	0.05	0.33	0.05	0.33	0.05	0.33	0.05	0.33
1983	Control	0.05 <sup>a</sup>	0.33							0.10	0.33					0.10	0.33
	High tephrafall <sup>b</sup>	0.26	0.55							0.37	0.81					0.53	1.00
	Blowdown	0.0	—							0.0	—					0.05	0.33

<sup>a</sup> Based on 4 days.

<sup>b</sup> 19 nests at this site.

TABLE 3. Maximum likelihood estimates (after Bart and Robson 1982) of daily "survival" rate for undamaged nests containing three artificial eggs. Standard errors of estimate are given in parentheses. Values with the same superscript are not significantly different.

Nest location	1983	1984
Control	0.9928 <sup>a</sup> (0.0051)	0.9965 <sup>a</sup> (0.0035)
High tephrafall	0.9493 <sup>b</sup> (0.0159)	0.9844 <sup>a</sup> (0.0077)
Blowdown	0.9966 <sup>a</sup> (0.0034)	0.9966 <sup>a</sup> (0.0034)

estimate cannot be applied directly to any nesting species.

We placed commercial wicker "canary" nests (7.5 cm diameter by 6 cm deep, dyed brown) in 4 × 5 arrays within each of the transect survey sites described above. Nests were placed ~100 m apart, in depressions with concealing cover (e.g. under a shrub, fallen tree, stump, etc.) and out of direct sunlight, to mimic those of the Dark-eyed Junco (Phelps 1968). Locations were marked by a red pin-flag placed 1 m north of the nest; nests were in place for at least 3 days before placement of eggs. Three fresh button-quail (*Turnix* sp.) eggs (mean size 2.0 × 2.5 cm, *n* = 3) were placed in each nest on 3 July 1983. In 1984, three somewhat larger (mean size 2.5 × 3.3 cm, *n* = 3) fresh Gambel's Quail (*Callipepla gambelii*) eggs were placed in nests on 12 July. Junco eggs average about 1.5 × 1.9 cm (Phelps 1968). Nests were checked for predation after 3, 10, and 15 days in 1983 and after 3, 6, 9, 12, and 15 days in 1984. Condition of nests and eggs (e.g. nest displaced, size and location of shell fragments or holes in eggs) were noted at each check. We assume our markers and disturbance did not differentially affect depredation rates. Differences in estimates of daily survival rates (Bart and Robson 1982) were considered significant at the *P* = 0.05 level (two-tailed test). Daily survival rate is the probability that an undamaged clutch will remain undamaged another day.

We rejected the null hypothesis that nests in all zones were equally likely to be damaged. Fifty-three percent of the artificial clutches in the tephrafall grid experienced some depredation in 1983, while 20% suffered damage in 1984 (Table 2). In contrast, only 5% of the clutches in the blowdown zone were damaged in either year. Estimates of daily survival rate, assuming constant survivorship during the 15-day period, ranged from 0.949 to 0.997 (Table 3). Thus, the probability of a 1983 tephrafall three-egg clutch escaping depredation for 10 days was 0.949<sup>10</sup>, or 0.59, compared with 0.97 for a blowdown clutch. The 1983 tephrafall-zone survival rate (Table 3) was significantly lower than any other. The 1984 tephrafall rate

was the lowest recorded that year, although no statistical difference was detected among the sites.

The intensity of predation also differed among sites. Depredated clutches in the tephrafall zone tended to lose all three eggs (Table 2), while clutches damaged elsewhere lost at most one egg.

Potential nest predators in the Mount St. Helens area include the Gray Jay (*Perisoreus canadensis*), Common Raven (*Corvus corax*), several rodents, small and large carnivores, and reptiles (Williams 1900, Maxson and Oring 1978, Smith and Andersen 1982, Thatcher 1968). Avian predators were rare in the blowdown zone and relatively uncommon at the tephrafall site during the study period (Table 1). Mammalian population levels, especially ground-dwelling rodents, were nearly equal at control and tephrafall sites, and somewhat lower at the blowdown site (MacMahon unpubl. data). An exception was the Cascade's golden-mantled ground squirrel (*Spermophilus saturatus*), which was not recorded at the control site and had not been recorded in the blowdown zone before 1984 (Andersen and MacMahon 1985b). Garter snakes (*Thamnophis* sp.) and alligator lizards (*Gerrhonotus coeruleus*) were seen at the tephrafall and control sites, but relative densities are unknown.

The low nest survivorship noted for the tephrafall site in 1983 (Table 3) may be responsible for the low number of breeding juncos found there in 1984 (Table 1). We speculate that the significant rise in nest survival rate at the tephrafall site between 1983 and 1984 (Table 3) was a consequence of a widespread, weather-related decrease in small mammal numbers between those years (MacMahon unpubl. data). Although a long-term rise in nest survival rate within the tephrafall zone is consistent with our view of posteruption community dynamics (see below), the 1984 level more likely reflected a short-term fluctuation in rodent density. No change in vegetation structure was apparent.

If junco nest density parallels the general decline in junco abundance from undisturbed clearcut to blowdown (Table 1), predator response to nest density would lead to the lowest survival rates in undisturbed sites. The observed variation in artificial nest survival rates (Table 3) suggests that any response to nest density, if present, was masked by other factors. We suggest that the relatively high predation rate in the tephrafall zone was the consequence of a near-normal species complement and density of potential predators, coupled with low levels of vegetation/ground cover and the uniformly gray substrate color. In the blowdown zone concealing cover was reduced, but so were the potential predators. This led to relatively low predation rates. The low level of predation at the control site was due to the high level of ground cover, the availability of alternative prey items, and, possibly, the absence of ground squirrels. This conclusion parallels that of Boag et al. (1984), who implicated shrub cover as a determinant of the

rate of predation by rodents on nests of Spruce Grouse (*Dendragapus canadensis*).

The probability of a ground nest suffering depredation is a complex function of habitat spatial heterogeneity (Bowman and Harris 1980) and the types and numbers of potential predators present (Maxson and Oring 1978, Parker 1984). Both factors are susceptible to change during succession. We speculate that predator density in the tephrafall zone will remain at current levels, but ground vegetation cover will increase to pre-eruption values. Thus, ground-nest predation levels should decrease. In contrast, predation levels within blowdown areas will rise as a more complete set of potential predators develops within a habitat featuring relatively low concealment cover.

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### Brood Parasitism of Eastern Kingbirds by Brown-headed Cowbirds

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Understanding why brood parasites lay eggs in the nests of hosts that reject eggs is hampered by insufficient data on the frequency with which parasites lay in rejecter nests, and by ignorance of which individuals practice this seemingly inappropriate behavior. Parasitism rates of rejecters can be determined only when host nests are observed during egg laying because most parasite eggs are rejected rapidly (e.g. Scott 1977). Even then, however, a certain percentage of parasitized nests may go undetected. Determining the selective value of host defense mechanisms also depends on knowledge of the frequency of parasitism, and the amount of reproductive loss caused by parasitism when it occurs (Rothstein 1976a).

Experimental investigations of brood parasite relations between Brown-headed Cowbirds (*Molothrus ater*) and Eastern Kingbirds (*Tyrannus tyrannus*) have demonstrated unequivocally that kingbirds are rejecters of cowbird eggs (Rothstein 1975, 1976b). Existing

data suggest that kingbirds are rarely parasitized: the percentage of kingbird nests containing cowbird eggs ranges from 0% to 0.8% (Robertson and Norman 1976, Goertz 1977, Lowther 1977). Friedmann (1963) also reported Eastern Kingbirds to be infrequent cowbird hosts. My purpose is to present estimates of actual rates of brood parasitism on Eastern Kingbirds by Brown-headed Cowbirds, including annual variation in parasitism; to describe the consequences of, and responses to, naturally occurring cowbird parasitism on kingbirds; and to test whether female cowbirds select kingbird nests on the basis of host egg size. For the last objective, I assumed that cowbird nestlings are disadvantaged when competing for food with equal-aged nestling kingbirds because of their smaller size. Because egg and hatchling size are correlated positively in both species (Nolan and Thompson 1979, Murphy 1981), I predicted that one mechanism cowbirds may use to reduce the kingbirds' advantage is to lay large eggs in nests containing large kingbird eggs.

I studied kingbirds in Erie Co., western New York, in 1979 and in Douglas Co., eastern Kansas, in 1980-

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