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The Influence of Human Disturbance on Tufted Puffin Breeding Success

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Burrow-nesting alcids are vulnerable to human disturbance (Amaral 1977, Manuwal 1978), but little quantitative information exists on the impact of researcher disturbance on estimates of alcid breeding success. We estimated our influence on Tufted Puffin (*Fratercula cirrhata*) reproductive success as part of a larger study of seabird ecology on the Barren Islands, Alaska (Manuwal and Boersma 1977).

The Barren Islands (58°55′N, 152°10′W) are located at the entrance to Cook Inlet in the Gulf of Alaska. The seven islands range in size from 60 to 17,000 ha. We studied the Tufted Puffin colony on East Amatuli Island from May through August 1978. Vegetation on East Amatuli is dominated by beach rye (*Elymus arenarius*), sedge (*Carex* sp. and *Honckenya peploides*), and cow parsnip (*Heraculum lanatum*) at lower elevations and alpine tundra plants (e.g. *Empetrum, Vaccinium, Lupinus, Potentilla*) at upper elevations. The island is treeless. The vegetation, climate, and breeding seabirds on the island were described by Bailey (1976), Manuwal and Boersma (1977), Manuwal (1979), and Simons (1980). The 1.5-ha study site was located above a rocky border along the island's eastern coast. Burrow density was estimated at approximately 830 active burrows/ha. Active burrows were defined as burrows in which Tufted Puffins laid eggs. We divided the puffin colony into three similar areas that received different levels of disturbance. Every effort was made to minimize unnecessary disturbance. Generally, only one of us visited the colony, and our activities usually flushed most of the breeding adult puffins from the vicinity. Approximately 2 h were spent collecting data during each visit, and adult birds generally did not return to their burrows until after our departure. We visited Area 1 every 5 days from late May to early June to determine egg-laying dates. We dug access holes to the nest chambers of longer burrows and covered the holes with weighted squares of plywood. Burrows that contained warm eggs were not checked again for approximately 45 days; they were then checked every 5 days to determine hatching dates, and every 3 days thereafter to collect chick growth data. Burrows in Area 2 were not checked until most eggs in Area 1 had hatched; nestlings were then weighed and measured every 3 days. Burrows in Area 3 were visited only once, 17 August, when nestlings in the other two areas were close to fledging. Burrow occupancy rates and chick sizes and weights were determined during this visit and compared with data from chicks in Areas 1 and 2. All chicks were weighed and measured using 100, 500, or 1,000-g Pesola spring scales and steel caliper. Statistical tests were taken from Dixon and Massey (1969) and Helwig and Council (1979), and significance was assumed at an alpha level of 0.05.

Reproductive success was significantly lower on heavily disturbed Area 1 (6 chicks fledged from 78 total burrows checked, including both active and inactive burrows) than in undisturbed Area 3 (15 chicks fledged from 32 total burrows checked; Chi-square test, $P < 0.001$; Table 1). Assuming that approximately 50% of all Tufted Puffin burrows on the Barren Islands have eggs laid in them (Amaral 1977, Manuwal and Boersma 1977), we estimate that our activities on the colony reduced fledging success from an undisturbed rate of 94% (15 chicks fledged/16 eggs laid; Area 3) to 18% (6 chicks fledged/34 eggs laid; Area 1) in the heavily disturbed area ($\chi^2 = 22.84$, $P < 0.001$).

It is also clear that the development of chicks in the most disturbed area was retarded. Even though logistic growth-rate constants (*K* values; Ricklefs 1967, 1968) of the nestlings in Areas 1 and 2 were similar, chicks from Area 1 were significantly lighter and had shorter wings than chicks from the less disturbed areas (ANOVA, $P < 0.001$; Table 1). Chicks were also significantly younger in Area 1 than in Area 2. Age

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TABLE 1. Reproductive success and nesting development of Tufted Puffins, Barren Islands, Alaska, 1978.

	Area and period of disturbance		
	1 Egg-laying to fledging	2 Nestling period[a]	3 One day
No. of burrows checked	78	—	32
No. of eggs laid	34	—	—
No. of eggs hatched	12	—	—
No. of chicks fledged	6	—	15
Growth constant (*K*)	0.103	0.101	—
Growth asymptote (g)	560.0	569.0	—
Average nestling development on 17 August[b]			
n	14	16	15
Age (days)	32 (A)	38 (B)	—
Weight (g)	471.0 (A)	548.0 (B)	538.0 (B)
Winglength (mm)	113.0 (A)	132.0 (B)	129.0 (B)

[a] Breeding success/burrow was not determined in Area 2 because data were collected only from burrows that were still active in late July.

[b] Areas with the same letter are not significantly different from each other using least-squares means.

determination was not possible for chicks in Area 3 because they were not first visited until late summer. The growth rates of nestlings in Areas 1 and 2 were close to those reported for other Alaskan colonies (Wehle 1983) and in previous years for the Barren Island colonies (Amaral 1977).

Chicks from Areas 2 and 3 achieved 96% of fledging weight (growth asymptote; Table 1) by 17 August. Four of 16 chicks (25%) fledged before 24 August. One of these chicks fledged between 17 and 21 August. In contrast, chicks from Area 1 averaged only 84% of fledging weight on 17 August. Only 1 of 14 chicks (7%) from Area 1 fledged in the period before 24 August. We suggest that these measurable differences in chick development were not a result of different growth rates among the three study areas but were an effect of disturbance during egg-laying or incubation that resulted in delayed hatching dates. Chicks in Area 2 hatched an average of 6 days earlier than those in Area 1.

Our activity in the colony during the incubation period apparently had two effects. First, it reduced breeding success directly in some nests due to desertion. Second, it may have lengthened the incubation period in nests that were temporarily deserted. Egg neglect resulting in extended incubation periods has been reported in a number of seabirds (Boersma and Wheelwright 1979, Murray et al. 1979, Boersma 1982), and it appears that Tufted Puffin embryos also may be capable of withstanding periods of abandonment early in incubation. We found three cold eggs during burrow checks that subsequently hatched chicks; one of these chicks fledged.

An alternative hypothesis, that adults in Area 1 laid later than those in the other two areas, also would explain our results. We feel that it is unlikely, however, for several reasons. Egg-laying by Tufted Puffins on the Barren Islands is highly synchronous (Amaral 1977, Manuwal and Boersma 1977), and the birds in Area 1 were not disturbed until just prior to laying. Postponing laying at that late date would have required retaining a well-developed egg, and we know of no evidence of this capability in alcids.

Our findings have implications for how estimates of Tufted Puffin reproductive success should be made. Clearly, disturbance during the incubation period can substantially lower breeding success and alter the apparent breeding chronology of the colony. Sensitive colonies should not be disturbed at all during the incubation period, and estimates of reproductive success should be made by combining data from several similar subcolonies that are visited at progressively later intervals during the season. Tufted Puffin nestling development was not adversely affected by periodic visits to collect growth data.

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Was Bachman's Warbler a Bamboo Specialist?

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Although the virtual extinction of the Bachman's Warbler (*Vermivora bachmanii*) has been considered to be natural (Stevenson 1972), a satisfactory explanation has yet to be proposed. Destruction of forest habitat per se does not seem to be involved in the decline. The riverine swamps of the southeastern United States have been extensively logged and drained, but there is no direct evidence that destruction of virgin forest habitats was a key factor in the warbler's disappearance. What little we know about the habitat preference of Bachman's Warbler does not indicate that it was as restricted to virgin forest as was the Ivory-billed Woodpecker (*Campephilus principalis*), whose dependence on mature forest follows from our knowledge of its feeding ecology (Tanner 1942). The degree to which the warbler occurred in second-growth forest is controversial (Hooper and Hamel 1977, Shuler 1977, Shuler et al. 1978). Urbston et al. (1979) found that one of the last strongholds of Bachman's Warbler, the I'On Swamp of South Carolina, was not a mature forest when most Bachman's Warblers were collected there and that most forest that was there had been logged extensively. However, the most recent observations of presumed breeding birds were in mature forest (Shuler et al. 1978; but see Hamel 1979 concerning validity of recent reports in I'On Swamp). Nevertheless, it seems unlikely that a small passerine would be completely dependent on virgin bottomland forests and find no other habitat type suitable: we have no parallel situation in any other bird of eastern North America, except the Ivory-billed Woodpecker. Therefore, it seems possible that some critical habitat or microhabitat upon which Bachman's Warbler was dependent has escaped identification.

Throughout the Neotropics, from Mexico to Argentina, bird species occur that are restricted in their habitat preference to bamboo thickets (*Chusquea* and *Guadua*; Bambusoideae); these bird species are primarily insectivores that glean arthropods from bamboo foliage and stems, although a few eat bamboo seeds (Parker 1982, Parker and Remsen MS). One species of bamboo, "cane" (*Arundinaria gigantea*), once occurred in extensive stands throughout the seasonally flooded swamplands of the southeastern U.S. Although cane is still present in much of its former range, the vast "canebrakes" that were the scourge of farmers and travelers are now greatly diminished.

William Bartram (*in* Harper 1958) frequently wrote of the extensive canebrakes encountered in his travels through the southeastern U.S. in the late 18th century. He used phrases such as "an endless wilderness of cane," "cane meadows always in view," "cane forests," "vast cane meadows," "wide-spreading cane swamps," and "cane swamps, of immense extent." Scenes such as that described at the turn of the century by Roosevelt (1962) along the Tensas River in northeastern Louisiana are essentially nonexistent today: ". . . canebrakes stretch along the slight rises of ground, often extending for miles, forming one of the most striking and interesting features of the country . . . ."

A variety of factors seem to have been involved in the decline of the great canebrakes. Canebrakes were valuable for cattle forage, and overgrazing of this resource contributed to their destruction (Hughes 1951, 1957). Because they were located on fertile floodplain soil and were more easily cleared than forest, many canebrakes were destroyed by clearing for agriculture (Hughes 1951, Meanley 1971). Fire control