

SHORT COMMUNICATIONS

Where were Kirtland's Warblers during the last ice age?—The nesting requirements of the Kirtland's Warbler (*Dendroica kirtlandii*) are highly specialized. It nests only on level or gently rolling sandy soil among young jack pines (*Pinus banksiana*) when they are about 2–4 m tall (8–20 years old) in nearly homogeneous stands. The nest is embedded in the ground and concealed under low vegetation. These conditions occur naturally only after extensive fires in jack pine woodlands. Very large tracts of potential habitat are necessary to provide a sufficient amount of forest in exactly the right stage at all times to sustain the nesting population. Although the range of the jack pine almost spans the continent, the bird nests in only one portion of northern Lower Michigan (Mayfield 1960:9–12). Here at any one time it has utilized only about 4,000 ha within the 100,000 ha of predominantly jack pine forest of the historical nesting range (Zimmerman 1956:31).

In the heart of its range the warbler has nested occasionally in suitable tracts as small as 30 ha, but this detail may be misleading because there have always been larger occupied tracts in the vicinity. The bird seems to be attracted only by extensive areas of the right kind. Even nonbreeding strays in nesting season (males seen in Wisconsin, Upper Peninsula of Michigan, Ontario, and Quebec) have been found in very large tracts somewhat similar in appearance to the nesting ground.

Until recently we supposed that suitable nesting conditions were widespread across the Midwest on the sandy outwash plains at the foot of the Wisconsin Glacier (Mayfield 1960: 24, 31). Now, however, we need to review that opinion. Pollen analyses have shown that jack pines were almost nonexistent in the Midwest 18,000 years ago at the height of the last glacial advance. The tree probably survived in that enormous region only in small isolated refugia, while at the same time jack pine covered most of the Appalachian highlands and the Atlantic Coastal Plain. It re-entered the Midwest about 10,000 years ago, replacing spruce because of its greater tolerance of repeated fires (Wright 1981, Critchfield 1985).

It is unlikely that the warbler was a significantly different creature in the late Pleistocene. It is a well-marked species, and Charles G. Sibley (pers. comm.) has expressed the opinion from DNA-based analysis that it probably separated from closely related *Dendroica* more than 100,000 years ago. We cannot be sure it has not changed its nesting behavior and habitat during the last 10,000 years, but its present rarity argues against its adaptability.

I suggest, therefore, that for a time near the end of the Pleistocene the bird's nesting range may have been restricted to the sandy coastal plain of the South Atlantic States. Similarly, other birds now breeding in the northern coniferous forest zone, may have been limited to the southeastern corner of the United States by the concentration of pinelands there. This circumstance, along with the possible origin of these species in the West Indies or beyond, may help explain why their fall migration route carries them southeast toward the sea instead of south across the midcontinent toward Mexico and Central America.

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Natal philopatry, site tenacity, and age of first breeding of the Semipalmated Sandpiper. —

There is a tendency for male-biased dispersal in birds and female-biased dispersal in mammals (Greenwood 1980). Considerable debate has centered on the reasons for such sex biases, primarily whether sex-biased dispersal exists as a means of avoiding harmful effects of extreme inbreeding (Greenwood et al. 1979, Greenwood 1980), or whether it results from intraspecific competition (Gauthreaux 1978, Moore and Ali 1984, Shields 1984, Liberg and von Schantz 1985). Pusey (1987) reviews both arguments.

Adults of many species of birds usually return to breed in areas where they have bred previously (Greenwood 1982). Therefore, in these species one would expect more obvious sexual biases in natal, compared to adult, dispersal, if sex-biased dispersal functions in inbreeding avoidance (Greenwood 1982), or to minimize intraspecific competition. It should, then, be most useful to examine sex biases in natal, rather than adult, dispersal. However, relatively few studies have examined sex biases in natal philopatry of birds (e.g., Greenwood 1980, Oring and Lank 1984).

The present note examines the effect of sex on natal philopatry, site tenacity, and age of first breeding from an eight-year study of a breeding population of Semipalmated Sandpipers (*Calidris pusilla*). The Semipalmated Sandpiper is a small, migratory shorebird with a monogamous, male-territorial mating system. I studied sandpipers at La Pérouse Bay, 40 km east of Churchill, Manitoba, in the summers of 1980 through 1987. During this period, I gradually increased the study area from 2 to 3 km². Approximately 40 to 130 pairs nested in the study area each year. Nests were mapped on 10× enlargements of aerial photographs (scale 1:2500, allowing accuracy to at least 3 m; Abraham 1980). Adult birds were given individual color-band combinations, while young nestlings were banded with one stainless steel band, and often a single color band. Adults were sexed by bill length and behavior (see Gratto and Cooke 1987). For a more complete description of the study site and methods see Gratto et al. (1985).

I defined natal philopatry as the return of birds banded as nestlings to breed in the study area. Natal site tenacity was defined as the distance from a bird's natal nest to the nest where it was first found breeding. Age of first breeding refers to the age a bird was first found with a nest. I might have missed the first breeding of a few individuals if their nests had been depredated very early, or if they had nested at the extreme edge of the study area (as did one female first found breeding at age 6). This should not have affected differences between sexes.

Because some individuals were first found breeding at age 4, returns of nestlings banded from 1980 to 1983 should be most complete (Table 1). Average return from these four years was 7 percent. Over all years, almost 90% of all young hatched in the study area were banded as nestlings. However, only 33.3% (8/24) of all yearling breeders from 1981 to 1987 (identified by the presence of partial postjuvinal wing molt, Gratto et al. 1983), were banded in