risk of injury or death (Montgomerie and Weatherhead 1988). However, observations of nest predation events under natural conditions are rare (Pettingill 1976) and observations of attacks on parent birds by predators during the course of nest predation are even more scarce. Brunton (1986) observed a Killdeer (*Charadrius vociferous*) killed by a red fox (*Vulpes vulpes*) while performing a distraction display. This observation of a Veery confronting a predator at the cost of its own life during active defense of the nest is to my knowledge, unprecedented. This observation supports speculation that adult birds assume risk of injury or death in the course of nest defense (Curio and Regelman 1985), and lends support to explanations of variability in nest-defense behavior that are couched in terms of cost-benefit analysis and the optimization of fitness (Montgomerie and Weatherhead 1988).

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Relationships of Clutch Size and Hatching Success to Age of Female Prothonotary Warblers

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ABSTRACT.—We obtained 1033 clutch sizes from 281 known-age female Prothonotary Warblers (*Protonotaria citrea*) nesting in nest boxes at Presquile National Wildlife Refuge in eastern Virginia from 1987 through 1998. Prothonotary Warblers typically nested twice during each breeding season; first clutches of all birds averaged 1.01 eggs greater than second clutches [4.96 ± 0.72 (SD) vs 3.94 ± 0.55]. Clutch size was significantly smaller in first nests of one-year-old warblers (4.64 ± 0.48) than in first clutches of females two to eight years old (5.05 ± 0.62). First clutches did not differ among age classes of birds older than one year. The mean size of second clutches was not significantly different among any of the age classes. One year old birds initiated laying significantly later than older birds (125.0 ± 6.4 vs 121.5 ± 7.7; Julian dates). The average number of infertile eggs in first clutches was larger in one year old females and differed significantly from that of older females (1.01 ± 0.90 vs 0.63 ± 0.87). The number of infertile eggs in second clutches did not differ significantly with female age. Significantly fewer eggs hatched in first nests of one year old birds than in those of older birds (3.75 ± 0.89 vs 4.33 ± 1.09). *Received 2 Dec. 1998, accepted 2 May 1999.*

The Prothonotary Warbler (*Protonotaria citrea*) is unusual among wood warblers (Parulidae) because it nests in secondary cavities. It shares this trait with only one other member of the 116 members of the subfamily Parulinae [Lucy's Warbler (*Vermivora luciae*); Curson et al. 1994]. It is likewise noteworthy among the birds of the eastern United States in that it migrates farther than the other small passerines nesting in secondary cavities. Determinants of clutch size of Prothonotary Warblers therefore may be of interest for comparison with other cavity-nesting passerines and with other Neotropical migrants. Several re-

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searchers have documented changes in reproductive success associated with age in cavity-nesting, passerine birds (Bryant 1988, McCleery and Perrins 1989, Sternberg 1989, Sæther 1990), but to date there have been few such data for a warbler.

Prothonotary Warblers are declining in the United States (Sauer et al. 1997), thus any knowledge of their demography may be useful in conservation of the species. In this paper we provide an analysis of a large set of measurements of reproductive performance of the Prothonotary Warbler that we have accumulated over the past 12 years. Specifically, we examine clutch size and infertility in this species and ask the question: Does clutch size and/or infertility of eggs change with age of females?

STUDY AREA AND METHODS

Our data were obtained from 1987–1998 in swamp forest along the James River near and on Presquile National Wildlife Refuge, Hopewell, Virginia (37° 20′ N, 77° 15′ W). The habitat of the study area is tidal swamp in which the dominant tree species are black gum (*Nyssa sylvatica*), red maple (*Acer rubrum*), and ash (*Fraxinus* sp.). These swamps have a relatively harsh environment where tree-surface temperatures regularly exceed 45° C and tidal amplitude in the swamp during spring tides often exceeds 1 m. Beginning in March 1987, we placed nest boxes made of salt-treated pine or red cedar at 100 m intervals along the creek banks. Box dimensions were 28 L × 9 W × 6 D cm and the entrance hole was 3.8 cm in diameter (see Blem and Blem 1991, 1992, 1994, for details). We gradually increased the number of nest boxes in the study from 141 in 1987 to 300 in 1993–1998.

We checked the contents of boxes 8–15 times during each breeding season. Old nest material was removed from the boxes in late winter. Eggs that failed to hatch were opened to determine fertility and degree of development. The present paper includes only those clutches that were incubated by females and only those eggs that failed to hatch because of infertility. Clutches that failed because nests were abandoned were not included in the analyses. Parasitism by Brown-headed Cowbirds (*Molothrus ater*) is relatively uncommon at our study site (<5% of all clutches), but nests containing cowbird eggs were excluded from our analyses. We recorded dates of first eggs and clutch sizes only for those nests visited often enough that we could be certain of laying dates. In some instances, we determined clutch size but nests were subsequently taken by predators and we were unable to determine fertility of the eggs. Sample sizes therefore vary among various subsets of the data. Because Prothonotary Warblers typically produce two clutches each season (Petit 1989, Blem and Blem 1992), we divided nests with eggs into two groups: first clutches in which first eggs were laid from 25 April through 20 May and second clutches in which first eggs were laid after 20 May. Recaptures of banded birds indicated that this division was accurate for this data set. Nest boxes were originally attached to trees. We moved them to metal poles in 1995, almost completely eliminating predation on nests. Since then many females have been recaptured during second broods in the same nest box. We captured adults by hand-netting them as they emerged from boxes and banded all birds with aluminum USFWS bands. In 1998, we used the criteria in Pyle (1997) to age adults, but older adults and many birds captured before 1998 could only be aged relative to previous captures. We designated such birds with a + (i.e., 3+) to indicate minimal age, and analyzed age classes accordingly.

All data are reported as means ± SD. Differences among groups were analyzed using nonparametric Kruskal-Wallis tests (χ^2 approximation; Zar 1984, SAS Institute Inc. 1990, Proc NPAR1WAY). In all statistical tests, a probability of 0.05 or less was accepted as significant ($P < 0.05$). All analyses were performed using SAS (Ver. 6; SAS Institute, Inc. 1990) on an IBM mainframe computer (VM operating system).

RESULTS

Sample size.—Over the 12 years we banded 2968 nestlings and 482 adult females. Birds were recaptured opportunistically, therefore sample sizes varied from year to year and individual age classes came from various years. We recovered 487 adults and 103 birds banded as nestlings. Recaptures during the same clutch were counted only once. Of all females banded as adults, 47.9% were recaptured at least once in subsequent years (n = 231). Only 1.7% of all nestlings were recaptured (n = 50). Some females (n = 112) were captured over several years and, therefore, are represented in several age classes in Tables 1 and 2.

Clutch size.—We obtained 1033 clutch sizes from 281 female Prothonotary Warblers of known age (Table 1). First clutch sizes differed significantly among age classes (χ^2 = 22.4, P = 0.002, df = 7), but there was no difference in second clutches (χ^2 = 5.0, $P >$ 0.05, df = 7). One year old female Prothonotary Warblers laid an average of 0.4 fewer eggs in first clutches (4.64 ± 0.48; n = 42) than did older females (5.03 ± 0.73; χ^2 = 17.7, $P < 0.001$, df = 1; Table 1). First clutches did not differ among age classes of birds older than one year (χ^2 = 4.6, $P > 0.05$, df = 6). First clutches of all birds averaged 1.01 eggs more than second clutches (4.96 ± 0.72 vs 3.94 ± 0.55; χ^2 = 356.8, $P < 0.001$, df =

TABLE 1. Clutch size of known-age female Prothonotary Warblers captured at Presquile National Wildlife Refuge, Virginia.

Age (years)[a]	First clutches[b]	Second clutches[b]	Julian date of first egg[b]
1	4.64 ± 0.48 (42)	3.81 ± 0.60 (11)	125.0 ± 6.4 (40)
1+	4.91 ± 0.72 (395)	3.86 ± 0.62 (128)	124.1 ± 5.5 (381)
2	4.94 ± 0.79 (33)	3.90 ± 0.32 (10)	123.2 ± 5.6 (32)
2+	5.04 ± 0.79 (211)	4.06 ± 0.46 (65)	121.4 ± 5.8 (205)
3	5.20 ± 0.42 (10)	4.25 ± 0.50 (4)	120.3 ± 2.5 (10)
3+	4.97 ± 0.59 (58)	4.12 ± 0.33 (17)	121.3 ± 6.2 (55)
4	4.50 ± 0.71 (2)	— (0)	121.0 ± 4.2 (2)
5–8	5.18 ± 0.53 (33)	4.00 ± 0.39 (14)	121.0 ± 6.1 (32)
Totals	4.96 ± 0.72 (784)	3.94 ± 0.55 (249)	123.0 ± 5.8 (757)

[a] Plus signs indicate that females were that age or older.
[b] Numbers in parentheses are sample sizes. Values are means ± SD.

1; Table 1). The mean of second clutches of one year old birds was 0.24 eggs fewer than that of females 2–8 years old (3.81 ± 0.60 vs 4.05 ± 0.54), but did not differ significantly among the age classes (χ^2 = 9.1, $P > 0.05$, df = 5; Table 1). We found no change in clutch size over consecutive years for 82 of 122 individuals; in 24 cases clutch size increased by one egg, in 14 cases clutch size decreased by one egg, and in two cases clutch size decreased by two eggs.

Nest initiation dates.—Nest initiation dates (Julian) differed significantly among age classes in the whole data set (χ^2 = 54.7, $P <$ 0.001, df = 7), but not among age classes of females 2 years old or older (χ^2 = 6.2, $P >$ 0.05, df = 5). One year old birds initiated laying of first clutches significantly later than older birds (125.0 ± 6.4 vs 121.5 ± 5.8; (χ^2 = 13.9, $P < 0.001$, df = 1). The mean date of nest initiation was remarkably stable among females greater than two years old, varying very little from 1 May (Julian date = 121).

Infertility rate.—The number of infertile eggs in first clutches was significantly larger in one year old females than in older birds (χ^2 = 3.9, $P < 0.05$, df = 1; Table 2), but the number of infertile eggs in second clutches did not differ significantly with female age (χ^2 = 8.7, $P > 0.05$, df = 7). Infertile eggs were more frequent in first clutches than in second (χ^2 = 8.8, $P < 0.01$, df = 1). We found no effect of age on frequency of clutches in which all eggs hatched, regardless of clutch size (χ^2 = 0.04, $P > 0.05$, df = 1). One year old birds hatched all eggs in 36.0% (18/50) of their clutches. Older birds hatched all eggs in 35.6% (235/660) of their clutches and there was no significant difference between the two groups (χ^2 = 0.005, $P > 0.05$, df = 1).

TABLE 2. Number of infertile eggs and nestlings per clutch of known-age Prothonotary Warblers captured 1987–1998 at Presquile National Wildlife Refuge, Virginia.

	Number of infertile eggs		Number of nestlings	
Age (years)[a]	First clutches[b]	Second clutches[b]	First clutches[b]	Second clutches[b]
1	1.00 ± 0.90 (28)	0.43 ± 0.53 (7)	3.70 ± 0.89 (28)	3.43 ± 0.79 (7)
1+	0.55 ± 0.75 (295)	0.42 ± 0.61 (67)	4.41 ± 0.92 (295)	3.58 ± 0.69 (67)
2	0.92 ± 1.41 (26)	0.50 ± 0.68 (10)	4.04 ± 1.64 (26)	3.40 ± 0.71 (10)
2+	0.66 ± 0.88 (179)	0.47 ± 0.79 (49)	4.36 ± 0.94 (179)	3.61 ± 0.86 (49)
3	0.90 ± 1.20 (10)	0.50 ± 0.71 (2)	4.30 ± 1.25 (10)	3.50 ± 0.71 (2)
3+	0.71 ± 1.01 (45)	0.21 ± 0.43 (14)	4.31 ± 1.18 (45)	3.86 ± 0.36 (14)
4	0.50 ± 0.71 (2)	— (0)	4.00 ± 0.00 (2)	— (0)
5–8	0.73 ± 0.87 (26)	0.33 ± 0.71 (9)	4.46 ± 1.17 (26)	3.55 ± 1.01 (9)
Totals	0.64 ± 0.87 (611)	0.42 ± 0.69 (158)	4.34 ± 1.01 (611)	3.59 ± 0.77 (158)

[a] Plus signs indicate that females were that age or older.
[b] Numbers in parentheses are sample sizes. Values are means ± SD.

DISCUSSION

In eastern Virginia, Prothonotary Warblers lay 2–8 eggs per clutch and clutch size varies significantly among years (Blem and Blem 1992). In 1986, we initiated a study to identify those factors that were responsible for those yearly differences. To lend explanatory strength to our analyses, we attempted to identify potential sources of variation. For example, date of clutch initiation is significantly related to clutch size (Blem and Blem 1992), while nest cavity volume, position of the nest, presence of old nest materials, and female mass are not (Blem and Blem 1991; Blem et al. 1999, unpubl. data). Female age is related significantly to Prothonotary Warbler clutch size in a manner similar to that found in several other cavity-nesting species (Klomp 1970, Sæther 1990), particularly the European Starling (*Sturnus vulgaris*; Kluijver 1935), House Martin (*Delichon urbica*; Bryant 1988), Pied Flycatcher (*Ficedula hypoleuca*; Sternberg 1989) and Great Tit (*Parus major*; McCleery and Perrins 1989). In all of these species, older females laid 0.4–1.0 more eggs per clutch than birds producing their first clutch. The increase in mean size of first clutches with age may be due to several factors including proximate factors such as increased development of reproductive tracts or enhanced ability to collect and process energy, thus allowing females to produce more eggs.

The effects of senility on clutch size are less well known. There seems to be no documented decreases of clutch size accompanying longevity in passerine birds. This might be due to the difficulty in obtaining clutch sizes from the rare individuals that reach more than a few years of age. In the present study we obtained clutch measurements from several birds more than four years old, including one each from six, seven, and eight year old birds. One female originally caught as an adult in 1990 was recaptured a total of 8 times from 1990–1997. Her first clutch sizes were 4 (1990), 5 (1992), 5 (1993), 5 (1995), 5 (1996), and 5 (1997). In 1997 the bird was at least eight years of age. The previous longevity record for Prothonotary Warblers was 5 years, 11 months (Kennard 1975).

Conservation measures, including intensive use of predator-proof nest boxes, have been successful in increasing local abundance of Prothonotary Warblers (Blem and Blem 1992). However, elimination of predation at nest boxes could skew age structures of warbler populations either by increasing production of young or by decreasing mortality of adult females nesting in boxes. Skewed age structures could then affect clutch size and infertility rates, this factor must be taken into account in any analysis of annual variations in clutch size. For conservation of the species, reduced clutch size and greater infertility of young birds seem to have only a modest impact on reproductive performance of Prothonotary Warblers. Furthermore, effects of senility were not obvious even in relatively old warblers.

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Hybridization Between Clay-colored Sparrow and Field Sparrow in Northern Vermont

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ABSTRACT.—A male sparrow showing hybrid characteristics between Clay-colored (*Spizella pallida*) and Field sparrows (*Spizella pusilla*) was first observed in Grand Isle, Vermont, in 1997. In 1998, the same hybrid defended a territory and mated with a female Field Sparrow. The pair produced one fledgling. The hybrid's signature song was composed of the buzzy notes of a Clay-colored Sparrow rising to a final trill as if copying a Field Sparrow's accelerating clear whistles. *Received 18 Dec. 1998, accepted 9 May 1999.*

I have found only two previous records of Clay-colored Sparrows (*Spizella pallida*) and Field Sparrows (*Spizella pusilla*) cooperating at a nest. Finch and Smart (1974) mention, without further details, a Clay-colored Sparrow found breeding with a Field Sparrow at Rockefeller Institute, Dutchess County, New York; "young were taken for study." The one example of hybridization presented by Knapton (1994) is the account by Brooks (1980) of a trio of adults, a male Clay-colored Sparrow and a pair of Field Sparrows, at a nest near Millbrook, Dutchess County, New York; however, "the fledged young appeared identical to young Field Sparrows." Carey and coworkers (1994) refer to the same report as "possible" hybridization. Hybridization between these two species is not unexpected because of their close phylogenetic relationship (Patten and Fugate 1998). Examples exist of apparent crossbreeding between Clay-colored Sparrows and other *Spizella* species, and between Chipping Sparrow (*Spizella passerina*) and Brewer's Sparrow (*Spizella breweri*; Knapton 1994, Pyle and Howell 1996).

Clay-colored Sparrows are rarely reported in Vermont (Faccio et al. 1997, 1998). In contrast, Field Sparrows may be abundant in proper habitat such as the abandoned overgrown fields and pastures of Grand Isle, a town on Lake Champlain in northwestern Vermont. There, on 29 May 1997, I identified a Clay-colored Sparrow by its song which consisted of two long buzzes. At 09:30, 11:00, and 16:30 EST, for a total of 30 minutes, I listened to the sparrow sing from elevated perches in a grassy clearing surrounded by red cedar (*Juniperus virginiana*), staghorn sumac (*Rhus typhina*), and common barberry (*Berberis vulgaris*). This sparrow was relocated 650 m north on 2 June, and last heard on 5 June.

From 23 July through 14 August, I observed and recorded a second Clay-colored Sparrow in a similar clearing 300 m southwest of the original location. I recorded the songs on a microcassette recorder and transferred the songs to a computer using either Creative

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