Soras in Tidal Marsh: Banding and Telemetry Studies on the Patuxent River, Maryland

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Abstract.—From 1993 to 1999, we conducted banding and telemetry studies of fall migrant Soras (Porzana carolina) in the historic rail hunting and exceptional stopover habitat of the Wild Rice (Zizania aquatica) marshes of the tidal Patuxent River. Drift traps equipped with audio lures produced 3,897 Sora and 417 Virginia Rail (Rallus limicola) captures during the seven-year study. Sora captures were characterized by a high proportion (70% to 90%) of young-of-the-year and a paucity of between-year recaptures (N = 12). Radio-telemetry studies depicted Soras as long-distance migrants with high stopover survival and a critical dependence on tidal freshwater marshes for migratory fattening. Here, the high productivity of Wild Rice, Smartweeds (Polygonum spp.) and other seed-bearing annual plants seem intrinsically linked to Sora migratory fitness. A stopover period of >40 days and mean mass gain of +0.6g/d suggests Soras are accumulating large fat reserves for long-distance flight. Radio tracking confirmed Soras as strong flyers with a demonstrated overnight (ten h) flight range of 700-900+ km. Given the potential size of fat reserves and the ability to use tail winds, it is conceivable for Soras to make nonstop flights from the Patuxent River to Florida, the Bahamas, or even the Caribbean. Given the potential size of fat reserves and the ability to use tail winds, it is conceivable for Soras to make nonstop flights from the Patuxent River to Florida, the Bahamas, or even the Caribbean. However, strong winds and tail winds make this flight range possible. The critical dependence of Soras and other seed-dependent, fall-migrant waterbirds on highly productive yet limited tidal freshwater marsh habitats make conservation of such areas a priority mission within the Chesapeake Bay.

Key words.—Porzana carolina, Sora, Rallus limicola, Virginia Rail, Zizania aquatica, migration, radio telemetry, tidal marsh, Patuxent River, Chesapeake Bay.

The freshwater tidal marshes of the Jug Bay region of the upper Patuxent River, an estuarine tributary of Chesapeake Bay, have long been known for a fall spectacle of maturing Wild Rice (Zizania aquatica) and an abundance of fall migrant waterbirds, especially Soras (Porzana carolina) (Meanley 1975, 1996). A diminutive rail, the Sora breeds at low densities in a wide variety of freshwater habitats across the northern continent and is likely the most abundant rail in North America (Melvin and Gibbs 1996). Fall migration begins in late summer and birds arriving from northern breeding areas concentrate in Atlantic coastal marshes. Arrival is closely timed with the maturing of Wild Rice, a favorite food. The Ojibwe (Chippewa or Anishinabe) people of the Great Lakes region, whose culture has historic ties to Wild Rice, or ‘manomin,’ have named the Sora “manoominikeshiinh,” meaning “one who shows where the rice is ripe for harvesting” (J. St. Arnold, Great Lakes Indian Fish and Wildlife Commission, pers. comm.). Tidewater tribes, such as the Powhatans of Virginia, were well aware of the arrival of Soras in tidal marshes and traditionally night-lighted them using fire pots in the bows of their canoes (Speck 1928). Birds were formerly so abundant they easily could be collected by swatting them from their roosts with sticks. Ancestral marshes of the Powhatan tribes occurred along the Pamunkey, Mattaponi and Chickahominy Rivers, which to this day remain important rail stopover habitats.

The hunting of Soras in coastal marshes by early American colonists was indelibly captured by naturalist and artist Alexander Wilson in his classic nineteenth century ornithological work. Soras are also a popular game bird in the Atlantic Flyway, and the decline in popularity of the Sora as a game bird in the Atlantic Flyway is attested to by the single sport-hunting recovery from our 3,900 bandings.
thology (Wilson 1812). Wilson painted the Sora against a sinuous tidal river, stalks of Wild Rice, and a punt boat with hunter discharging his black powder shotgun. With the advent of the center-fire shotgun in the latter nineteenth century, Sora hunting developed into a popular shooting sport, especially prior to the Migratory Bird Treaty Act of 1918 that empowered the Federal government to curtail wanton market hunting and to set limits on the sport harvest of migratory game birds. Even then, daily bag limits as high as 50 birds attracted many shooting enthusiasts, including dignitaries such as General Billy Mitchell, whose participation on the Patuxent helped popularize rail hunting as a sporting pastime (Mitchell 1933). Whereas many fresh-tidal marshes were well known locally and regionally for rail shooting, including the upper Potomac and Anacostia Rivers at Washington, D.C. (Coues and Prentiss 1883), the Patuxent marshes remained the most well-known rail hunting area in the Chesapeake region. While no quantitative information regarding historic population trends or harvest of Soras in Patuxent River marshes exists, our interviews with several old-time rail hunters indicate that present day Sora numbers have declined and with it, the popularity of the species as a game bird.

This study was motivated by the apparent decline in Sora use of historic Patuxent River stopover habitat, the paucity of information about Sora stopover ecology and migration, and the need for better management and conservation of the species as a game bird. Moreover, the study of Soras during stopover offers one of the few opportunities to potentially capture large numbers of birds and assess species status. These objectives are in concert with several priority research and conservation needs as emphasized by Conway et al. (1994) and Melvin and Gibbs (1994, 1996).

**METHODS**

**Study Area**

The study area is located along a ten-km stretch of tidal-emergent marsh, some 600 ha in extent, commonly referred to as the Wild Rice marshes of the Jug Bay region of the upper Patuxent River, near Upper Marlboro, Maryland (38°47'N, 76°42'W, Fig. 1). The size and pristine nature of these marshes has led to their inclusion as a site component of the Chesapeake Bay National Estuarine Research Reserve, Maryland. The Patuxent River marshes are classified as tidal freshwater marshes (Cowardin et al. 1979; Odum et al. 1984; Tiner and Burke 1995), or less frequently, fresh estuarine river marshes (Stewart 1962). They are bordered upstream by tidal freshwater swamps (forested) and downstream by brackish marshes. Lying just below the fall line, the fresh-tidal reach of the Patuxent River receives runoff from a watershed that lies within the Baltimore-Washington corridor, one of the most heavily populated and developed areas of the United States. As high nutrient and sediment loads associated with such development have suppressed the productivity of submerged aquatic vegetation of Chesapeake Bay (Orth and Moore 1983; Kemp et al. 1983), inter-tidal emergent plants like Wild Rice have benefited from the enriched waters brought twice daily on the tide. In this regard, the emergent marshes of the Patuxent River are likely as luxuriant and productive today as at any time in the past.

The subspecies of Wild Rice of the Patuxent is the tall, broadleaf coastal form known as southern Wild Rice (Zizania aquatica var. aquatica, Oelke et al. 2000). This species has minimal salt tolerance and its distribution in the estuary closely parallels that of Spatterdock (Nuphar advena) and Pickerelweed (Pontederia cordata). In association with Wild Rice, the marshes contain a highly diverse assemblage of freshwater plants that are distributed along a depth gradient (Anderson et al. 1968; Odum et al. 1984; Tiner and Burke 1995). Plants that occur in deeper zones include such broad-leaved emergents as Spatterdock, Pickerelweed, Arrow Arum (Peltandra virginica), and Arrowhead (Sagittaria latifolia), those that occupy high marsh include Rice Cutgrass (Leersia oryzoides), Walter Millet (Echinocloa walteri), River Bulrush (Schoenoplectus fluviatilis), Dotted Smartweed (Polygonum punctatum), Arrow-leaved Tearthumb (P. sagittatum), Halberd-leaved Tearthumb (P. arifolium), Tidemarsh Waterhemp (Amaranthus cannabinus), Jewelweed (Impatiens capensis), Bur-marigold (Bidens laevis) and Cattail (Typha spp.). Wild Rice typically occurs in river-bordering pure stands or in mixed vegetation at intermediate depths. Wild Rice and other freshwater emergent plants grade downstream to brackish marsh dominated by Black Needlerush (Juncus roemerianus) and Cordgrasses (Spartina spp.), especially S. alterniflora (Anderson et al. 1968).

**Capture Techniques**

Large-scale capture and bandings and conventional VHF radio-telemetry methods were the principal investigative techniques used to study Soras during stopover and migration. Trapping methods were designed specifically for Sora and Virginia Rails (Rallus limicola). Improved capture techniques were developed in 1993 based on Seth Low clover leaf traps (Low 1935), as originally modified by Stewart (1951, 1954) for use with Clapper Rails (Rallus longirostris, Kearns et al. 1998). Traps were constructed from 2.5-cm mesh galvanized wire and drift fences from standard 2.5-cm mesh, 46-cm high poultry wire. A critical modification included ramped funnels of 1.3-cm mesh hardware cloth that greatly improved retention of rails. Catch boxes were made of 1.3-cm mesh vinyl-coated wire to minimize bill abrasion of trapped birds. Capture success was enhanced by use of
audio playback of rail vocalizations. One minute of rail calls were played on a 50% duty cycle to help lure rails to drift traps. The audio tract included 40 s of Sora calls (“keek,” “kerwee,” and “whinny,”) and 20 s of Virginia Rail calls (“kiddick” and grunts). Initial use of cassette tape recordings proved unreliable and solid-state record-
ing with special programming was developed for long-term, high-quality sound reproduction (Kearns et al. 1998). The final design featured the one-min rail recording, a playback delay capability to adjust the off time up to ten min, and a 24-h timing circuit to provide programmable turn-on capability for the following day. Trap lines varied in configuration depending on marsh topography, but typically each consisted of two cloverleaf traps evenly spaced along 46+ m of drift fence with a playback sound system (audio unit, battery, solar charging panel and speaker) located centrally between the traps. In 1997, the effect of audio lure on capture success was tested by alternating every other trap line with playback for two-day periods. The study was conducted for 23 rotations (46 days) from 9 Sept until 24 Oct.

Sexing and Aging Soras

The accuracy of field sexing techniques based on live bird morphological and plumage characters described by Pospichal and Marshall (1954) was tested. Fall plumage characters easily separated Soras by age, i.e., adults, or after-hatching-year (AHY) birds, that were in definitive basic plumage and young-of-the-year, or hatching-year (HY) birds, that were in juvénal plumage or a stage of transition to basic I plumage (see molts and plumages in Melvin and Gibbs 1996). Criteria for sexing Soras were based on the premise that males are generally larger (measures of body mass, culmen, toe, and tarsus) than females and male adults have richer plumage and brighter physical features than females. For example, the large, chrome-yellow bill of males often contrasts with the smaller olive-green bill of females. Two adult sex-linked features noted by Pospichal and Marshall (1954: Fig. 1) were examined: the extent and pattern of the auricular patch (isolated posteriorly and/or anteriorly indicating male, connected both anteriorly and posteriorly depicting female) and the superciliary line (distinctly or indistinctly broken indicating male, connected both anteriorly and posteriorly depicting female). The auricular patch and superciliary line are not developed and therefore do not pertain to sexing fall migrant HY birds. To test the sexing criteria, DNA techniques were used to determine the sex of a random sample of Sora captures. The goal was to sex 100 Soras in 1997 of about equal sex and age. Six birds contributed by hunters were used to provide a sample of known-sex individuals for development of a sex-linked marker. DNA tests were conducted on 40 µl blood samples collected from the medial metatarsal vein of trapped Soras. Samples were stored in ethanol and processed by D. Zaitlin of the National Aviary, Pittsburgh, Pennsylvania.

Food Value of Rice and Smartweed Seeds

Because of the documented importance of various smartweeds and Wild Rice to fall migrant Soras, proximate analysis and bomb calorimetry were conducted to compare the food value and energy content of these foods. A systematic sample of mature seeds of Wild Rice and three species of smartweeds common to the Patuxent marshes were collected in three areas of the marsh from a minimum of three plants each. Samples were pooled, mixed, and dried in an oven for two weeks at 60°C. Seeds were then ground to a powder in a food mill and sent to the University of Maine food laboratory for analysis (A. Bushway, Department of Food Science, 5736 Holmes Hall, University of Maine, Orono, Maine).

RESULTS

Summary of Captures and Bandings

A total of 3,897 Soras and 417 Virginia Rails were captured for banding during the seven-year period, 1993-1999 (Table 1). Discarding the 1993 and 1994 startup years (traps were not fully deployed and modified), an average 655 Soras and 66 Virginia Rails were captured each fall, 1995-1999.
during a ten-week trapping period using ten trap lines/year. Over these five standardized trapping years, capture success for Soras varied nearly four-fold (296 versus 1,118) while Virginia Rail captures varied two-fold (41 versus 92). Good numbers of Soras began arriving in the marsh as early as the third week in August and peak captures occurred in early to mid-September (Fig. 2). Capture success increased following cold fronts that brought flights of birds to the marsh, as depicted in the capture histogram for the 1995 fall season (Fig. 3). Soras began departing the marsh with the first frosts in October (see also Telemetry Studies).

An exceptional flight of birds occurred in fall 1998 that yielded the largest capture of 1,118 Soras and 92 Virginia Rails. Among Soras, 88.7% of captures were HY birds (992 birds). HY Soras exceeded AHY captures in all banding years and ranged from 70.6% to 90.1% (mean = 80.3 ± 2.95 SE percent, N = 7, Table 1). Not surprisingly, HY Sora captures were highly correlated with total captures ($r_s = 0.99, P < 0.01$), whereas AHY Soras were not ($r_s = 0.65, P > 0.05$). Because of the lack of established ageing criteria, fall migrant Virginia Rails could not be confidently separated as HY and AHY captures. However, it is noted that Sora and Virginia Rail captures were highly correlated ($r_s = 0.96, P < 0.01$), which provides evidence that the numbers of Virginia Rails captured each year also was driven by the fall flight of young birds. To examine whether there was temporal variation in the capture of AHY versus HY Soras, differences in mean percent of AHY captures was tested in each of five arbitrary capture periods, late August through early November, using captures from six banding years (1994-1999). Mean percent of AHY Sora captures ranged from 15.1% to 22.8% but were not different across capture periods ($P > 0.5$, Table 2).

Another distinct feature of Sora trapings was a paucity of between-year recaptures; only twelve recaptures were recorded during the seven-year study (Table 1), the highest number predictably occurring during later years, i.e., five in 1998 and three in 1999. These recaptures accounted for 4.0% and 5.1% of AHY captures in those years, respectively. Eleven of twelve recaptures were banded HY and recaptured the following fall, whereas a single Sora banded HY was recaptured two years after banding. All twelve recaptures were trapped in the same section of marsh and three were caught on the same trap line of initial capture. Notably, no AHY Soras banded during the seven-year study (N = 674) were either recaptured during fall trapping or later recovered, that is, shot by hunters or found dead. However, one AHY Sora, a bird banded in fall 1995, was recaptured during a small spring trapping effort in April 1996. Only a single Virginia Rail recapture was recorded during our study: an HY male trapped in 1997 was recaptured on the same trap line in fall 1999.

### Table 1. A summary of seven years of fall captures of Soras and Virginia Rails using clover-leaf drift traps in the tidal freshwater marshes of the Patuxent River, Maryland. Trapping was standardized to ten trap lines and a ten-week trapping period from 1995-1999.

<table>
<thead>
<tr>
<th>Year</th>
<th>Soras Captures</th>
<th>% HY</th>
<th>Recaptures</th>
<th>No. with transmitters</th>
<th>Virginia Rails Captures</th>
<th>Total captures</th>
</tr>
</thead>
<tbody>
<tr>
<td>1993</td>
<td>126</td>
<td>70.6</td>
<td>0</td>
<td>0</td>
<td>38</td>
<td>164</td>
</tr>
<tr>
<td>1994</td>
<td>496</td>
<td>81.7</td>
<td>1</td>
<td>0</td>
<td>49</td>
<td>545</td>
</tr>
<tr>
<td>1995</td>
<td>754</td>
<td>74.0</td>
<td>1</td>
<td>0</td>
<td>82</td>
<td>836</td>
</tr>
<tr>
<td>1996</td>
<td>392</td>
<td>73.2</td>
<td>0</td>
<td>20</td>
<td>42</td>
<td>434</td>
</tr>
<tr>
<td>1997</td>
<td>715</td>
<td>90.1</td>
<td>2</td>
<td>40</td>
<td>73</td>
<td>788</td>
</tr>
<tr>
<td>1998</td>
<td>1,118</td>
<td>88.7</td>
<td>5</td>
<td>53</td>
<td>92</td>
<td>1,210</td>
</tr>
<tr>
<td>1999</td>
<td>296</td>
<td>83.8</td>
<td>3</td>
<td>53</td>
<td>41</td>
<td>337</td>
</tr>
<tr>
<td>Totals</td>
<td>3,897</td>
<td>82.6</td>
<td>12</td>
<td>166</td>
<td>417</td>
<td>4,314</td>
</tr>
</tbody>
</table>

*a Only a single Virginia Rail recapture was recorded: a bird banded HY in 1997 was recaptured in fall 1999.
*b HY: hatching year.
Only two recoveries were reported from the 4,300+ Sora and Virginia Rail bandings. The first was a Virginia Rail banded in October 1998 and found dead three months later from an apparent collision at a light post near Daytona Beach, Florida, a straight-line distance of 1,150 km from the Patuxent River study area. Virginia Rails are believed to fly at low altitudes during migration and such deaths by collision have been previously reported (Conway 1995). The second was an HY Sora banded in fall 1999 and shot by hunters in fall 2000 in the Wild Rice marshes of the Maurice River, another historic rail hunting marsh located in southern New Jersey (near Millville, New Jersey, about 160 km ENE of the Patuxent study area). Virginia Rails seemed less abundant in tidal marsh as they accounted overall for about one-tenth of our rail captures (9.7%). Known to prefer shallowly flooded zones of high marsh, fewer Virginia Rails may have been available for capture because of placement of traps in mid intertidal areas of greater water depth (Sayre and Rundle 1984; Conway 1995). Peak captures of Virginia Rails occurred later than that of Soras, indicating a later arrival (Fig. 3). By mid-October Sora captures were well on the decline and many Soras were actively departing on migration.

Figure 2. The onset and duration of northerly cold fronts in relation to Sora and Virginia Rail capture success in fall 1995. Captures tended to increase following northerly weather fronts that brought flights of migrant rails to the marsh in late August and September. A pre-dawn audio lure was used to enhance capture success. Soras were departing the study area on migration with arrival of October cold fronts.

Figure 3. Histogram of Sora and Virginia Rail captures for the seven-year study, 1993-1999. Sora captures peaked in early to mid September, versus early to mid October for Virginia Rails, and outnumbered Virginia Rail captures by about nine to one.
DNA Sexing and the Effect of Audio Lure on Rail Captures

DNA sexing of 100 Soras in 1997 indicated a field sexing error of 21% for HY birds (17 of 81) and 11% (2 of 19) for AHY birds. Of 19 total errors, 16 (84%) were mistakes in sexing females as males. Among young, this reflects errors primarily in mistaking larger females for males, i.e., a result of overlapping size (Table 3). Among adults, the error reflects the accuracy of the use of the auricular patch as the primary sex determining factor. In contrast, use of the superciliary line in determining sex was unsuccessful because “indistinctly broken” as defined by Pospichal and Marshall (1954), could not be adequately interpreted as an objective feature. Because the superciliary line was indistinct in most birds, it was concluded that this feature had little facility in sexing adult Soras.

Results of alternating trap lines with and without audio playback in 1997 revealed that the audio lure increased Sora captures by a factor of 2.1 (476 captures with lure, 226 without lure: $\chi^2_1 = 46.0$, $P < 0.001$). To test for the effect of playback on sex-specific capture rates, a correction for sex, as determined from DNA sexing, was first applied. Results showed that although more HY males were captured with playback than without (1.05 vs. 0.74 males/female, respectively), in neither case did the proportion of sexes differ from a 50/50 ratio ($\chi^2_1 = 0.4$, $P > 0.8$, and $\chi^2_1 = 2.2$, $P > 0.1$, respectively). For AHY birds, sex ratios favored males both with and without playback (1.71 vs. 1.65 males/female, respectively). However, as with HY birds, neither proportion of sexes differed from 50/50 (with lure: $\chi^2_1 = 1.63$, $P > 0.2$, without lure: $\chi^2_1 = 0.43$, $P > 0.5$). Finally, there was no difference in the age composition of the catch, i.e., AHY vs. HY birds, associated with the two methods ($\chi^2_1 = 2.53$, $P > 0.1$). AHY birds made up 13% of captures with audio lure and 8% of captures without the lure.

**Table 2. Mean percent of adult (AHY) Soras trapped in five arbitrary fall capture periods for six banding years 1994 through 1999.**

<table>
<thead>
<tr>
<th>Capture period</th>
<th>Mean % AHY in captures</th>
<th>Total Sora captures (%)&lt;sup&gt;a&lt;/sup&gt;</th>
</tr>
</thead>
<tbody>
<tr>
<td>≤10 Sep</td>
<td>15.1 ± 2.0 SE A&lt;sup&gt;b&lt;/sup&gt;</td>
<td>1,474 (39.2)</td>
</tr>
<tr>
<td>11-20 Sep</td>
<td>21.2 ± 3.0 SE A</td>
<td>1,005 (26.7)</td>
</tr>
<tr>
<td>21-30 Sep</td>
<td>22.8 ± 2.9 SE A</td>
<td>613 (16.3)</td>
</tr>
<tr>
<td>1-10 Oct</td>
<td>16.1 ± 4.2 SE A</td>
<td>423 (11.3)</td>
</tr>
<tr>
<td>&gt;10 Oct</td>
<td>18.7 ± 4.0 SE A</td>
<td>243 (6.5)</td>
</tr>
</tbody>
</table>

<sup>a</sup>Total Sora captures for all periods = 3,758.
<sup>b</sup>Values within column sharing the same letter are not different: individual 2-tailed $t$-tests ($\alpha = 0.05$).

**Table 3. A summary of culmen, tarsus, middle toe, and body mass measurements for 100 known age and sex Soras trapped 8-22 September 1997, in the Wild Rice marshes of the tidal Patuxent River. Sex was determined by DNA analysis of whole blood.**

<table>
<thead>
<tr>
<th>Age-sex</th>
<th>N</th>
<th>Culmen (mm)</th>
<th>Tarsus (mm)</th>
<th>Toe (mm)</th>
<th>Body mass (g)</th>
</tr>
</thead>
<tbody>
<tr>
<td>AHY-M</td>
<td>9</td>
<td>21.8 ± 0.36&lt;sup&gt;a&lt;/sup&gt; A&lt;sup&gt;b&lt;/sup&gt;</td>
<td>35.3 ± 0.63 A</td>
<td>38.0 ± 0.74 A</td>
<td>79.0 ± 1.35 A</td>
</tr>
<tr>
<td></td>
<td></td>
<td>(20.0-23.3)</td>
<td>(31.6-38.0)</td>
<td>(34.4-42.0)</td>
<td>(75-85)</td>
</tr>
<tr>
<td>HY-M</td>
<td>30</td>
<td>20.4 ± 0.16 B</td>
<td>34.5 ± 0.25 A</td>
<td>37.3 ± 0.28 A</td>
<td>73.5 ± 1.73 A</td>
</tr>
<tr>
<td></td>
<td></td>
<td>(18.2-22.3)</td>
<td>(31.7-36.8)</td>
<td>(33.8-40.7)</td>
<td>(54-89)</td>
</tr>
<tr>
<td>AHY-F</td>
<td>10</td>
<td>19.2 ± 0.18 C</td>
<td>31.8 ± 0.33 B</td>
<td>33.9 ± 0.40 B</td>
<td>64.1 ± 2.08 B</td>
</tr>
<tr>
<td></td>
<td></td>
<td>(18.3-20.2)</td>
<td>(29.8-33.3)</td>
<td>(31.2-36.1)</td>
<td>(53-76)</td>
</tr>
<tr>
<td>HY-F</td>
<td>51</td>
<td>19.0 ± 0.08 C</td>
<td>32.5 ± 0.17 B</td>
<td>34.7 ± 0.20 B</td>
<td>64.9 ± 1.06 B</td>
</tr>
<tr>
<td></td>
<td></td>
<td>(17.9-20.3)</td>
<td>(29.3-35.1)</td>
<td>(32.4-37.9)</td>
<td>(46-85)</td>
</tr>
</tbody>
</table>

<sup>a</sup>Means ± SE with range shown in parenthesis.
<sup>b</sup>Means within columns sharing the same letter do not differ: individual 2-tailed ‘t’-tests ($\alpha = 0.05$).
Body Mass and Mass Change During Stopover

Mean values of body mass for a sample of 100 known age and sex Soras (Table 3) showed that adult males are heaviest followed by HY males, AHY and then HY females; body mass values exhibited considerable overlap between age-sex categories. Mean body mass calculated from large-sample field captures for combined years 1995-1999, showed the same ranking and overlap (Table 4), albeit the data are subject to measurable sexing error especially for HY birds. Soras ranged from 40 g to 126 g and individuals below 55 g were most often HY birds near or even possibly below lean body mass. These individuals appeared stressed from the energetic demands of migratory flight, perhaps from late hatching or otherwise lack of building sufficient body stores prior to migration.

Change in body mass for Soras during stopover was measured for within-year recaptures, i.e., birds captured a second time within the same fall with a known period of residency. To exclude possible negative effects of capture trauma on body mass, the analysis was limited to birds recaptured ≥ten days after initial banding. For the five years with the highest number of bandings (1994-1998), 141 Soras were recaptured from ten days to 52 days after initial banding. Most of these recaptures, especially those in the initial two week (ten-to-24 day) interval, exhibited a wide variation in mass gain, including some mass loss (twelve or 8.5% of birds lost mass during this period). A fitted linear regression (Fig. 4) revealed a mass increase of +0.61 g/d ($t_{139} = 8.0$, $P < 0.001$). The mean mass gain for Soras in the late 25- to 52-day recapture interval was 2.6 times greater than that for birds in the early ten-to-24 day interval (22.1 ± 1.32 SE g [N = 39] versus 8.6 ± 0.86 SE g [N = 102], respectively, $t_{139} = 8.4$, $P < 0.001$). This indicates that Soras gain mass relatively slowly during early stopover and more rapidly with the approach of migration departure. The relationship of the rate of mass gain to initial body mass of the 141 recaptures was found to be negative (Fig. 5, $m = -0.022$ g/d, $t_{139} = -4.7$, $P < 0.001$). This result is consistent with the notion that body mass is a correlate of physiological condition and that mass gain, i.e., refueling rate during stopover, is inversely related to initial body mass.

Proximate Analysis of Rice and Smartweed Seeds

The results of proximate analyses and bomb calorimetry tests show that three common smartweeds of the Patuxent marshes are comparable to Wild Rice in gross nutrient and energy content and all are consistently high in carbohydrate, low in fat and comparable in ash content (Table 5). Only protein levels showed measurable differences with Wild Rice and Arrow-leaved Tearthumb being about five percentage points higher in protein than Halberd-leaved Tearthumb and Dotted Smartweed.

Telemetry Studies

A customized transmitter attachment was developed for Soras in 1996 by test marking

| Table 4. Mean body mass of fall migrant Soras captured in drift traps in the Patuxent River marshes from 1995 to 1999. Birds were arbitrarily aged and sexed in the field and therefore are subject to measurable sexing error, especially among HY birds. |
|-----------------|-----------------|-----------------|-----------------|
|                | HY              | AHY             |
|                | Male            | Female          | Male            | Female          |
| Mean body mass (± SE) | 72.3 ± 0.24 A$^a$ | 62.5 ± 0.23 B | 76.1 ± 0.53 C | 64.0 ± 0.48 D |
| (47-126)$^b$    | (40-100)        |                 | (54-117)        | (48-86)         |
| N = 1,659       | N = 1,123       |                 | N = 373         | N = 205         |

$^a$Means with different letters are different: individual 2-tailed $t$-tests ($\alpha = 0.05$).

$^b$Range of values.
20 Soras with radio transmitters and tracking them in the field. A single mortality was attributed to a poorly fit, non-stretch harness that was believed to predispose the Sora to predation. Using the refined attachment technique in 1997 and 1998, an additional 90 Soras were instrumented and monitored in the field until migration or transmitter battery failure (Haramis and Kearns 2000). No mortalities were recorded and 60 Soras (67%) were known to migrate from the study area. An additional 23 Soras were believed to depart on migration based on a characteristic over-night loss of signal. Seven birds remained in the marsh and were tracked until early winter when their transmitters failed. During stopover, Soras were characteristically sedentary in an area of marsh where they were initially captured and released. This pattern continued until the onset of migration when birds spent considerably more time flying at night, especially just after dark.

Monitoring Soras in Migration

By monitoring telemetry signals from bluffs overlooking the study area, an abrupt increase in signal strength was indication that a rail had taken flight. Typically a bird would circle the marsh a few times gaining altitude, and then depart on a direct southerly bearing. Major land features and river courses appeared to play no role in the chosen flight direction. Cold northerly weather fronts bringing near freezing or subfreezing air temperatures triggered Sora migration. The first of such fronts typically arrived in early October (Fig. 2). Most birds migrated on nights with favorable tail winds and stars clearly visible, usually the first or second night following passage of a strong weather front. Clearly visible stars, or some portion thereof in the night sky, seemed essential for

Table 5. Results of proximate analyses and bomb calorimetry on a grab sample of seeds from Wild Rice and three species of smartweeds collected from Patuxent River marshes.

<table>
<thead>
<tr>
<th>Species</th>
<th>% Ash</th>
<th>% Protein</th>
<th>Calculated carbohydrate</th>
<th>Extractable fat %</th>
<th>Energy Kcal/g</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Zizania aquatica</em></td>
<td>1.66</td>
<td>17.16</td>
<td>71.01</td>
<td>2.17</td>
<td>4.22</td>
</tr>
<tr>
<td><em>Polygonum arifolium</em></td>
<td>2.27</td>
<td>12.88</td>
<td>74.12</td>
<td>2.38</td>
<td>4.18</td>
</tr>
<tr>
<td><em>Polygonum sagittatum</em></td>
<td>3.18</td>
<td>17.32</td>
<td>70.13</td>
<td>3.76</td>
<td>4.34</td>
</tr>
<tr>
<td><em>Polygonum punctatum</em></td>
<td>2.50</td>
<td>11.89</td>
<td>73.40</td>
<td>3.70</td>
<td>4.13</td>
</tr>
</tbody>
</table>

ªHalberd-leaved Tearthumb.
ºArrow-leaved Tearthumb.
ªªDotted Smartweed.
initiation of migration. Of 26 documented departures in 1998, 20 left on clear nights, six on partly cloudy nights and none on completely overcast nights (test against equal probability: $\chi^2 = 24.3, P < 0.001$). Most Soras migrated in mid-to-late October (Fig. 6) and by mid November few birds remained in the marsh. Most birds departed on clear evenings in a 40-min window following arrival of complete darkness, a period starting about one h after sunset (Fig. 7). Making the conservative assumption that transmitter-marked Soras arrived in the marsh on the date of initial capture, average length of stay determined from known departure dates was 46.3 ± 3.7 SE days in 1996 (N = 16), 45.5 ± 2.8 SE days in 1997 (N = 33), and 44.8 ± 3.8 SE days in 1998 (N = 26).

A total of 61 transmitter-marked Soras were detected down range, most of which were passing overhead during nocturnal migration (Fig. 8). Most of these birds were located by manual tracking from automobiles at sites from the Potomac River (+72 km) to the coastal marshes of North Carolina (+370 km). Birds could be tracked predictably because they all followed the same general bearing due south. Exact flight paths were modified only by the strength and direction of tail winds. Because most tail winds had a westerly component, it was generally an issue of how far to the east the birds would be blown off course. Soras migrated in a corridor that passed directly over the major western tributaries of the Chesapeake Bay: the Potomac, Rappahannock, York and James Rivers. Most frequent passage occurred just east of Currioman Bay on the south shore of the Potomac River (+72 km), within ten km east of Williamsburg, Virginia (+180 km), then east and nearly parallel to the Chowan River to the Mattamuskeet and Pamlico Sound area of North Carolina (+370 km) (Fig. 8). Only three birds were tracked beyond coastal North Carolina during a single nighttime migration. These birds passed Seabrook Island, South Carolina, at about 05.00 h covering a straight-line distance from the Patuxent study area estimated at 725 km. We note if these birds flew straight to the Hatteras area and then either down the coast or over the Atlantic to Seabrook Island, the distance would have been considerably farther, at least 900 km (see also Discussion). Each bird passed this point in about a ten-h flight that indicated an average flight speed in the range of 72 km/h to 90 km/h. During the late December 1999 aerial survey of Florida wetlands, three Soras were located in freshwater emergent marsh of the upper St. Johns River basin, a distance of about 1,250 km from our Patuxent River study area. Two birds were located just west of Merritt Island and the third just west of Sebastian, Florida, north of Blue Cypress Lake. Vegetation cover mapping of the area pro-

![Figure 6. Migration departure date of 71 transmitter-marked Soras from the Patuxent River marsh during the three-year period 1996-1998. Most Soras (64.5%) departed between the 15-day period 18 October to 1 November, 12.7% departed before 18 October and 22.5% after 1 November. The median date of departure was 26 October and peak (mode) was 20 October. Very few Soras remained in the marsh by the onset of winter.](image)

![Figure 7. Migration departure time in relation to sunset for 64 transmitter-marked Soras on the Patuxent River study area, 1996-1998. Two thirds (66%) of Soras departed in a 40-min window following arrival of complete darkness, or beginning about 60 min after sunset.](image)
vided by the St. Johns River Water Management District (R. Brust, Florida Fish and Wildlife Commission, Fellsmere, Florida, pers. comm.) indicated all three birds were located in wetlands classified as freshwater shallow marsh, i.e., herbaceous or graminoid communities dominated by such species as Sawgrass (*Cladium jamaicense*), Maidencane (*Panicum hemitomon*), Cattails, Pickerelweed, Arrowhead (*Sagittaria spp.*), or other grasses and broad-leaved herbs.

Flight speed of 19 Soras was measured during the first 72 km of migration, from the Patuxent study area to the south shore of the Potomac River. For 17 of the 19 records, flight speed ranged from 50 km/h to 90 km/h and averaged $71 \pm 2.4$ SE km/h. Two birds covered the distance at the exceptionally high speeds of 108 km/h and 121 km/h. These high speeds could only be achieved with unusually strong tail winds aloft, winds on which it is thought that Soras would not normally migrate. Although wind speeds aloft could not be verified, the general observation was that Soras could average about 48-56 km/h in calm air. This was confirmed by following three departing birds down the Patuxent River with a high speed motor boat. Soras also seem to avoid turbulence and prefer to migrate in laminar flow air with tail winds between 16 km/h and 32 km/h. These conditions typically occur on the second and third nights following initial passage of strong northerly or northwesterly cold fronts.

**DISCUSSION**

The Value of Sora Banding

With development of successful audio-enhanced trapping techniques that doubled our capture rate, we accumulated 3,897 Sora bandings, a total that more than tripled the North American bandings for the species (M. Gustafson, USGS Bird Banding Laboratory, pers. comm.). Given this success, we quickly note that these bandings were not accomplished without considerable investment in time and effort. Our typical banding season ran for ten weeks using ten trap lines with an average catch of eight to ten rails per day. We suggest that the most efficient trapping program would be to rotate trapping effort between different sections of marsh and focus maximum effort following cold fronts. Predawn use of playback seemed to attract arriving migrants and on several occasions when timed with low tides, we trapped as many 30 to 50 rails per day. Our exceptional one-day catch was 120 Soras.

Unfortunately, the routinely small samples of AHY Soras captured each fall (averaging <20% of captures) coupled with very limited recaptures precluded any meaningful application of capture-recapture methods for population and survival estimation (Pollock *et al.* 1990). In addition, the lack of hunter recoveries, a surprising outcome, negated the use of more traditional recovery
model estimation (e.g., Brownie et al. 1978). While this annual banding process fell short of such approaches to population study, it still provided valuable information on the size of the fall flight (captures per effort) and overall reproductive success (large-sample age ratios). We note that while HY birds remain difficult to sex accurately, retention of juvenal plumage during fall provides for accurate measure of age ratio. We suggest that improved banding data for population and migration study might be obtained by simultaneously operating a number of banding stations at strategic locations down the flyway. This of course would require greater effort and logistical organization to achieve.

A single hunter recovery from our 4,314 bandings of Soras and Virginia Rails indicates that hunting of these diminutive rails is mostly a sport of bygone days, at least in the Atlantic Flyway. Until the advent of the cooperative Migratory Game Bird Harvest Information Program (HIP) by the U.S. Fish and Wildlife Service and state wildlife agencies, a program that requires registration by all migratory game bird hunters, there was no information available on how many hunters pursued rails and no method of estimating harvest. Preliminary statistics forwarded by the HIP program (P. Padding, U.S. Fish and Wildlife Service Migratory Bird Management Office, pers. comm.) show that during the recent five-year period 2000-2004, 967 rail wings were contributed to the parts survey of which 952 (98%) were about equally divided between Soras and Clapper Rails. While this indicates that Sora and Clapper Rails are the most heavily hunted rails in the flyway, the low hunter participation in the parts survey and less than stochastic nature of contributions precludes meaningful estimate of species-specific harvest. The HIP program reports that from 2002 to 2004, about 2,600 hunters declared to have pursued rails annually in the U.S. portion of the Atlantic Flyway, and although imprecise, total annual rail harvest is estimated to range from 5,000-50,000 birds. Virginia, New Jersey, South Carolina, and Florida are identified as the most important harvest states for rails in the Atlantic Flyway.

Tidal Freshwater Marsh as Sora Habitat

Fresh estuarine river marshes are unique in the diversity and productivity of seed-bearing annual plants that provide the food needed to replenish body stores of migratory birds like Soras. By comparison, the brackish and salt marsh plant communities have an impoverished diversity and limited seed supply for rails and other granivorous or seasonally granivorous birds. A study of Sora fall food habits along the Housatonic River in Connecticut showed this clearly (Webster 1964). Soras collected from freshwater marsh consumed 98% seeds (by volume) while those collected in brackish marsh consumed 91% invertebrates. Plants such as Wild Rice, smartweeds, and millets are primary to attracting large numbers of migrant Soras and other waterbirds to Patuxent marshes (Meanley 1975, 1996). In the past the numbers were stunning, e.g., during the first week of September 1960, Meanley estimated 22 million Red-winged Blackbirds (Agelaius phoeniceus) and 10,000 Bobolinks (Dolichonyx oryzivorus), known locally as reed birds, on the Patuxent marshes. Today Bobolinks have greatly declined but Red-winged Blackbirds remain the most abundant passerine in the fall marsh.

Wild Rice is recognized as one of the most important wildlife foods to migrant rails, song birds (Meanley 1961, 1965; Webster 1964) and numerous ducks (McAtee 1911, 1917; Martin and Uhler 1939; Moyle and Hotchkiss 1945). While our proximate analyses show smartweeds and Wild Rice to be nutritionally equivalent (Table 5), the attractiveness of Wild Rice may lie in its high digestibility while developing on the panicle, or what Meanley (1996) referred to as the ‘milk’ and ‘dough’ stages of seed development. Early arriving birds may glean rice directly from the panicle, but because rice shatters (falls) over a short period of about three weeks in September, it may have limited availability. Once rice has fallen, feeding is limited to picking rice from inter-tidal mud. Smartweeds on the other hand are indeterminate flowering plants that continue to produce and hold seed well into fall. Be-
cause of this, seeds of smartweeds, especially the large-seeded Halberd-leaved Tearthumb, may have a longer period of availability than Wild Rice. Some evidence of this is provided by the higher frequency of occurrence of smartweed seeds versus rice from Sora food habit studies on the Patuxent (Wilke and Meanley 1942; Meanley 1996).

The high carbohydrate content of rice and smartweed seeds make them an excellent diet for lipogenesis. As a general pattern birds are known to fatten more quickly for migration by feeding on either relatively low protein-high fat diets, in which case the fats are assimilated directly (e.g., Red Knots \([\textit{Calidris canutus}]\) feeding on eggs of the Horseshoe Crab \([\textit{Limulus polyphemus}]\) in Delaware Bay [Haramis \textit{et al.} 2007]), or on high carbohydrate diets, such as represented by rice and smartweed seeds, where fatty acids are produced from \textit{de novo} synthesis in the liver (McWilliams \textit{et al.} 2004).

Insights on Sora Migration

Our success in documenting transmitter-marked Soras departing on migration supports the long-believed influence of cold fronts on triggering migration (e.g., Bent 1926), and identifies a possible strong dependence on visible stars for navigation. Although a weak flying bird when flushed in the marsh, we have demonstrated that indeed Soras can manage long-distance flights of 700-900+ km in a single night at average speeds of 70-90 km/h. The long stopover and mass gains made on the Patuxent also support the notion that Soras are storing large quantities of fat to undertake long-distance flight. While we tracked Soras relatively easily from Maryland to coastal North Carolina, we could not follow them out over the Atlantic Ocean. We observed Soras to maintain flight well out to sea over Hatteras at the risk of not making landfall. Based on bearing and flight speed as they passed the Cape Hatteras-Cape Lookout area, we would predict them to reach the vicinity of the Bahamas Islands in just under 18 h (straight line distance of about 1,300 km from the Patuxent study area). Thus, a Sora departing the Patuxent marsh at 18.30 h and averaging 72 km/h flight speed, is estimated to arrive in the Bahama Islands about 12.30 h the next day, requiring five+ hours of diurnal flight over water.

Are Soras capable of this flight? Evidence from three birds reaching Seabrook Island, South Carolina, an estimated distance of about 700-900 km, indicates it is possible. Gains in body mass also suggest fat stores in the range of 25 to 30 g should provide sufficient fuel. From the shorebird flight range model developed by Castro and Myers (1989), Soras were estimated to be able to cover 1,400+ km on 30 g of fat while flying at a calm air speed (estimated) at 50 km/h. While these shorebird models have not been validated for Soras (i.e., Soras are not as efficient in flight as shorebirds), Soras are known to make efficient use of tail winds aloft which could substantially extend their range with no additional flight cost. Our average measured speed of 72 km/h would indicate that use of tail winds could extend Sora flight range by 40-50%, and at the likely attainable speed of 90 km/h, extend range by nearly 100%.

Because fall migrants tend to follow wind patterns about high pressure systems (see Moore \textit{et al.} 1995: Fig. 5.3), Soras can be predicted to track prevailing winds south or southeasterly on departure and southwesterly on the back side of the cell. Thus, successful migration is perhaps a matter of good timing, so that winds that carry Soras out to sea off North Carolina, might carry them first south and eventually southwesterly back to the Georgia-Florida coast later in the flight. Our lack of success in detecting Soras migrating directly along the Carolina-Georgia coastline seems consistent with this pattern. Whereas data is lacking for Sora migration beyond coastal North Carolina, evidence gained from actively tracking migrating birds serves to underscore navigation skills and wind patterns aloft as critical components to successful migration.

Soras are well known winter residents of the Caribbean, Bermuda, the Netherland Antilles, Trinidad and Tobago, south to northern South America, including Columbia, Ecuador, Venezuela, and Guyana (Melvin and Gibbs 1996 and citations there-
in). In contrast, Virginia Rails winter mostly in Atlantic coastal and Gulf marshes of the deep south and are apparently rare or unknown in the Caribbean islands and south of northern Mexico (Conway 1995).

The wind-driven nature of Sora migration might be the primary factor underlying the apparent lack of site fidelity and thus the lack of between-year recaptures observed during fall bandings on the Patuxent River. Another possible explanation might be that adults have a different migration flight path or chronology than young-of-year that reduces their catchability. For instance, adults may depart the breeding ground later than HY birds, take a different flight path, or either overfly or make only a brief stop before continuing. Yet a third possibility is simply the ‘cost of migration,’ i.e., high mortality especially for HY birds that are inexperienced and have less body reserves to sustain long flights, especially over open ocean. This notion, although unverified, might be argued from the general demographic pattern that high mortality tends to go hand-in-hand with high fecundity, a basic precept of ‘r’ selection. Soras are highly fecund, i.e., they average ten eggs in the nest (Melvin and Gibbs 1996), and the wide swings in numbers of fall bandings as driven by recruitment success, suggests the species fits an “r” selected demography.

**CONSERVATION CONSIDERATIONS**

Our findings underscore the critical value of tidal freshwater marshes as primary stopover habitat for Soras and other migrant waterbirds in the Atlantic coastal plain. Although tidal freshwater marshes are characteristic of most Chesapeake Bay tributaries, as well as estuaries south along the Atlantic coast (Odum et al. 1984), most of these marshes are sharply zoned and of limited size (see Tiner and Burke 1995: Fig. 6-1). Large marsh tracts like those of the Patuxent are at a premium, e.g., even along the ca. 70 km tidal Patuxent River well developed freshwater emergent marsh occurs along <10% of this distance. We note that an unusual extent of Wild Rice marsh, likely the largest in the Chesapeake Bay area, occurs along a 16-km reach of the Chickahominy River, a tributary of the James River, near Williamsburg, Virginia.

The limited extent and high ecological value of tidal freshwater marshes make these habitats worthy of special stewardship, protection, and management. For the Patuxent marshes this has been provided through designation as part of NOAA’s National Estuarine Research Reserve (NERR) system, a management partnership at the federal, state, and county level. The stewardship role, as expressed in a Memorandum of Understanding between local counties and the state of Maryland, is dedicated to wetland protection, research, and education, while maintaining the marsh in a natural state. Major threats include water quality issues such as pollution, sediment and nutrient burdens, as well as changes in vegetative composition of the marsh, including control of invasive species, such as Common Reed (*Phragmites australis*) and Purple Loosestrife (*Lythrum salicaria*). The value of stewardship and partnering within government to mediate threats or otherwise meet the management needs of the NERR recently was demonstrated by response to the catastrophic loss of rice to grazing by an overpopulation of resident Canada Geese (*Branta canadensis*) (Haramis and Kearns 2004, 2007). Goose herbivory was not only eliminating large tracts of rice but leaving inter-tidal mud flats barren of vegetation and vulnerable to invasion by less desirable species. In response to this problem, co-managers formulated a five-year program that successfully reestablished rice and reduced numbers of geese. The program used protective fencing, widespread seeding of rice, and Maryland’s September resident Canada Goose hunting season to remove 1,900+ geese from the Jug Bay area. This successful program served to alert wetland managers to the threat of resident Canada Geese to our mid latitude marshes, especially given the recent large increase in the flyway population to about one million birds (Atlantic Flyway Council 1999; Hindman et al. 2004).

Another threat to the Patuxent marshes is the possible appearance of South American Nutria (*Myocastor coypus*), a large, fur-
A bearing mammal capable of rapid population growth and destruction of emergent wetlands through grazing (Willner et al. 1979). Nutria were first released in the 1940s in marshes along the Blackwater River on the eastern shore of the Chesapeake Bay, where eventual overpopulation helped accelerate widespread conversion of emergent marsh to open water (Bounds and Carowan 2000; GMH, unpubl. data). A federal program to eradicate Nutria in Maryland was established in 2004 and has demonstrated excellent success in removing over 11,000 animals from eastern shore marshes. However, dispersing Nutria remain problematic in establishing satellite populations at distant locations, including the western shore of the Bay (S. Kendrot, USDA-APHIS, pers. comm.). Until such populations are located and removed, this exotic mammal will continue to be a threat to Chesapeake Bay’s tidal wetlands.

More long-term issues involve such factors as global change, e.g., global warming, and the continued impact of human population growth in the watershed. The potential ecosystem effects of both factors are numerous and complex. For instance, rising sea level alone could radically alter vegetation and substantially reduce the extent of our estuarine marshes in the next 100 years (Poff et al. 2002; Cahoon et al. 2006; Erwin et al. 2006) and continued rapid pace of suburban development and urbanization in the upper watershed could further degrade water quality by increasing nutrients, sediment, and pollutants to the estuary and threatening further fragmentation of lands bordering riparian corridors.

Actions that prevent wetland loss and secure natural land buffers for all watercourses in the Patuxent drainage will have the greatest benefit to water quality. Likewise, preservation of natural borders in the estuary will allow for natural processes to mediate rising water levels due to global warming. Protective regulations that hinge on Maryland’s Tidal Wetlands Act and the Federal Clean Water Act have helped reduce the rate of loss of Maryland’s wetlands in recent decades (Tiner and Burke 1995) and passage of Maryland’s Critical Area Act in 1984 restricts development or alteration of lands within a 300 m perimeter of tidal waters, thus helping to create a strong buffer zone for the Bay’s tidal boundaries. Other important government programs that help preserve ecologically important lands bordering the tidal Patuxent include the Greenways Plan and Program Open Space. The Patuxent Greenway Plan aims to prevent the fragmenting effects of development through acquisition or easement of lands bordering the river. Likewise, Maryland’s Program Open Space is also designed to acquire lands to conserve natural resources and provide outdoor recreation. Supported by funds generated from the state’s real estate transfer tax, Program Open Space has provided millions of dollars to enable counties to purchase ecologically valuable lands which include many parcels along the Patuxent River. Whereas this suite of regulations and programs provides a level of direct protection to our tidal wetlands, water quality issues especially from non-point urban, and to a lesser degree, agricultural sources in the upper watershed are predicted to continue to be the most difficult and challenging problem for the Patuxent River in the future.

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LITERATURE CITED


McAtee, W. L. 1911. Three important wild duck foods. United States Department of Agriculture, Bureau of Biological Survey, Circular Number 81, Washington, D.C.


Moyle, J. B. and N. Hotchkiss. 1945. The aquatic and marsh vegetation of Minnesota and its value to


