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# Premigrational Movements and Behavior of Young Mallards and Wood Ducks in North-central Minnesota

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# Premigrational Movements and Behavior of Young Mallards and Wood Ducks in North-central Minnesota

by

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## Abstract

Movements and behavior of 89 young mallards (*Anas platyrhynchos*) and 48 young wood ducks (*Aix sponsa*) were monitored on a 932-km<sup>2</sup> study area in north-central Minnesota in late summer and fall, 1972-74, with telemetry, visual observation, and aerial surveys. Initial flights of both species were confined to the natal (brood) marsh; first flights away from the natal marsh occurred in the third week after fledging in both species. First flights of young mallards and wood ducks away from their natal marshes were not significantly different between the sexes (mallard,  $\bar{x}$  = 4.95 km for females and 5.83 km for males; wood ducks,  $\bar{x}$  = 2.31 km for females and 2.64 km for males). However, flights away from the brood marshes by wood ducks were significantly shorter than for mallards.

As young mallards and wood ducks grew, their daytime use of the natal marshes decreased in an irregular pattern as both species began daily flights between day- and night-use areas. Locally reared mallards made longer daily flights between use areas than did wood ducks, but wood ducks changed use areas with greater frequency before 1 October. Despite often extensive movements,

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most locally reared mallards and wood ducks remained in the vicinity of their brood marshes throughout fall until migration.

Movement of young birds to new habitat was not the result of random searching and thus fortuitous discovery of nearby areas. Instead, birds seemed to learn of new habitat and develop movement patterns by associating with other birds; locally reared young always moved in the company of flocks of conspecifics that included adults and older immatures.

Differences in movement patterns between the sexes of young birds and between young and adult birds cause them to be differentially distributed by age and sex on and near the breeding grounds. These differences are ultimately reflected in the distribution of the hunter harvest. We have interpreted generalizations about such phenomena, developed from analysis of continent-wide mallard banding data, using our data obtained from individually marked birds. We document (a) greater distances moved by early than by late-hatched young in the postbreeding period before migration, (b) differential movement of age and sex cohorts that explains greater hunting mortality of young than adults and of females than males near natal marshes, (c) differences in length and timing of postbreeding movements of adult male mallards and the postfledging movements of immature male mallards that help explain the northerly continental recovery distribution of young males, and (d) differential timing and rate of movement by birds through harvest areas (early departure of males and some return of females to natal marshes after the beginning of hunting) that explain differences in the timing of hunting season recoveries. Behavioral differences between the age and sex cohorts in the fall waterfowl population on and near their breeding grounds in north-central Minnesota can explain observed differences in survival and recovery rates of adult and young birds.

The behaviors observed suggest to us that restrictive harvest regulations such as small-area closure may have little or no local benefits at the breeding grounds because premigratory assemblages of birds make extensive movements. In particular, protection of postbreeding adult females and locally reared young might only occur by closing large areas or scheduling extreme delays in the season opening, neither of which may be compatible with equitably apportioning waterfowl harvest at higher latitudes. Additional research on the local effects of restrictive regulations, and on age- and sex-specific differences in the timing, rate, and direction of fall movements of postbreeding waterfowl is needed.

The premigrational activities of young Anatidae have not been studied with the detail accorded waterfowl during the breeding and brood-rearing periods. Hochbaum (1944, 1955) reviewed the activities of North American prairie ducks and the topic of waterfowl movements in general and provided casual observations on the movements of young birds. Some details of the behavior and premigratory movements of young redheads (*Aythya americana*) were discussed by Williams (1944) and Low (1945), of young American black ducks (*Anas rubripes*) by Wright (1954) and Ringelman and Longcore (1982), of young ring-necked ducks (*Aythya collaris*) by Mendall (1958), of young wood ducks by Stewart (1958) and Grice and Rogers (1965), and of young mallards by Raitusuo (1964).

We describe the fall movements and behavior of young mallards and wood ducks from fledging until the onset of migration in north-central Minnesota. Differences are quantified between species, ages, and sexes, in movements, behavior, and habitat use, while birds are in the vicinity of the natal marshes. We relate these data to recent reviews of the distribution and derivation of the

mallard hunting harvest. We also address whether harvest regulations can be designed to protect adult females and locally reared young, and provide suggestions for further research in postbreeding ecology. This work was conducted as a part of a long-term investigation of the postbreeding ecology of ducks in forested north-central Minnesota (Kirby 1976, 1989; Kirby et al. 1976, 1981, 1983; Gilmer et al. 1977).

## Study Area

The study area was centered in the northwest portion of the Chippewa National Forest, Beltrami County, about 25 km east of Bemidji, Minnesota. Regular aerial searches were conducted for radio-equipped birds within a 932-km<sup>2</sup> area (Fig. 1), and searches were also conducted in several other counties in northwestern, western, and central Minnesota each year. Ducks were trapped and fitted with radio transmitters on four lakes where large numbers of waterfowl congregated in late summer (Fig. 2). These lakes contained large, interspersed stands

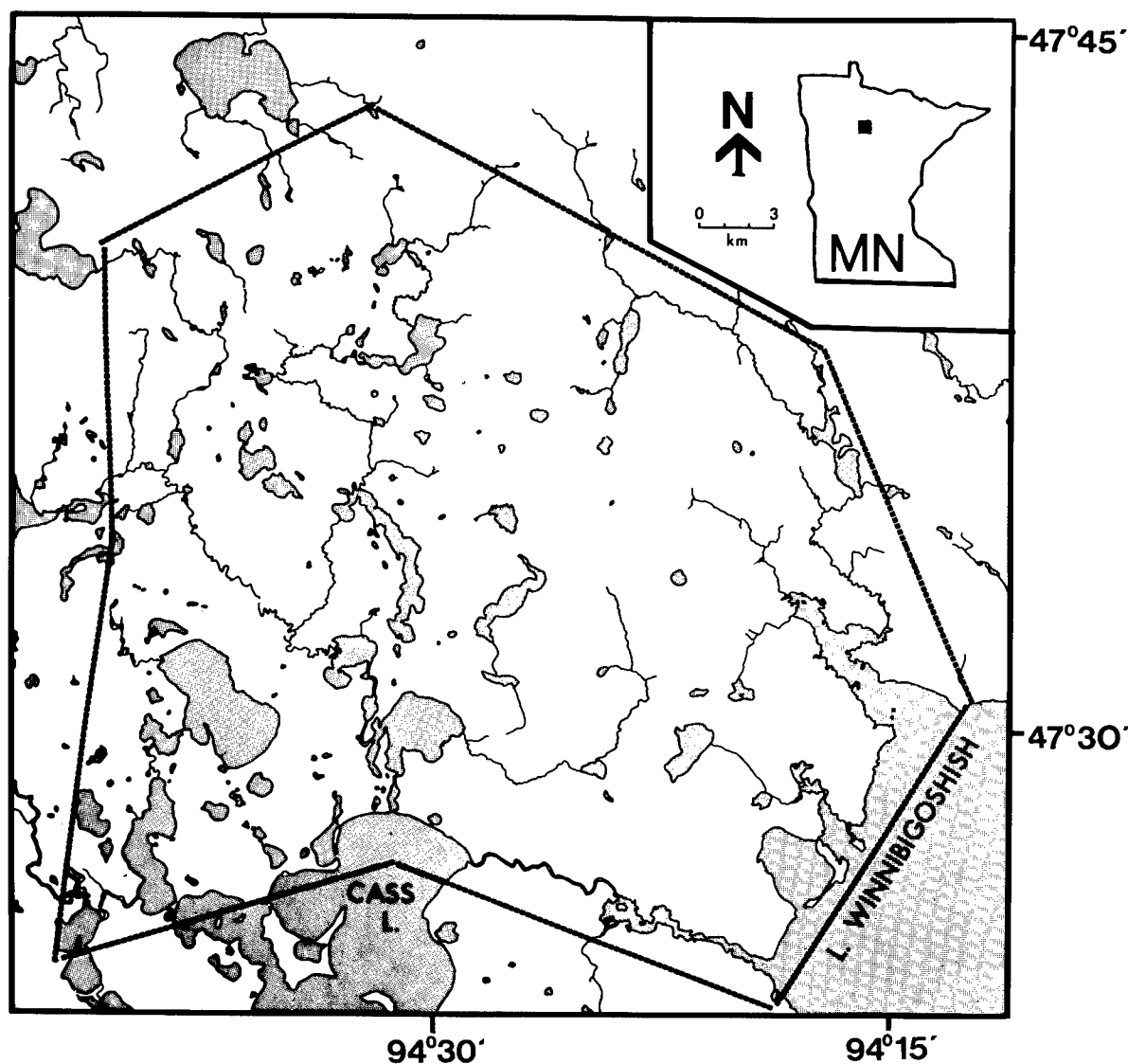


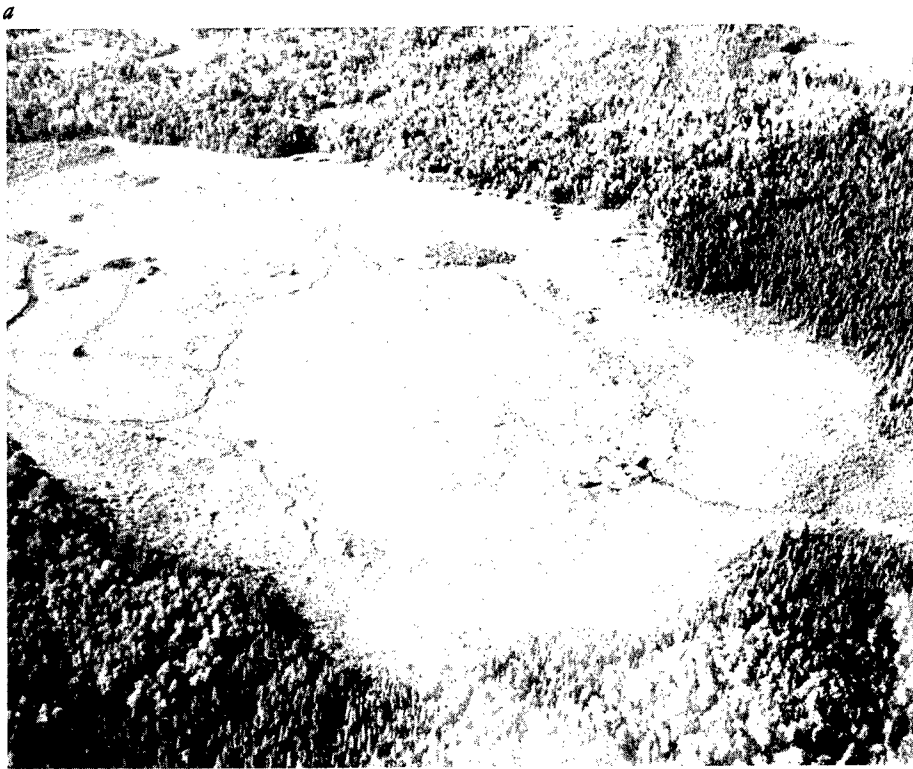
Fig. 1. The study area in north-central Minnesota showing permanent wetlands that were searched regularly for radio-equipped birds.

of annual wild rice (*Zizania aquatica*), tule bulrush (*Scirpus acutus*), cattails (*Typha* spp.), and common reed (*Phragmites australis*). Wetland classification follows Cowardin and Johnson (1973). Other aspects of the study area are presented by Kirby (1973), Kirby et al. (1976), and Gilmer et al. (1977).

## Methods

Both flightless and newly fledged mallards and wood ducks were captured in late July, early August, and mid-

September of 1972–74 by nightlighting, usually from an air-thrust boat. Each bird was fitted with a breast-mounted radio package (Gilmer et al. 1974) and a metal U.S. Fish and Wildlife Service leg band (Fig. 3). Because our study area was large, birds were radio-tracked primarily from aircraft equipped with receiving antennas. The principal aircraft used for aerial work was a Cessna 172 with a pilot and two radio operators—observers, except during a part of 1974 when an amphibious STOL-equipped Cessna 185 was the primary aircraft. Antennas on 9.2-m towers and on motor vehicles and boats equipped with removable masts were also used.



*b*



Fig. 2. Wetland habitat typical of that upon which waterfowl were captured during late summer 1972-74. Most birds were located at night in (a) dense stands of wild rice, or (b) a mixture of rice, bulrush, and floating leaf vegetation such as water lilies (*Nuphar variegatum*, *Nymphaea tuberosa*) or watershield (*Brasenia schreberi*).



**Fig. 3.** An immature male mallard with an attached breast-mounted radio transmitter. The antenna loop fits behind the wings and an adjustable strap around the neck of the bird holds the transmitter in place.

Diurnal ground or water searches for marked birds were conducted 1 or more times a day, allocating search effort for each bird evenly between morning and afternoon. Daylong monitoring was regularly conducted on wetlands that contained several marked birds. Aerial searches for radio-equipped birds were conducted an average of 5 times a week throughout the study period each year. A single search often located birds in the morning and

then again in the afternoon in a separate flight, or included separate flights at dusk or after dark. Birds were located at night 3 or more times a week by using antennas on towers and antenna-equipped boats and vehicles. Aircraft were used to locate birds at night when the ground was snow-covered or when sufficient moonlight was available to permit identification of the wetlands harboring the birds. Much aircraft tracking was conducted

at dawn and dusk to identify movement between day- and night-use areas.

In all searches, the area of a bird's most recently known location was searched first. If unsuccessful, then the search was expanded to cover all areas the bird had used. Finally, adjacent drainages, large lakes, and other known preferred areas for each species were searched. When a bird was located from an aircraft, its position was determined by aerial triangulation techniques similar to those described by Seidensticker et al. (1970) and Gilmer et al. (1981). Otherwise, standard triangulation techniques were used. Records were maintained of areas searched where birds were not found as well as where they were found. An intensive aerial search of the entire study area was made within an average of 60 h of the determination that a bird had possibly left the study area.

Visual observations to evaluate the general behavioral response of newly marked ducks to the radio package were made during the first week after capture. Visual observations were also made when birds used new areas, did not move noticeably between observations, or when radio signals indicated sustained inactivity. In addition, we observed birds whenever possible to do so without disturbing them.

Because telemetry triangulation error was a concern, we used several practical methods to be precise and accurate. These included siting fixed-location antennas on towers to reduce distances between the towers and wetlands and to make the angles between adjacent tower sites as near 90° as possible. Aerial telemetry techniques were practiced each year before tracking marked birds by locating planted transmitters in precisely known places throughout the study area until an accuracy corresponding to a location of <50 m error was obtained consistently by all staff. Similar practice on the ground and water with antennas on towers and vehicles resulted in errors of <10 m. Triangulation error was consistently <1 m for hand-held receivers with loop antennas, which were most often used to precisely locate dead and crippled birds, to find birds in dense cover, and to monitor signals for indication of movement. All telemetry triangulation was performed as a series of averages of numerous readings so that the confidence limits of the error polygons were minimized. Checks on accuracy and precision, with known-location transmitters, gave us confidence that we were capable of consistently locating a bird to within 10 m from the ground or water and 50 m from the air.

Four years of use allowed us to consider transmitter operational life as being at least 75 days—some lasted 90 days. If a duck carrying a radio transmitter that had operated less than 75 days could not be located after

searching the entire study area, we concluded that the bird had flown elsewhere, but we continued telemetry searches to determine whether any returned. The chances of a transmitter being rendered completely inoperative by a predator or by shotgun pellets were considered slight (Kirby et al. 1981).

Beginning in late September and continuing through the third week of October of each year, the waterfowl population on the 932-km<sup>2</sup> study area was monitored by semiweekly aerial surveys on all permanent wetlands and beaver (*Castor canadensis*) flowages. Wood ducks were counted during late evening flights into night-use areas. Hunting parties, defined as any group hunting from the same boat or blind, or over the same set of decoys, were similarly counted from aircraft on opening days, weekends, and during midweeks of the waterfowl season each year.

We estimated the age of captured birds from plumage development (Gollop and Marshall 1954; W. E. Steffen, Northern Prairie Wildlife Research Center, Jamestown, North Dakota, unpublished report, 1961). This age was used to estimate the date of fledging, unless the duckling was observed flying before the calculated date or was known to be incapable of flight after the calculated date.

We chose the beginning of the hunting season each year (1 October) as a logical break in analysis. Hunting season activities had been shown to substantially affect the behavior of young and adult waterfowl on the Chippewa National Forest (Kirby et al. 1976). Movements of young were analyzed by 10-day intervals from day of fledging through departure from the study area. Proportional use of natal marshes and other habitat was calculated as the fraction of telemetry locations on various sites. Continuous tracking of individual birds and visual observations of bird movements were used to determine the distance, direction, and duration of movements of the young birds until they departed on fall migration.

Habitat was classified according to the scheme of Cowardin and Johnson (1973). We were unable to assess habitat choice by calculating usage versus availability because bird movements expanded with increasing age; consequently, we could not make an assessment of availability. Instead, we used rank correlation techniques to compare day and night use of shorelines, wetland complexes, and emergent vegetation in the vicinity of areas used by radio-equipped birds.

Birds hatched within the calendar year of banding and captured while still flightless were known to have been reared on the study area. The analysis of these birds was held separate from those captured as flying young and perhaps reared elsewhere. We refer to the former as

“locally reared” young and the latter or combinations of the two groups as “immature” birds.

## Results

Habitat use and predation occurring within 1 week of capture may have been related to attaching the radio to the bird. Thus, no data from days 1–7 after radio attachment were used in subsequent analyses. After omitting data from predation losses in the first week and from two initial transmitter failures, we had data from 133 young birds (32 mallards and 23 wood ducks captured as Class III ducklings; 56 mallards and 22 wood ducks captured as flying immatures) available for analysis.

### *Fledging*

#### Mallards

Flightless mallard broods are capable of swimming distances of 3.9 km in 24 h (Ball 1973) and 1-day-old wood ducks can swim 1 km/h (Stewart 1958), but we found no evidence that fledged birds made long distance forays entirely by swimming. Although individual birds sometimes swam 0.5–1.0 km along a shore in 24 h, they usually flew across larger expanses of open water. Except for one late-hatched bird, the dates of first flight of all locally reared mallards to which we attached transmitters were between 28 July and 7 August. The first flying movements of all but one mallard, which departed 3 days

after fledging, were confined to the marsh on which they fledged (natal marsh).

First flights of locally reared birds away from the natal marsh were recorded each year (Table 1). Although locally reared males made first flights an average of 5 days earlier and flew an average of 0.88 km farther than did locally reared females, differences between the mean values for the sexes were not significant. The maximum straight-line distance any young mallard could fly without leaving the area on which it fledged was about 2.5 km. Flights away from the natal marsh occurred with other mallards in either early morning or late evening. Otherwise, all mallards, both young and adult, were relatively sedentary during daylight hours.

#### Wood Ducks

Much wood duck daytime activity during the first weeks after fledging was centered about favored loafing areas. Except for some young birds associated with flocks of molting drakes, locally reared wood ducks remained in small groups of 3 to 7 birds—rarely as many as 12.

First flights of wood ducks away from their natal marshes occurred in their third week of flying, similar to mallards (Table 1), but because our sample of radio-equipped birds included late-hatched young, dates of these flights extended from 12 August until 19 September. Young male wood ducks flew away from the natal marsh an average of 5 days later than did females, but to areas farther away. With our small samples, these differences were not statistically significant. The range of movements observed for individual wood ducks in this

Table 1. *Time and distance characteristics of first flight of young mallards and wood ducks away from natal marshes in north-central Minnesota.*

Species and sex	N	Number of days after flight could have occurred that a departure was documented			Distance of flight (km) <sup>a</sup>
		$\bar{x}^b$	Min.–max.	$\bar{x}^c$	
<b>Mallard</b>					
Female	18	21	0–37	4.95	0.61–18.42
Male	9	16	1–29	5.83	0.69–28.58
<b>Wood duck</b>					
Female	11	16	2–26		
	10 <sup>d</sup>			2.31	0.25– 5.56
Male	12	21	1–31	2.64	0.80–10.88

<sup>a</sup>Measured as the minimum distance from the previous location on the natal marsh to the location on the new area.

<sup>b</sup>Differences between sexes not significant:  $t = 0.264$  (25 df,  $P \gg 0.05$ ) for mallards;  $t = 1.294$  (21 df,  $P \gg 0.05$ ) for wood ducks.

<sup>c</sup>Differences between sexes not significant:  $t = 0.097$  (25 df,  $P \gg 0.05$ ) for mallards;  $t = 0.306$  (20 df,  $P \gg 0.05$ ) for wood ducks.

<sup>d</sup>Does not include one bird whose first move away from the natal marsh was migratory in September.

Table 2. Percentage of days in which radio-equipped locally reared mallards and wood ducks were located at least once away from their natal marsh, and fidelity of site use by 10-day intervals from time of first flight through 30 September 1972-74.<sup>a</sup>

Period (days)	Number of birds <sup>b</sup>		Percentage of locations away from natal marsh <sup>c</sup>			Site use index <sup>d</sup> $\bar{x}$ visits/10 days		
	Male	Female	Male	Female	Both	Male	Female	Both
<b>Mallard</b>								
1-10	11	20	10	20	17	1.59	1.59	1.59
11-20	10	18	26	31	29	1.96	1.47	1.61
21-30	6	16	46	57	55	1.69	1.79	1.75
31-40	5	16	50	64	60	2.08	1.92	1.96
41-50	5	14	78	78	75	2.08	2.44	2.33
51-60	5	14	85	84	84	1.30	1.89	1.69
61-70	2	4	100	86	90	1.00	1.41	1.25
<b>Wood duck</b>								
1-10	14	12	2	13	7	2.70	2.44	2.56
11-20	12	11	11	20	16	2.27	2.38	2.33
21-30	12	10	39	48	43	1.92	1.85	1.89
31-40	9	9	60	58	59	1.82	1.85	1.85
41-50	9	8	67	50	59	1.79	1.92	1.85
51-60	6	4	75	86	80	1.61	1.16	1.37

<sup>a</sup>Only data for birds within 30 km of their natal marsh included.

<sup>b</sup>Decreases with time because of departure or death of birds, or because data for a given age fell beyond 30 September for the bird in question.

<sup>c</sup>No more than one location a day per bird used in analysis. Every bird was not located every day and some birds departed or returned in midperiod. % = (number of days with locations away from the natal marsh/total number of days on which locations were obtained) × 100.

<sup>d</sup>Total number of locations in this 10-day period divided by the number of different areas used. Telemetry locations were considered different if on different discrete water bodies, or if on the same wetland, separated by at least 1,000 m of shoreline, or if on rivers or streams, separated by ≥1,000 m (measured point-to-point). Discrete lake bays, if of generally homogeneous habitat, were considered a single location if the maximum straight-line distance between any two locations on the bay shore was less than 1,000 m. The index was calculated individually for each bird present during the period and then a  $\bar{x}$  calculated for the entire sample.

period was much less than that observed for mallards, and the distances flown were significantly shorter for wood ducks than for mallards ( $t = 2.026$ , 48 df,  $P < 0.05$ ).

### *Use of Natal Marshes After Fledging*

#### Mallards

The proportion of daylight hours spent away from natal marshes increased for both mallard sexes with time (Table 2). Although females initially spent more time away from the natal areas than males, proportionately more males than females departed the study area entirely, confounding attempts to strictly compare the sexes. Notwithstanding, the differences between the sexes in the use of natal areas, from about 40 days after first flight, disappeared for those birds remaining on the study area. The Site Use Index (Table 2) showed that throughout

the period following first flight, each site used in the daytime averaged more than one visit each 10-day period. The generally increasing, then finally decreasing, Site Use Index values were similar between the sexes and reflected selection of favored day-use areas after initial sampling of many different areas near the natal marshes.

Use of areas other than the natal marshes for night activities (Table 3) showed a pattern of general increase by females until the last two 10-day periods after first flight, and an irregular increase by males throughout the period before 30 September. Use of sites by females, similar to males, averaged slightly more than once in each 10-day period. Both sexes of mallards used proportionately more different areas at night than during the day. Rate of change of night-use areas within each 10-day period remained high through September. Male use of the natal marsh for night activities (Table 3) paralleled their transitory fidelity to the natal area in general; that is, they quickly began using areas other than the natal marsh at

Table 3. *Percentage of nights in which radio-equipped locally reared mallards and wood ducks were located at least once away from their natal marsh, and fidelity of site use by 10-day intervals from time of first flight through 30 September 1972-74.*<sup>a</sup>

Period (days)	Number of birds <sup>b</sup>		Percentage of locations away from natal marsh <sup>c</sup>			Site use index <sup>d</sup> $\bar{x}$ visits/10 days		
	Male	Female	Male	Female	Both	Male	Female	Both
<b>Mallard</b>								
1-10	11	20	—	50		—	1.00	
11-20	10	18	75	43	55	1.00	1.15	1.12
21-30	6	16	57	66	63	1.25	1.16	1.23
31-40	5	16	50	71	68	1.00	1.30	1.25
41-50	5	14	40	82	73	1.67	1.27	1.35
51-60	5	14	85	59	67	2.00	1.23	1.37
61-70	2	4	100	33	67	1.00	1.00	1.00
<b>Wood duck</b>								
1-10	14	12	0	18	10	1.43	1.37	1.47
11-20	12	11	50	33	41	1.00	1.20	1.11
21-30	12	10	56	71	64	1.45	1.13	1.32
31-40	9	9	80	75	77	1.00	1.61	1.30
41-50	9	8	75	43	54	1.49	1.56	1.47
51-60	6	4	100	100	100	1.00	1.00	1.00

<sup>a</sup>Only data for birds within 30 km of their natal marsh included.

<sup>b</sup>Decreases with time because of departure or death of birds, or because data for a given age fell beyond 30 September for the bird in question.

<sup>c</sup>No more than one location a day per bird used in analysis. Every bird was not located every day and some birds departed or returned in midperiod. % = (number of days with locations away from the natal marsh/total number of days on which locations were obtained) × 100.

<sup>d</sup>Total number of locations in this 10-day period divided by the number of different areas used. Telemetry locations were considered different if on different discrete water bodies, or if on the same wetland, separated by at least 1,000 m of shoreline, or if on rivers or streams, separated by ≥1,000 m (measured point-to-point). Discrete lake bays, if of generally homogeneous habitat, were considered a single location if the maximum straight-line distance between any two locations on the bay shore was less than 1,000 m. The index was calculated individually for each bird present during the period and then a  $\bar{x}$  calculated for the entire sample.

night. Their use of areas other than the natal marsh after dark was about 50% until the last two periods when it increased dramatically. In contrast, females first increased time away from the natal marsh at night, then increased time on the natal marsh later in fall; they generally spent night hours on areas closer to the natal marsh than did males. To some extent, this paralleled the movements of some females to and from the study area as a whole (see later discussion of Table 5). Nonetheless, this pattern may have been largely a consequence of the shorter movements made by females during daylight hours (see following discussion of Table 4) which aided their return to the natal marshes at night.

Some young-of-the-year birds were located substantial distances from the study area before 30 September (e.g., Agassiz National Wildlife Refuge, 145 km northwest, and Bowstring Lake, 45 km east). Band recoveries showed that other birds were either out of northern Minnesota or out of the State entirely before the beginning

of the hunting season. Direct recoveries of birds in northwestern Minnesota and north-central South Dakota showed that young mallards leaving the study area followed routes similar to those of adult birds during the premigration period (Gilmer et al. 1977). Those birds that remained on the study area, however, did not travel far from their natal marshes during either day or night (Table 4). Maximum mean distances from the natal area for both day and night locations were reached in the sixth and seventh 10-day periods—approximately at the end of September and when the population of flying birds on the study area was reaching a peak.

Some changes in movements of locally reared birds in late September were related to the arrival of large numbers of birds from outside the study area. Newly arrived birds joined the larger flocks of locally reared young and other mallards already present on the study area, and were observed on the same day- and night-use areas as had been frequented by the early fall population. Mallard

flocks seemed more wary and restless with the addition of the new birds, but no major changes in habitat use were noted. These larger flocks traveled farther and attracted birds from all of the lakes that they visited. The result was that more "different" areas were visited. Local birds joining these larger flocks, or in the flock that formed the nucleus of the larger group, visited more different areas later in fall than they did in summer. The Site Use Index for daytime locations (Table 2, periods 5-7) reflected this change. All members of these large daytime flocks did not necessarily remain together on the same areas at night. This was reflected in the Site Use Index for night locations (Table 3).

#### Wood Ducks

Although daily use of natal marshes by wood ducks changed throughout the period before 1 October, they continued to use these areas during the period before migration more than mallards did. Day use of natal marshes decreased gradually throughout the season for both sexes (Table 2) but most birds returned occasionally. Night use of the natal marshes by both sexes also decreased, but irregularly. The birds were generally

replacing movements centered on the brood-rearing lakes with movements centered on favored night locations as their age increased. After the second 10-day period, when most birds had made flights off their brood lake, wood ducks of both sexes joined evening and morning flights to nearby beaver flowages, meandering streams, and adjacent rice lakes. Although many birds developed this pattern soon after leaving the original lake, flights were usually occurring in both directions, into and out of most wood duck habitat on the study area. Few birds consistently used the same areas for long periods, although phases of active movement between lakes were often interspersed with extended periods of no movement between water areas. All wood ducks maintained either day or night contact with their natal marshes until immediately before migration in September.

The Site Use Indices for the daytime locations of the birds (Table 2) were consistently near 2.00 by mid-August, which indicated about 2 days use of any area within a given 10-day period, albeit with much overlap in site use between consecutive 10-day periods. Use per site decreased immediately before migration. More different areas were used at night by both sexes of wood

Table 4. Distances (km) of radio-equipped locally reared mallards and wood ducks from their natal marshes by 10-day intervals from time of first flight through 30 September 1972-74.<sup>a</sup>

Period (days)	Day						Night				
	Mean			Maximum			Mean			Maximum	
	Male	Female	Both	Male	Female	Both	Male	Female	Both	Male	Female
<b>Mallard</b>											
0-10	0.12	0.48	0.35	1.29	3.20	—	2.76	—	—	8.29	
11-20	1.83	1.64	1.70	2.77	11.54	0.00	1.63	1.36	0.00	11.54	
21-30	4.82	2.78	2.97	13.79	12.49	2.22	1.61	1.79	7.71	9.98	
31-40	4.07	2.34	2.80	15.74	10.12	3.78	2.11	2.34	7.56	2.29	
41-50	3.08	3.50	3.38	14.46	12.95	1.43	2.98	2.58	3.65	11.96	
51-60	6.10	3.59	4.16	9.06	12.69	6.59	4.30	4.93	8.45	12.26	
61-70	7.47	1.68	3.42	12.27	2.27	7.32	0.72	4.01	12.02	2.16	
<b>Wood duck</b>											
0-10	0.02	0.13	0.07	1.04	1.18	0.00	0.31	0.02	0.00	1.85	
11-20	0.16	0.33	0.25	1.60	3.20	0.69	0.82	0.77	5.26	3.58	
21-30	1.61	0.90	1.25	3.42	3.45	1.18	0.73	0.99	6.95	1.60	
31-40	2.00	1.44	1.72	7.62	6.26	1.09	1.03	1.05	1.84	1.48	
41-50	2.73	2.21	2.48	6.88	11.91	1.19	0.43	1.28	2.61	1.50	
51-60	5.52	7.29	6.34	10.04	11.84	—	—				

<sup>a</sup> All locations on the same discrete water body from which the bird first flew were arbitrarily given values of "0" for these calculations. Depending on the site, birds could move 1.7-2.5 km before leaving the area for which zero values applied. Only birds within 30 km of their natal marsh were included in these calculations. Sample sizes for each period as in Tables 2 and 3.

ducks than were used during the day (Table 3). Nonetheless, the total use by wood ducks of all night-use areas visited by the locally reared birds was rather constant before migration. Our counts of birds flying into or out of night-use areas remained similar from day to day on many areas in August, even though the radio-equipped birds were moving between roosts. These counts suggested that a general shuffling of the population was occurring.

Throughout the period 1 August–30 September, young wood ducks that remained on the study area were on the average <7.3 km from their natal marshes (Table 4). Although the mean daytime distance from the natal marsh for both sexes increased throughout the season, distances from the natal marsh at night remained short ( $\bar{x} < 1.3$  km) and rather constant, indicating that evening concentration areas were stable near the original brood lakes. When we considered the range of movements by these young birds in conjunction with the fidelity we observed for day- and night-use areas, we concluded that most young wood ducks became familiar with only a relatively small part of the study area before migration.

Adult wood ducks monitored in fall in 1972–74 (Gilmer et al. 1977) demonstrated movement patterns similar to those of young birds. Adults moved from one side of the study area to the other, but once an initial large move was accomplished, they too developed daily movement patterns that they used for the remainder of the premigratory period. This behavior seems to be typical of the species in north-central Minnesota. Limited movement of wood ducks before migration has also been reported in Iowa (Hein and Haugen 1966) and Illinois (Parr et al. 1979).

### *Ultimate Departure From the Area*

A large proportion of the radio-equipped locally reared mallards and wood ducks that were still alive on 30 September each year, and—we presume—similar proportions of young reared throughout the study area, remained on the study area throughout the period before migration: female mallard, 71%; male mallard, 55%; female wood duck, 42%; and male wood duck, 50%. The large proportion of wood ducks that left was a consequence of normal earlier migration for wood ducks than mallards. Both the wood duck and mallard data illustrate differential migration of the sexes of young birds.

The number of mallards and wood ducks on the study area actually appeared to increase throughout the entire

pre migratory period according to ground and aerial counts. This is not inconsistent with birds leaving, because total numbers of the more visible flying young and postmolting adult females (compared with flightless broods and molting adult females) increase throughout the summer as late broods finally fledge, and birds concentrate, especially in evening and morning flights. Additionally, since part of our radio-equipped sample departed the study area, some unknown portion of the increase in birds we observed was undoubtedly because of ingress of young from elsewhere. A portion of the premigratory population of young birds thus stays, another portion leaves and, to some unknown extent, young birds from elsewhere appear soon after early broods are flying.

Nearly concentrations of mallards that we discovered off the study area were on the large wild-rice lakes in north-central and northwestern Minnesota and, as judged from band returns, on large lakes and wetlands in North Dakota, South Dakota, and Manitoba. Concentration areas for wood ducks included scattered beaver flowages and meandering streams throughout the wooded portion of Minnesota. One large concentration, at Roseau River Wildlife Management Area on the Minnesota–Manitoba border, may have been the northern terminus of premigratory movements for the north-central portion of Minnesota. We commonly found radio-equipped birds there, mixed with concentrations of wood ducks that were far in excess of the population expected from locally breeding birds (R. L. Jessen, personal communication).

### *Mallards*

Locally reared mallards departed the study area throughout the period 1 August–30 September (Table 5); locally reared males left as late as the fourth 10-day period after first flight, and females departed through the sixth 10-day period. Only females left the study area and returned before 1 October. By 30 September, the sex ratio of locally reared young remaining on the study area was definitely skewed in favor of females (Fig. 4).

Although total numbers of flying mallards on the study area increased from August through September (young fledged and new birds arrived), some locally reared birds departed, but these events did not occur simultaneously. For example, in 1974 mallards increased from 399 (9 September) to 824 (22 September) and then 1,194 (28 September) on the lakes and wetlands surrounding the brood-rearing lakes. Departure of birds from their natal areas occurred before the largest influx of mallards from elsewhere.

Table 5. *Departure of radio-equipped locally reared mallards and wood ducks from the study area before 1 October 1972-74, by 10-day intervals from time of first flight.*

Period <sup>a</sup> (days)	Number alive on the area during the period <sup>b</sup>			Number departing <sup>c</sup>			Proportion departing <sup>d</sup>		
	Male	Female	Both	Male	Female	Both	Male	Female	Both
<b>Mallard</b>									
1-10	11	20	31	1	1	2	0.09	0.05	0.06
11-20	10	18*	28	3	1	4	0.30	0.06	0.14
21-30	7	16*	23	1	2 (1)	3 (2)	0.14	0.12 (0.06)	0.13
31-40	5	16	21	1	1 (0)	2	0.20	0.06 (0.00)	0.10
41-50	5	14*	19	0	2	2	0.00	0.14	0.11
51-60	4	14**	18	0	3 (2)	3	0.00	0.17 (0.11)	0.21
61-70	2	4	6	0	0	0	0.00	0.00	0.00
<b>Wood duck</b>									
1-10	14	12	26	0	0	0	0.00	0.00	0.00
11-20	12	11	23	0	1	1	0.00	0.09	0.04
21-30	12	10	22	3	1	4	0.25	0.10	0.18
31-40	9	9	18	0	1	1	0.00	0.11	0.06
41-50	9	8	17	3	4	7	0.33	0.50	0.41
51-60	6	4	10	0	0	0	0.00	0.00	0.00

<sup>a</sup>Final periods of all birds were truncated by the 30 September limit for this table.

<sup>b</sup>Birds not accounted for by departures either were taken by predators, or did not enter the table because the period in question for them was after 30 September. Certain additional circumstances apply only to female mallards: \*bird left in this period, but returned in the next; \*\*bird left in this period, but returned after 1 October.

<sup>c</sup>Numbers in parentheses in these and the following columns are calculated with the return of a bird as a negative departure.

<sup>d</sup>(Number departing)/(number alive on the area during the period).

### Wood Ducks

Local wood ducks departed the study area throughout the period 1 August-30 September (Table 5) but none left during the first 10 days after fledging. The high number of departures in the fifth 10-day period occurred during the last half of September, when many adult wood ducks were also departing on southward migration. Departure dates for locally reared birds that left before 1 October ranged from 30 August to 29 September ( $\bar{x}$  = 21 September). This was equivalent to the average of Gilmer et al. (1977) for adult wood ducks in this area (24 September  $\pm$  5 days). By 30 September, the remaining population of locally reared wood ducks was skewed in favor of males (Fig. 4).

Wood ducks are difficult to locate in late summer and fall. Thus, we have no data to compare their magnitude of influx into our area with that observed for mallards. However, we believe that some birds entered as well as left our study area because banding records analyzed by Stewart (1972; 1977a,b,c; 1979) showed that fall dispersal

movements by postbreeding wood ducks are common in both the northern and southern portion of the species' range. Counts of wood ducks at evening roosts showed typical increases to peaks before migration as have been reported elsewhere for the species at higher latitudes (Grice and Rogers 1965; Hein and Haugen 1966; Lingle 1978).

### *Flock Movements Before the Hunting Season*

#### Mallards

Flocks of flying mallards were on many of the study area lakes in early August of each year, 6 weeks before the beginning of the hunting season. Gilmer et al. (1977) showed that these birds are mostly females that have unsuccessfully attempted nesting, and immature birds of both sexes. As the season progresses, females that have successfully reared broods join these birds, which then

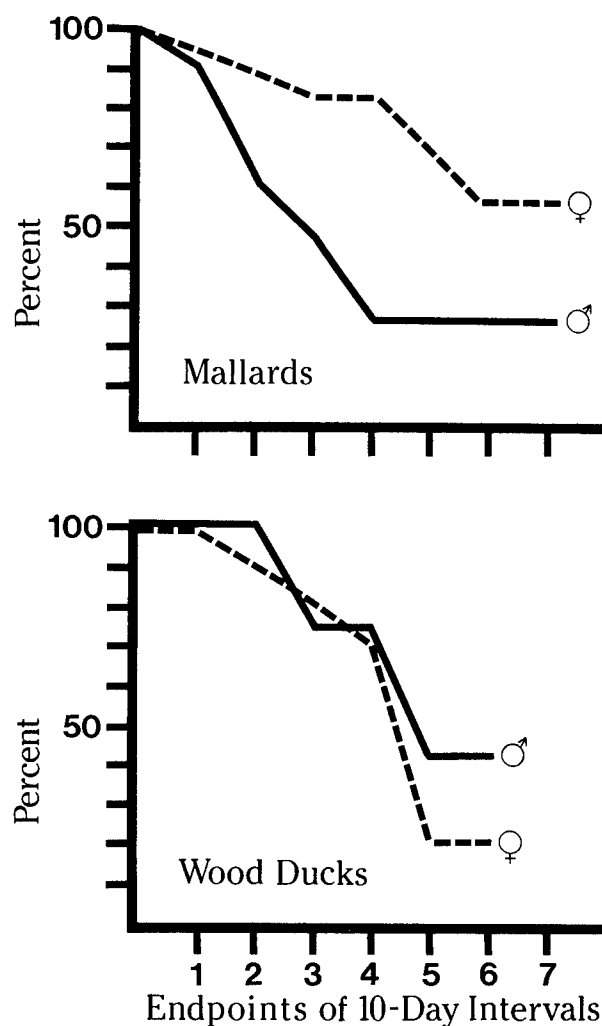


Fig. 4. Proportion of young mallards and wood ducks remaining on the north-central Minnesota study area by 10-day intervals from the time of first flight in late July through 30 September, 1972-74.

become semicohesive flocks of mixed species using discrete water areas (Kirby et al. 1976). We compiled records of consecutive movements of radio-equipped birds and plotted these as movements between day- and night-use areas in 1972-74 (Fig. 5). No areas used only for night activities by mallards were ever located.

We never recorded locally reared mallards moving to new areas, either during day or at night, except in the company of other mallards. Despite often dawn-to-dusk observation of radio-equipped young mallards over three seasons, we obtained no indication that locally reared mallards found new habitat by random searching and

thus merely fortuitous discovery of nearby areas. Instead, young birds were always found with conspecifics and initially made movements to and from the natal lake in company of flocks making morning and evening flights. Flying young on isolated bays of large lakes often made no moves off these areas until flocks from elsewhere began using the natal area, whereas young birds reared on the large night-use areas often used a new daytime loafing area each day by joining a different flock each morning. Naive birds apparently joined flocks of birds that were familiar with other areas. By changing flocks on either the day- or the night-use area, young birds progressively visited more new areas.

#### Wood Ducks

Telemetry revealed that some adult wood ducks flew morning and evening between use areas soon after renewing flight feathers (Gilmer et al. 1977). These flights were usually direct, made in small groups, and often occurred in the first or last minutes of twilight. This behavior persisted throughout the period before migration, and was also typical of young birds.

Day- and night-use areas used consecutively by radio-equipped wood ducks were located throughout years 1972-74, as they were for mallards. Figure 6 illustrates movements for wood duck flocks. As observed for mallards, all areas used at night by wood ducks were also used by the species during the day. During each fall, the movements came to resemble the spokes of a wheel around lakes and beaver flowages used at night.

Locally reared wood ducks showed a consistent tendency to move up drainages that entered the natal lakes. In the company of a small group of other wood ducks, the radio-equipped birds often could be found on the same stream or river from day to day, but the birds would be found farther up the drainage as days progressed. When flocks of birds from adjacent natal lakes mixed on these day-use areas, we often found that interchange of radio-equipped birds took place on the first encounter. We presume that the same mechanisms that allowed naive young mallards to learn of new habitats were also present in wood duck flocks; that is, the locally reared wood ducks discovered new habitat by making movements with other wood ducks between day- and night-use areas.

#### *Effects of the Hunting Season*

Hunter counts on 169 discrete water areas showed that almost all waterfowl habitat on the Chippewa National Forest received hunter use at some time during the season, with heaviest use on opening day and subsequent

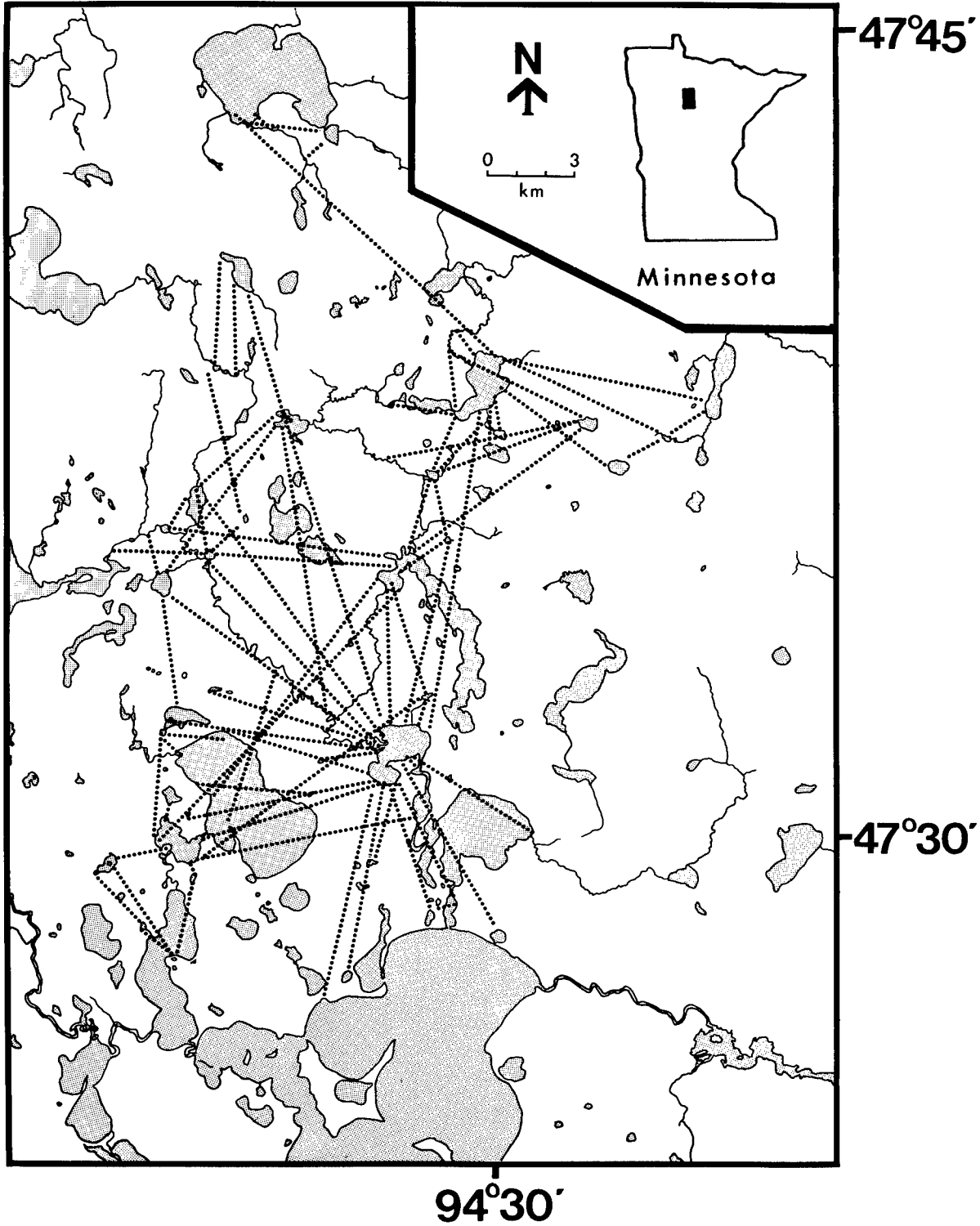


Fig. 5. Mallard flock movements by 30 September 1972-74 on the west half of the study area. Documented flights by radio-equipped birds have been used to develop a composite presentation of movements occurring before the hunting season.

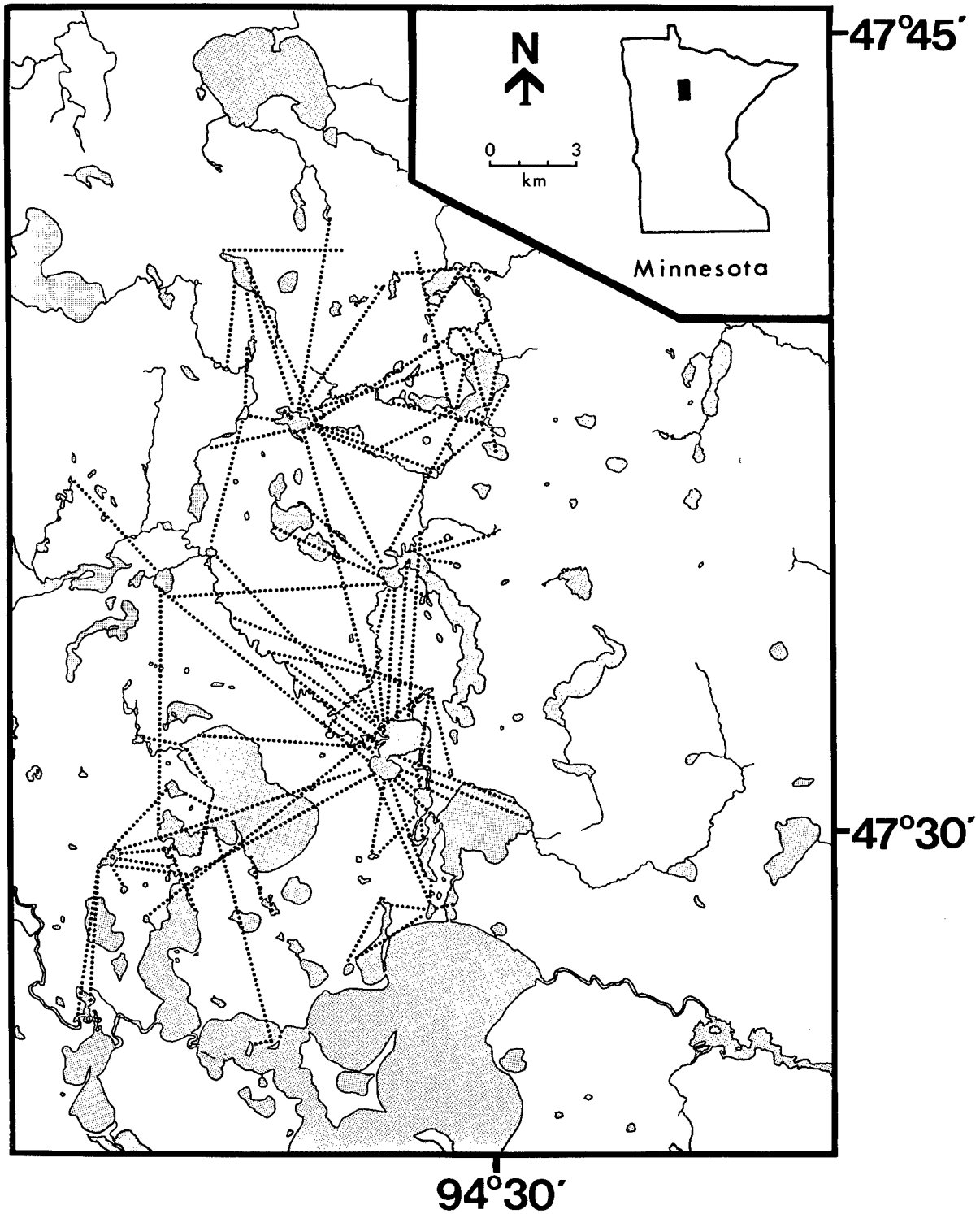


Fig. 6. Wood duck flock movements by 30 September 1972-74 on the west half of the study area. Documented flights by radio-equipped birds have been used to develop a composite presentation of movements occurring before the hunting season.

weekends (Kirby et al. 1976). The number of young radio-equipped birds remaining on the study area during the 3 years varied from highs of 83% of the mallards and 73% of the wood ducks in 1972 to lows of 50% of the mallards and 29% of the wood ducks in 1974. On opening day, hunters shot 22% of the radio-equipped young mallards and 9% of the young wood ducks that remained on the study area during their first waterfowl season (direct recoveries; Table 6).

#### Mallards

Aerial waterfowl surveys comparing number of birds before and after the opening of hunting season revealed a dramatic decrease in the number of waterfowl on the area after opening day (Kirby 1976). Mallards decreased to 10% of the pre-season total in 1972, to 20% of the pre-season total in 1973, and to 47% of the pre-season total in 1974. Forty percent of the male mallards equipped with transmitters as flying young birds departed the study area on opening day when they were first disturbed by hunters; smaller proportions of the other radio-equipped cohorts of young mallards left at that time (Table 6).

All 11 of the young birds recovered by hunters, or shot but not recovered on the opening day of the waterfowl season, were taken on either their normal day-use areas or as they entered their usual night-use areas. None of the young mallards fitted with transmitters used entire-

ly new areas during the hunting season. Most birds not initially taken by hunters, including the radio-marked sample, moved about the study area until they found wetlands free of disturbance on opening day. This movement occurred within 2 to 3 h after noon when shooting began at 1200 h (Kirby et al. 1976). Some birds had no contact with hunters on the opening day of the hunting season. Nonetheless, the large number of hunting parties in the field each year on 1 October (270 in 1972 on a Sunday, 197 in 1973 on a Monday, and 153 in 1974 on a Wednesday) meant that there were no large areas free from disturbance in the vicinity of the normal day-use areas of many flocks. Many birds thus left the study area completely. Locally reared young birds generally remained and sought refuge in smaller, more isolated portions of their usual day-use locations. All radio-equipped mallards not killed or crippled by hunters returned to their usual night-use areas on opening day in the 3 years of study; during 1973 and 1974 shooting ended at 1600 h.

Because young birds that moved about the study area inevitably came in contact with hunters, only relatively sedentary birds escaped being killed. The latest ultimate, presumably migratory, departure of an uninjured radio-equipped mallard from the study area was 25 October 1974. A crippled bird recuperated throughout October and departed with the last flock of mallards on the study area on 9 November 1972 (Kirby et al. 1981).

Table 6. Fate of radio-equipped young mallards and wood ducks on the 932-km<sup>2</sup> study area, north-central Minnesota, opening day of the hunting season, 1972-74.<sup>a</sup>

Species, age and sex	Recovered by hunter		Unrecovered kill		Crippled		Departed the area		Remained on the area	
	N	(%)	N	(%)	N	(%)	N	(%)	N	(%)
<b>Mallard</b>										
Local male	1		0		1		0		4	
Local female									10	
Immature male	1		2				6		6	
Immature female <sup>b</sup>	5		1				1		13	
Total	7	(14)	3	(6)	1	(2)	7	(14)	33	(65)
<b>Wood duck</b>										
Local male									6	
Local female	1								4	
Immature male	1						1		6	
Immature female							1		2	
Total	2	(9)					2	(9)	18	(82)

<sup>a</sup>Local = bird reared locally—that is, captured as flightless young; immature = bird captured after fledging.

<sup>b</sup>Includes one bird that left the study area 20 September and returned on opening day.

During the rest of the waterfowl season, 14 of the 33 young mallards that remained on the study area on opening day were shot by hunters on or adjacent to the study area. Two locally reared female mallards departed the study area 3 days before and 2 days after the opening, but returned to the area and were shot by hunters 5 and 15 days after the opening, respectively, in 1973. No radio-equipped young male mallards that departed the study area during late summer or during the hunting season returned later in the year during the periods their transmitters should have been operative. In sum, 16 (48%) of the young mallards remaining on the study area after the opening were recovered or crippled by hunters, and 27 (51%) of the 53 radio-equipped birds (locally reared and immatures) present on the study area at any time in October were recovered, or were shot, not retrieved, and subsequently died on the study area. Of the entire sample of radio-equipped mallards thought to still be alive at the beginning of the hunting season on 1 October (84 birds), an additional 10 were killed by hunters south of the study area. If cripple loss off the study area is estimated to be 0.19 following Martin and Carney (1977), and the reporting rate of radio-equipped birds is assumed to be about 1.0 (Kirby 1989), then the proportion of the radio-equipped sample lost to hunting during the first season following banding (direct recovery rate) was minimally 0.463.

#### Wood Ducks

Two young wood ducks were recovered by hunters on the study area on opening day (Table 6). Two of the 18 young wood ducks remaining on the study area after the opening day during the 3 years of study were recovered by hunters on the area later in the season. Two additional birds were also recovered on the study area: one that departed the area 29 September returned and was recovered 7 October, and another that departed 4 October returned and was recovered 11 October. Both were locally reared females. In sum, six (33%) of the young wood ducks on the study area in early October were recovered there by hunters. The two birds shot opening day and three of the birds shot later were bagged on their normal day-use areas; one bird was shot illegally after hours on a night-use area. Of the entire sample of radio-equipped wood ducks thought to still be alive at the beginning of the hunting season on 1 October (46 birds), an additional eight were killed by hunters south of the study area. With similar assumptions regarding cripple loss and reporting rate of wood ducks as previously given for mallards, the proportion of the

radio-equipped sample lost to hunting during the first season following banding (direct recovery rate) was minimally 0.337.

Behavior of young wood ducks during the hunting season could not be distinguished from their behavior in late September. Use of new habitat by wood ducks in October was attributed to the first stages of fall migration; we tracked several radio-equipped birds to the south and south-southwest as they left the study area each year. An exception was a bird that moved to an adjacent lake, perhaps coincidentally, on opening day of the hunting season. Wood duck numbers declined sharply on the study area in the last week of September when migration commenced, and numbers continued to decrease rapidly throughout the first week of October. Night concentrations ceased to be apparent as the total number of birds decreased, although the night-use areas frequented earlier in the year continued to be used by some birds. By the end of September, most of the radio-equipped birds were spending all of their day and night hours on areas remote from the early concentrations on brood-rearing lakes.

With daily telemetry monitoring and specific hunter counts, we found that birds not taken by hunters actually never used wetlands on which they could have contacted humans. The latest known date a radio-equipped young wood duck was on the study area was 15 October, when the transmitter on an immature male failed.

#### *Habitat Use Near the Natal Marshes*

There are theoretical reasons to believe that waterfowl, similar to other species, choose discrete patches for feeding, and that other characteristics such as freedom from disturbance, availability of nearby wetlands, and numbers and distribution of conspecifics determine the suitability of a site. Knowledge of the general characteristics of sites used by fledged, radio-equipped birds permitted a reasonable first approximation of how habitat types were distributed in the vicinity of all fledged young birds while they remained on and near the natal marshes (Tables 7 and 8). In general descriptive terms, areas of lakes with circumneutral bog (sedge or shrub phase) shorelines containing wild rice and emergent vegetation were important mallard day- and night-use habitat. Lakes with similar shorelines and areas of shrub swamp, but with greater amounts of emergent and emersed vegetation, were important wood duck night-use areas. Lakeshore with brushier shorelines and a greater representation of emersed aquatics were used by wood ducks during daylight hours.

Table 7. Frequency distribution of shoreline characteristics within 500 m of areas used by fledged young mallards and wood ducks 1 July–30 September, 1972–74, on the 932-km<sup>2</sup> study area in north-central Minnesota.

Habitat type <sup>a</sup>	Mallard <sup>b</sup>				Wood duck <sup>c</sup>			
	Day		Night		Day		Night	
	N	(%) <sup>d</sup>	N	(%)	N	(%)	N	(%)
a. Flooded uplands	3	3	2	4	5	4	2	3
b. Shallow/deep-marsh aquatics	12	11	9	17	5	4	3	5
c. Hardwood swamp	2	2	2	4	5	4	4	7
d. Shrub swamp	30	27	17	32	28	23	19	32
e. Circumneutral bog—shrub phase	54	49	30	57	46	37	31	52
f. Circumneutral bog—sedge phase	61	57	37	70	54	44	24	40
g. Circumneutral bog—ericaceous phase	8	7	2	4	2	2	1	2
h. Acid bog	8	7	1	2	2	2	1	2
i. Softwood swamp	8	7	5	9	8	6	2	3
j. Sand-gravel beach	22	20	7	13	24	20	12	20
k. Overhanging upland brush	19	17	6	11	37	30	15	25

<sup>a</sup>Habitat types c–i are communities 10, 9, 12, 11, 13, 14, and 15, respectively, of Cowardin and Johnson's (1973) classification. "Flooded uplands" are inundated areas without wetland vegetation. "Shallow/deep-marsh aquatics" are the species found in Cowardin and Johnson's (1973) communities 3–8 (seasonal and semipermanent wetlands). Habitat types j and k are nonwetland lakeshore designations.

<sup>b</sup>Data are 1,711 telemetry locations on 110 day-use sites and 336 telemetry locations on 53 night-use areas.

<sup>c</sup>Data are 1,619 telemetry locations on 123 day-use sites and 303 telemetry locations on 60 night-use areas.

<sup>d</sup>% = (number of times the habitat was present/total number of different sites used by the species, either day or night) × 100, rounded to the nearest percent.

Table 8. Ranks of habitat use (1 = highest) of fledged young mallards and wood ducks on the 932-km<sup>2</sup> north-central Minnesota study area before 30 September, 1972–74.

Habitat <sup>a</sup>	Mallard <sup>b</sup>		Wood duck <sup>c</sup>	
	Day	Night	Day	Night
<b>Wetland complex</b>				
Nonpermanent	5	6	6	6
Beaver flowage	6	4	5	5
Lakes	1	1	1	1
River channel	2	3	2	3
River marsh	4	5	4	4
River mouth	3	2	3	2
<b>Emergent vegetation</b>				
Bulrush	4	4	3	4
Common reed	5	5	5	5
Wild rice	1	2	2	2
Emerged aquatics	2	1	1	1
Other	3	3	4	3

<sup>a</sup>The first five wetland complexes and the emergent vegetation communities are from Cowardin and Johnson (1973) and Kirby (1973).

<sup>b</sup>Data are 1,711 telemetry locations on 110 day-use sites and 336 telemetry locations on 53 night-use areas.

<sup>c</sup>Data are 1,619 telemetry locations on 123 day-use sites and 303 telemetry locations on 60 night-use areas.

Kendall's coefficient of rank correlation ( $\tau$ ), applied to the frequency distribution of shoreline characteristics of mallard and wood duck day- and night-use areas (Table 7), showed differences ( $P = 0.0004$ – $0.0078$ ) for all combinations of species and time; that is, both species were using portions of the entire study area wetland community with differing intensities, day and night. Because the wetland types used most by young birds are typical of larger lakes on the study area (Cowardin and Johnson 1973), we increased the scale of analysis and assessed correlations among ranks of use of wetland complexes (Table 8), which are defined on the basis of physical and botanical characteristics of shorelines (Cowardin and Johnson 1973). Similarly, we decreased the scale of analysis by assessing correlations among ranks of use of specific emergent vegetation that previous observation (Gilmer et al. 1977) had indicated was most often used by postbreeding birds (Table 8). The result of these rank correlation analyses (again Kendall's  $\tau$ ) within species was that only wood duck day and night use of wetland complexes was correlated ( $P < 0.05$ ). Comparing mallard and wood duck habitat use, the species were significantly correlated in both their day and night use of wetland complexes and their use of emergent vegetation communities at night.

## Discussion

The asynchronous postbreeding periods of mallard females on the study area, resulting from differences in individual bird behavior, differential nest success, and differential brood survival, have an important net effect on the development of movement patterns near the natal marshes. A small but possibly constant number of flying adults are in the population at all times before large numbers of flying birds arrive from outside the Chipewewa National Forest. We believe the older birds encourage movements by locally reared young, and possibly serve to initially coordinate movement patterns of all mallards near favored brood-rearing lakes in late summer.

Similarly, movements of flying adult wood ducks may have encouraged locally reared young to initiate movements between adjacent water areas in mid- to late summer. The species differed in their flocking behavior, however. Even when many wood ducks were on the same lake, they were usually scattered along the shore, and there appeared to be no tendency to consolidate and coordinate movements within a single flock as was observed early in the year for mallards. Hartowicz (1965) also documented a lessening of obvious flock movements of wood ducks in midsummer in Missouri.

### *Effects of Fall Dispersal*

Hochbaum (1955) concluded that there was a "... universal urge for juveniles to use their wings; and once in the air, they moved out and away from home..." He viewed the functionings of these wanderings as threefold: refinement of flight technique, strengthening of flight muscles, and acquisition of geographical knowledge of value in homing orientation during the following spring. Hochbaum regarded the summer movements of young ducks as random wanderings, but modified this generalization with the qualification that randomness applied to compass direction only; the travel always appeared to be toward favorable habitat. Williams (1944) and Low (1945) concluded that young redheads did not congregate and that they departed the natal marshes in all directions as soon as they could fly. Mendall (1958) believed that young ring-necked ducks began random wanderings soon after they could fly, but added that they sometimes remained near favorable areas for several weeks.

The preceding generalizations do not describe what we observed on the north-central Minnesota breeding grounds. It is true that observation of unmarked young

mallards and wood ducks on our study area would give the impression that young birds depart in all directions soon after they can fly. However, our radio-equipped sample allowed us to monitor the development of movement patterns by many individuals, and clearly showed that movements were not random, that they were made in the company of conspecifics, and that extensive movements for the average young bird occurred only after substantial time.

The rate of movement away from the natal areas for both young mallards and wood ducks appeared to be limited by the slow increase in the number of wetlands with which each bird becomes familiar. This follows from the observation that the movements of locally reared young are circumscribed almost entirely by the activities of flocks of conspecifics, which are usually making only relatively short moves between day- and night-use areas at the time the young are fledging. Our finding that radio-equipped young birds do not make random explorations of the habitat near their natal marshes thus explains why young birds do not immediately leave the area from which they fledged (even though they may leave the natal lake) unless they join a flock from elsewhere which will take them away from the natal marsh at a rate greater than would otherwise occur.

Our telemetry observations showed that most mallards and wood ducks remained on their natal marshes for several weeks after fledging. Because increase in age correlated, in both species, with the trend for movement out and away from the natal marsh, the common observation that early broods travel more than late broods (Hochbaum 1944; Mendall 1958) can now be given some biological basis. Our telemetry data showed that late-hatched young do not appear to travel as far simply because they do not have the time to develop large-scale movement patterns before migration. Gollop (1965) also showed that late-hatched broods near Kindersley, Saskatchewan, were recovered in significantly higher proportions in the vicinity of the banding site than were early hatched broods, and that this difference was evident through an 8- or 9-week period.

Differential movements of each species, and of the sexes within species, have significant population consequences. The sex ratios of the radio-equipped birds, and we presume all locally reared birds, differed greatly from 1:1 in the vicinity of the natal marshes by 1 October. One might therefore hypothesize that recovery rates between the sexes would be different for these birds. Cowardin (1976) investigated this possibility on our study area and found that greater numbers of female mallards were recovered within 20 km of the banding site than

expected. The mean maximum limit of female mallard movement during weeks 2–6 postfledging was only 10.34 km—well within the 20-km radius used for analysis by Cowardin (1976), and an obvious reason for the discrepancy observed. The difference between the sexes was made even more extreme by the tendency of young male mallards to leave earlier and travel farther from the banding site (natal marsh). Additionally, some young female mallards (and wood ducks) returned to the vicinity of the banding site after an initial departure from the study area, a phenomenon not observed in young male birds. March and Hunt (1978) similarly found a higher proportion of recoveries of locally reared female mallards in the vicinity of the banding site in Wisconsin.

Gilmer et al. (1977), Benson (1983), and Bartelt and Trost (1989) have shown that wood duck immatures of both sexes, and adult females, migrate later than adult males in Minnesota. In accordance with Benson's (1983) observations, the percentage of locally reared birds of both sexes remaining on the area into October was higher than the percentage of breeding males remaining on the study area in 1968–74 (17%; Gilmer et al. 1977). Our data, however, showed that a larger percentage of young female than male wood ducks departing northern breeding areas before 1 October.

We believe that the philopatry documented for young female mallards and wood ducks while still on and near the natal marshes might be typical behavior for northern hemisphere waterfowl in general. This is because waterfowl exhibit substantial homing by females, the selective advantage being that benefits accrue to females that return to areas where they were successfully hatched and reared (Greenwood 1980; Greenwood and Harvey 1982). For example, Lessells (1985) described the value of homing for Canada geese (*Branta canadensis*) in the English midlands as being the need for females to assess the suitability of brood-rearing sites. Familiarity with the site would aid such assessments and would permit earlier nesting. Thus, it may be advantageous to "learn" the vicinity of the natal marsh well instead of broadening knowledge of larger or more distant areas. The behaviors exhibited by young females—but not young males that do not home to natal areas—seem to be those that would increase efficiency in subsequent nesting attempts.

### *Habitat Use*

Gilmer et al. (1975) and Kirby et al. (1985) found that mallard pairs on the southwest part of our study area spent 50% of the day and 65% of the night on the shores of lakes, and that birds, except those initially captured

on large sand lakes, spent the remaining time on nonpermanent wetlands. This habitat use by mallard pairs differed from habitat use by mallards in fall in that open shoreline types on large lakes and small wetlands received much use. Proximate causes of this disparity seem to relate first to the need for seclusion by pairs in spring and conversely a tendency to aggregate in large flocks in fall. Second, availability of some wetlands differed from spring to fall in that many of the lakes used heavily by mallards in fall lacked emergent vegetation in spring, and many of the nonpermanent wetlands used by mallards in spring were unavailable (dry) in fall. Another difference between fall and spring use of the study area by mallards was the different use of riverine habitat at night. Ball (1973) suggested that susceptibility to predation was a cause of avoidance of shoreline night roosts by mallard and wood duck broods. Kirby et al. (1985) found that mallard pairs moved from river channels and lakeshores to river marsh areas at night, possibly also because of predation on shorelines. Less use of river marsh at night in fall may have been a reflection of the greater safety from predation offered mallards by thick emergent stands in the open water lakes, although food was relatively more abundant in these areas also.

Extensive growth and spread of wild rice stands is an important change in northern wetlands in late summer. We found that birds spent consecutive days and nights only on areas that contained wild rice, except for beaver flowages, which are highly productive in other ways (Beard 1953; Kirby 1973). As the season progressed and submerged vegetation began to die, all mallards equipped with radio transmitters, and apparently most of the mallard population on the Chippewa National Forest, moved at night to beaver flowages or to wetlands that contained large emergent stands of wild rice. This supports the earlier findings of Morse (1941) and Stoudt (1944), who documented the apparent preference of mallards in north-central Minnesota for wild rice habitat throughout the pre hunting season.

Much of the wetland habitat used by wood duck pairs in spring was not initially or consistently available to wood ducks in fall. Ephemeral, temporary, seasonal, and some semipermanent wetlands were usually dry in August, but became recharged later in the year. Although we did not find radio-equipped wood ducks returning in great numbers to wetland types used in spring (Gilmer 1971), they did use hardwood forest areas flooded by rain in fall, and extensively used flooded shrub swamps on small permanent wetlands and new beaver flowages. Thus, they were quick to respond to changing water conditions and used nonpermanent water areas in fall.

### *Implications for Management*

The behavioral repertoire of young mallards and wood ducks does not prepare them for contact with hunters in late fall. Hunter pressure on our study area removed many locally reared young from the population on opening day and the first part of the season. Thereafter, maintenance of pre-hunting season behavior patterns or return to these patterns after a period of restricted movement was fatal for many of the remaining young. This contrasts with movements of birds captured as flying young who possibly were not from the study area, as well as with the majority of the mallard population on the Chippewa National Forest that left the study area on opening day when they were initially disturbed. Thus, the movement patterns that had developed and that attached young birds to favored sleeping, resting, and feeding sites near the natal marshes were a disadvantage in the presence of hunters; these behaviors in areas of high hunter activity resulted in substantial harvest of locally reared birds.

The restriction of locally reared waterfowl activities to areas used previously in the season explains why extensive hunting pressure on a production area can effectively destroy locally breeding populations in a single season. Birds that remain near natal marshes as late as the beginning of the hunting season do not move long distances and thus remain vulnerable to hunters until they migrate. Anderson and Henny (1972) believed that association with young birds made an adult hen more vulnerable to hunters. Our data from the Chippewa National Forest populations indicate that this is true to the extent that adults have the same activity patterns near natal marshes as do the young.

Knowledge of waterfowl behavior and population dynamics during the postfledging period and hunting season is necessary to effectively manage locally reared ducks. Yet waterfowl behavior is difficult to study during this period, and at best yields only partial conclusions. Despite the difficulty, we wish to underscore the importance of such knowledge. In support of this view, we reiterate the most important management findings of our work by comparing the findings regarding young birds, together with those of Gilmer et al. (1977) regarding adult waterfowl on the same area, with a recent comprehensive analysis of mallard banding data (Munro and Kimball 1982).

Munro and Kimball (1982) found highly significant differences in the continental test statistic when recovery distributions of locally reared and immature mallards were compared, with significant differences found in the

Great Lakes reference area (encompassing the Chippewa National Forest) and adjacent Missouri River Basin area. Alternative explanations provided for this phenomenon included an influx of immatures into the United States from northern regions or earlier movement of more physiologically advanced immatures from the banding site. Our results support the conclusion that a combination of effects is involved. We observed early hatched young moving earlier and farther from the brood marshes (biotelemetry data) and an influx of mallards into the Chippewa National Forest before the hunting season in aerial censuses. Similar circumstances probably apply throughout northern States and the Canadian Provinces where recovery distributions differ significantly between locally reared and immature birds.

Munro and Kimball (1982) further found highly significant differences in the continental test statistic when recovery distributions of immature and adult mallards were compared; the prevailing difference was a more northerly distribution of immatures. A prolonged attachment to brood marshes of more vulnerable first-year birds and successfully nesting females would be capable of causing this difference in recovery distribution. Biotelemetry data support this speculation. Gilmer et al. (1977) showed that most adult male mallards actually left northern Minnesota entirely following the breeding season, although some returned later during fall migration. Unsuccessful females also departed the area. Our telemetry studies showed that successful females and many of the young reared on the Chippewa National Forest remained on or near their brood marsh until after the beginning of the hunting season. This provides support for the argument of Munro and Kimball (1982), and for earlier similar speculation that timing of migration differed for young birds (Gollop 1965; Jessen 1970).

Munro and Kimball (1982) found that the most pronounced differences in recovery distribution were between immature and adult male mallards. Again, the early departure of adult male mallards to molting areas north of Minnesota (Gilmer et al. 1977) all but guarantees different recovery distributions for male mallards banded in the north-central part of the State. Postfledging dispersal of young male mallards is not the equivalent of postbreeding movements of adult birds. To the extent that postbreeding movements of mallards elsewhere follow this pattern, differences in recovery distributions similar to those found in Minnesota should be expected.

Munro and Kimball (1982) also found age- and sex-specific differences in the timing of recovery (harvest) that suggested differential vulnerability and, perhaps, in-

licated "subadult" age classes. Munro and Kimball (1982) also allowed that differential timing and rate of movement of birds through harvest areas could explain differences in the timing of recoveries. Our data provide support for the latter view because birds departed from our study area asynchronously. Particularly important was the finding that some young females actually returned to the study area (and their natal marshes) after absence during the first part of the hunting season, a phenomenon increasing the discrepancies in the distribution of young birds early in the hunting season. The sudden departure of most mallards on our study area after the opening of the hunting season (but not the majority of the radio-equipped locally reared birds) strengthens the case for differential timing in migration of young-of-the-year birds versus other birds, or perhaps early versus late-hatched young, but provides no insight into the question of existence of "subadult" age classes.

We can also speculate on the interaction of harvest regulations and their ultimate effect on the birds present in north-central Minnesota at the beginning of the hunting season. The regulations in effect in 1973 and 1974, which included closure at 1600 h, allowed ducks to maintain pre-hunting season activity patterns (Kirby et al. 1976) and shifted a significant proportion of the total harvest of mallards banded in Minnesota out of State (Kirby et al. 1983). This suggests that a refuge in "time" was afforded these birds by Minnesota's shortening of the late afternoon hunting period. Analyses of survival rates between years of sunset closure and years of 1600 h closure, although inconclusive because of the low power of the tests, nevertheless showed a trend toward lower survival of adult and young female mallards and higher survival of adult and young male mallards during years of 1600 h closure (Kirby et al. 1983).

The seemingly incongruous result of the combination of regulations in effect during years of 1600-h closure can be explained by our telemetry study. Females, both young and adult, were closer to the brood marshes at the opening of the hunting season, on the average, than were male mallards. Hunting pressure in north-central Minnesota is substantial. Thus, birds remaining on or near the brood-rearing marshes ran a high risk of eventually coming into contact with hunters because hunter-free areas are scarce, despite the refuge in time afforded by the 1600-h daily closure. Similarly, because a large part of the waterfowl population of our study area departed immediately after opening day, the probability of remaining birds coming into contact with the still large contingent of hunters on subsequent days of the season was increased until more northern birds arrived to aug-

ment the study area population. Olson (1967), Boyd (1971), and Hochbaum and Walters (1984) showed that the probability of hunting mortality for an individual duck increases with decreasing flock size. Additionally, Hochbaum and Walters (1984) showed that duck vulnerability, which is low at the beginning of hunting seasons when ducks demonstrate avoidance behaviors to new stimuli, is inversely proportional to current rather than cumulative hunting effort. This means that avoidance learning does not protect birds against lower levels of hunting effort later in the season and that vulnerability on a given marsh increases as the season progresses and populations decline (Hochbaum and Walters 1984). Thus, the substantial mortality that occurred in locally reared young and females near the natal marshes, despite the 1600-h closure, probably resulted from a combination of increased probability of naive birds encountering a hunter early in the season and continued high and then increasing vulnerability later in the season as populations declined.

The northern Minnesota mallard population presently appears not to be maintaining its numbers except through pioneering of additional birds each year (Cowardin and Johnson 1979; Kirby and Cowardin 1986). An apparently appropriate solution to the problem of substantial kill of locally reared young and adult females has been suggested on numerous occasions (Martin and Carney 1977; Munro and Kimball 1982)—to delay the opening date until such time that larger numbers of the species in perceived difficulty are present on the brood marshes. This was recently attempted on a large scale in Manitoba (Caswell et al. 1985) where survival rates of adult mallards, especially females, were improved by delaying opening dates and reducing bag limits for large areas on the breeding grounds. Because northern water areas freeze early, however, such rearrangements in hunting season frameworks are difficult to carry out if a concurrent goal is to maintain equivalent hunting opportunity. Alternatively, area closures have been suggested to protect female birds or more vulnerable species (Hochbaum and Walters 1984). These have often had limited success, with harvests sometimes higher when birds are encouraged to remain on or near areas of high hunter activity. In many instances, total benefits accrued to locally reared young and breeding females are often slight because of extensive premigratory movements (the present study) and mortality resulting from daily flights in and out of the refuge areas (Jahn and Hunt 1964). Such arguments also have been countered by others who state that benefits are of little total consequence (without extensive area closure) because the probability remains

that a bird not killed on or near brood marshes would nevertheless be subject to substantial hunting mortality elsewhere (Cowardin and Johnson 1979).

The sequence of events observed in young waterfowl during late summer in north-central Minnesota was probably typical of occurrences throughout much of the forested Lake States region. Our data suggest the need to critically appraise harvest regulations that emphasize sex, age, and species differences in order to protect locally reared birds. Given the behavior of premigratory assemblages of waterfowl near natal marshes, the local effects of such regulations might be much less than expected and the continental effects insignificant for some species and detrimental for others. Similarly, our data suggest that small-area closures have little likelihood of significantly increasing survival of locally reared birds and adult females remaining near the breeding grounds into the hunting season. Both daily and seasonal premigratory movements of these cohorts are great enough to require very large closures if protection of birds near natal marshes is a priority.

The effects of postbreeding movements and preferential habitat use by adult and young birds should be addressed when considering area-specific regulations that are intended to protect locally produced young and adult females remaining on and near breeding areas after breeding. We emphasize the great need for a better understanding of timing in movements of waterfowl, particularly the differences between movements of the various ages and sexes. We also stress the necessity for clearly understanding waterfowl-habitat relations during the postbreeding period. Studies of postbreeding waterfowl can provide major insight into questions on waterfowl distribution, and the relations between chronology of migration and hunter harvest. Similarly, a greater understanding of the survival benefits that accrue to the individual bird in a postbreeding waterfowl flock, particularly through study of flock structure and dynamics, will clarify many aspects of age-related and time-specific survival and fecundity. Scientific waterfowl management must have such data to properly and effectively manage this resource.

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**Key words:** Behavior, biotelemetry, habitat use, mallards, *Anas platyrhynchos*, migration, Minnesota, movements, postbreeding, premigratory, wood ducks, *Aix sponsa*.

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The following is a list of recent *Fish and Wildlife Research* publications.

1. Life History and Status of the Endangered Cui-ui of Pyramid Lake, Nevada, by G. Gary Scoppettone, Mark Coleman, and Gary A. Wedemeyer. 1986. 23 pp.
2. Spread, Impact, and Control of Purple Loosestrife (*Lythrum salicaria*) in North American Wetlands, by Daniel Q. Thompson, Ronald L. Stuckey, and Edith B. Thompson. 1987. 55 pp.
3. Taxonomy, Life History, and Ecology of a Mountain Mahogany Defoliator, *Stammodes animata* (Pearsall), in Nevada, by Malcolm M. Furniss, Douglas C. Ferguson, Kenneth W. Voget, J. Wayne Burkhardt, Arthur R. Tiedemann, and John L. Oldemeyer. 1988. 26 pp.
4. Demographic Characteristics of a Maine Woodcock Population and Effects of Habitat Management, by Thomas J. Dwyer, Greg F. Sepik, Eric L. Derleth, and Daniel G. McAuley. 1988. 29 pp.

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