This is to certify that the

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SOCIOBIOLOGY OF BREEDING DRAKE
MALLARDS IN NORTHERN IOWA

presented by

DeWaine Howard Jackson

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Harold H. Prince
Major professor

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SOCIOBIOLOGY OF BREEDING DRAKE MALLARDS IN NORTHERN IOWA

By

DeWaine Howard Jackson

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ABSTRACT

SOCIOBIOLOGY OF BREEDING DRAKE
MALLARDS IN NORTHERN IOWA

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Breeding activity of drake mallards (*Anas platyrhynchos*) was studied during 1977 and 1978 in north-central Iowa on a 137-ha marsh and satellite wetlands within 16 km. Drought conditions prevailed in 1977 and water levels returned to normal in 1978. Although nearly twice as many drakes were observed in 1977 compared to 1978, pursuit flight activity and behavior indicative of actively breeding birds was not as frequent. The number of pairs was similar between years, yet traditional census methods showed an increase in the number of indicated pairs for 1977. This suggests a larger breeding population in 1977 and confounds the response by mallards to drought. Drakes not observed with a hen spent less time on the study area and utilized 3.4 times more area than drakes observed with a hen. Although drakes without hens appeared to be available for breeding, they did not appear to interfere with breeding pairs.

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I am especially grateful to Ken Reynolds, Gary Littauer, Richard Sayles, and Ronald Andrews for their enthusiastic field assistance.

I appreciate the cooperation of the Cerro Gordo County Conservation Board in allowing the study to be conducted on Zirbel Slough.

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INTRODUCTION

Disparate sex ratios are common to many avian populations and particularly to waterfowl. Early conceptual notions that the type of mating system created the unbalanced sex ratio have been replaced by the concept that unbalanced sex ratios are consequences of differential mortality in males and females resulting ultimately from intense sexual selection in nonmonogamous mating systems (Willson and Pianka 1963, Selander 1965, 1972).

In the mallard (*Anas platyrhynchos*) ratios ranging from 40 to 70 percent drakes have been documented. Although the mallard has one of the most balanced sex ratios of all common game ducks, the margin of surplus drakes appears to be increasing (Bellrose 1976). The extent of disparity existing in mallard populations depends on region, season, and method of data collection (Bellrose et al. 1961). Although the presence of extra drakes is now widely accepted, the breeding activities of the surplus drakes has not been determined.

The mallard is basically monogamous (Johnsgard 1960, Humburg et al. 1978) and pairing generally occurs on the wintering grounds prior to spring migration (Hochbaum 1944, Sowls 1955, Weller 1965). Breeding activity of pairs returning to production areas is dependent on proper environmental cues such as weather and habitat conditions. Under suitable conditions a pair selects an appropriate section of habitat and initiates reproductive efforts. Breeding habitat used by mallards

is not stable and appropriate conditions are not always present, especially in years when drought reduces the number and size of wetlands.

The high energy expenditure by the female during reproduction accentuates the importance of mate and habitat selection. In a discussion of male and female display and courtship roles, Weidman and Darley (1971) have concluded that the female is an essential element in social display and that social display promotes pair formation. A male's most obvious reproductive activity is to insure that the offspring of his mate are actually his. Thus his behavior consists of the early defense of the territory (and/or the female) and the later abandonment of the territory and his mate as she nears hatching.

Information presented by Humburg et al. (1978) indicates that although surplus drakes occasionally mated with a renesting female and while they "... appeared available for breeding, they did not seem to interfere with breeders in the system." Apparently some of the unmated drakes in the population are not essential during the breeding season. The present research was designed to describe in greater detail, the behavior, breeding activities, and the importance to the breeding system of mated and unmated drake mallards.

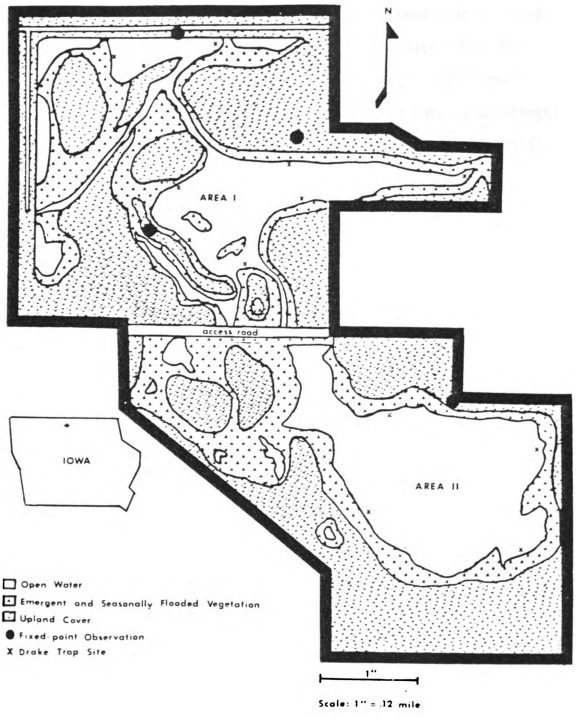
STUDY AREA

The main study area was Zirbel Slough, a 137.5 ha public hunting area located in north-central Iowa. The wetland complex is located 10.5 km southeast of Clear Lake, Sections 8 and 17, T95N, R21W, Mount Vernon Township, Cerro Gordo County, Iowa (Figure 1).

Zirbel Slough consists of approximately 61 ha of marsh and open water and 76.5 ha of uplands. The dominant upland vegetation during the nesting period is bromegrass (*Bromus inermus*) and bluegrass (*Poa pratensis*), with reed canary grass (*Phalaris arundinacea*) and prairie cord grass (*Spartina* spp.) occupying moist upland sites. These major cover species are intermixed with seasonal grasses and forbs, goldenrod (*Solidago* spp.), milkweed (*Asclepias* spp.), daisy fleabane (*Erigeron pumilus*), sunflowers (*Helianthus* spp.), and sweetclover (*Melilotus alba*), that provide limited cover throughout the nesting period. Major emergent hydrophytes during early spring include sedges (*Carex* spp.), cattail (*Typha* spp.), common threesquare (*Scirpus americanus*) and bullrushes (*Scirpus* spp.). Other emergents, arrowhead (*Sagittaria* spp.), water-plantain (*Alisma* spp.), burreed (*Sparganium* spp.) and smartweed (*Polygonum* spp.) become abundant in late June and early July and provide considerable cover for broods.

Water level on the study area changed dramatically between years. Precipitation one year prior to the 1977 field season was 20.6 cm below normal while precipitation one year prior to the 1978 field

Figure 1. The Zirbel Slough study area.


N
AREA I
access road
IOWA
AREA II
Open Water
Emergent and Seasonally Flooded Vegetation
Upland Cover
Fixed point Observation
X Drake Trap Site
1"
Scale: 1" = .12 mile

season was 16.5 cm above normal (Table 1). Precipitation during the four month field season in 1977 had little effect on the water level of the study area. A 45.7 cm decrease in water level occurred during the 1977 field season. The water level on the study area that was maintained during the 1978 field season was 25.4 cm greater than the highest level obtained during the 1977 field season. Additional habitat areas used for foraging, loafing, and territory establishment were present in 1978 because the high water flooded many areas that were without water in 1977.

Table 1. Precipitation (cm) statistics for Zirbel Slough 12 months prior to and during the 1977 and 1978 field seasons.

Time period	Year 1977	Year 1978
Total precipitation 12 months prior to the field season (March-February)	54.1	91.2
Departure from mean for 12 months prior to the field season (March-February)	-20.6	+16.5
Total precipitation during the field season (March-June)	41.0	30.3
Departure from mean during the field season (March-June)	+7.4	-3.3

METHODS

Sex Ratios

To estimate sex ratios, male and female mallards were counted within a 16 km radius of Zirbel Slough between 25 March-7 April in 1977 and 1978. Nine counts in 1977 and seven counts in 1978 were completed on either entire groups of mallards exposed on open water areas or segments of larger flocks partially concealed by vegetation. Counts were on undisturbed flocks only and in many cases two observers with spotting scopes would count the same group of birds from two different locations to obtain the greatest accuracy. Counts were conducted between 07:00-18:00 h and each took approximately 0.5 h.

Trapping and Marking

Trapping and marking began just after the migrants had left the study area. Eleven modified clover-leaf traps, containing a live semi-domestic hen mallard as a decoy, were used between 12 April-6 June in 1977 and between 13 April-2 June in 1978. Each trap was checked twice daily, once early in the morning and again at sunset. Traps were placed in areas where aerial pursuit flights, pairs,and mating activity had been consistently observed. Traps were relocated when vegetation began to obscure the trap and/or capture rate declined significantly. Hens located on nests were captured with a bail type

nest trap similar to that described in Doty and Lee (1974). A colored polyvinyl nasal saddle bearing an alpha-numeric code, and a U.S. Fish and Wildlife Service leg band was placed on each captured mallard. Three different colors of florescent paint were applied in specific combinations to the under wings and tail of each bird. Both years, back mounted radio transmitters (Dwyer 1972) were placed on 6 to 8 drakes during each of three 4-15 day intervals.

Ground Counts

The number of mallards using the area during the breeding season was estimated by weekly ground counts (Dzubin 1969b) between 29 April-8 July 1977 and 14 April-7 July 1978. Counts were made by making 0.5 h observations of the census area and then walking a fixed route to flush birds not previously visible. Counts were made by two and three observers in 1977 and 1978, respectively. Each mallard was classified into one of four categories: single drake, pair, single hen, or flock. Duplicate observations were minimized by recording bird identification numbers when possible, time of the observation, and location of the bird (or direction of flight).

Fixed-point Observations

Fixed-point observations were made between 1 May-27 June 1977 and 14 April-30 June 1978 from three 3.5 m high observation platforms and 1 natural vantage point. Fixed-point observations were made on alternate days in 1977 and daily in 1978. Nearly all observation periods (ranging from 0.5-3 h in length) were conducted between

sunrise and 10:00 h and/or 16:00 h to sunset. Location, consort, and activity of all marked and unmarked mallards were recorded at the beginning and then monitored throughout the observation period. Activity was categorized on the basis of social interactions such as courtship or aggressive behavior. These observations were then used to calculate total number of mallards, pairs, and pursuit flights on a per hour basis.

Observation of Marked Birds

Mallards marked with nasal saddles or both nasal saddles and radio transmitters were monitored on a daily basis from late March through mid-July of each year. Spotting scopes were used to identify nasal saddle markings and/or paint combinations on marked birds. For each observation on a marked bird, the date, time, location, consort, and behavior were recorded. Approximately 20 and 30 man hours per day were spent searching and observing marked birds during April-June of 1977 and 1978, respectively. Generally, searching for marked birds included ground surveillance for birds on Zirbel Slough in the morning, then a search of satellite wetlands within 16 km of Zirbel Slough during midday and surveillance again on Zirbel Slough in the afternoon. An attempt was made to record two locations per day for birds on Zirbel Slough and one location per day for birds on satellite wetlands. Ground surveillance for drakes marked with radio transmitters began immediately after the first radio was attached (19 April in both years), while aerial surveillance was done on a routine basis from early May to late June in both years. Daily searches were made for all drakes with radio transmitters on Zirbel Slough and in an 800 sq km area

(16 km radius) surrounding Zirbel Slough. When individuals with radio transmitters were not located within this area, attempts were made to locate the birds by aerial surveillance. An aerial search within the 800 sq km area was used during each flight to verify ground surveillance. Major wetland complexes between 16 km and 322 km from Zirbel Slough were then searched. When possible, visual observations of birds located with radio telemetry were made to determine the birds' status (i.e., with or without a mate). The ground and aerial search patterns within the 800 sq km area were based on the distribution of satellite wetlands surrounding Zirbel Slough. Although aerial searches of known larger wetland complexes beyond the 800 sq km area were emphasized, some drainage channels and sheetwater areas were also searched. The status of the bird, the length of time the marked bird stayed on the study area, and movements of the bird were determined from these observations.

RESULTS

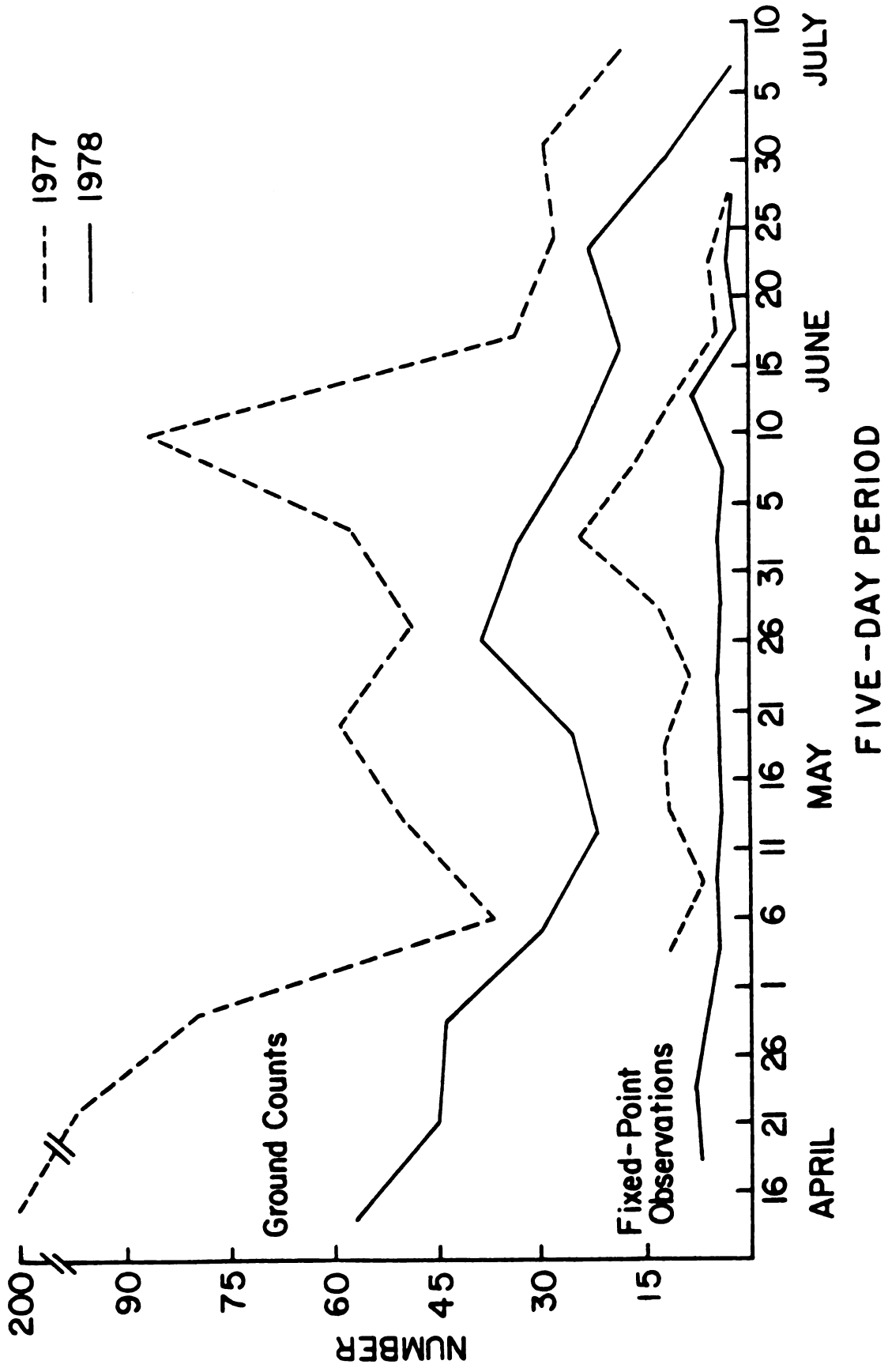
Population Observations

Each year the highest number of mallards on the area was counted just after spring arrival (Figure 2). The total number of mallards on Zirbel Slough ranged from 18 to 200 birds in 1977 and from 2 to 57 birds in 1978. Although the ground counts were correlated by date between years ($r = 0.71$, 9 df, $P < 0.02$), there was a significantly higher mean number of mallards observed per ground count in 1977 compared with 1978 ($t = 3.13$, 20 df, $P < 0.01$). The large number of birds counted during the 10 June census in 1977 was not repeated in 1978.

Mallards observed per hour per five-day period on fixed-point observations averaged 10.5 ± 5.7 and 4.8 ± 2.0 in 1977 and 1978, respectively (Figure 2). Numbers observed during fixed-point observations tended to remain constant in 1978 while the numbers observed in 1977 were more variable and tended to parallel ground counts.

The sex ratio of mallard flocks present in early April 1977 (9 counts, 56.4 ± 0.6% drakes, n = 460) was not significantly different ($t = 2.1$, 14 df, $P > 0.05$) from the ratio observed in 1978 (7 counts, 54.8 ± 0.5% drakes, n = 386). The combined sex ratio of both years was 55.7 ± 1.8% drakes, which deviates significantly from 50:50 ($X^2 = 10.9$, 1 df, $P < 0.005$).

Figure 2. Total number of mallards observed on ground counts and number observed per hour per five-day period during fixed-point observations on Zirbel Slough in 1977 and 1978.


1977
1978
Ground Counts
Fixed-Point Observations
NUMBER
200
90
75
60
45
30
15
16
21
26
1
6
11
16
21
26
31
5
10
15
20
25
30
5
10
APRIL
MAY
JUNE
JULY
FIVE-DAY PERIOD

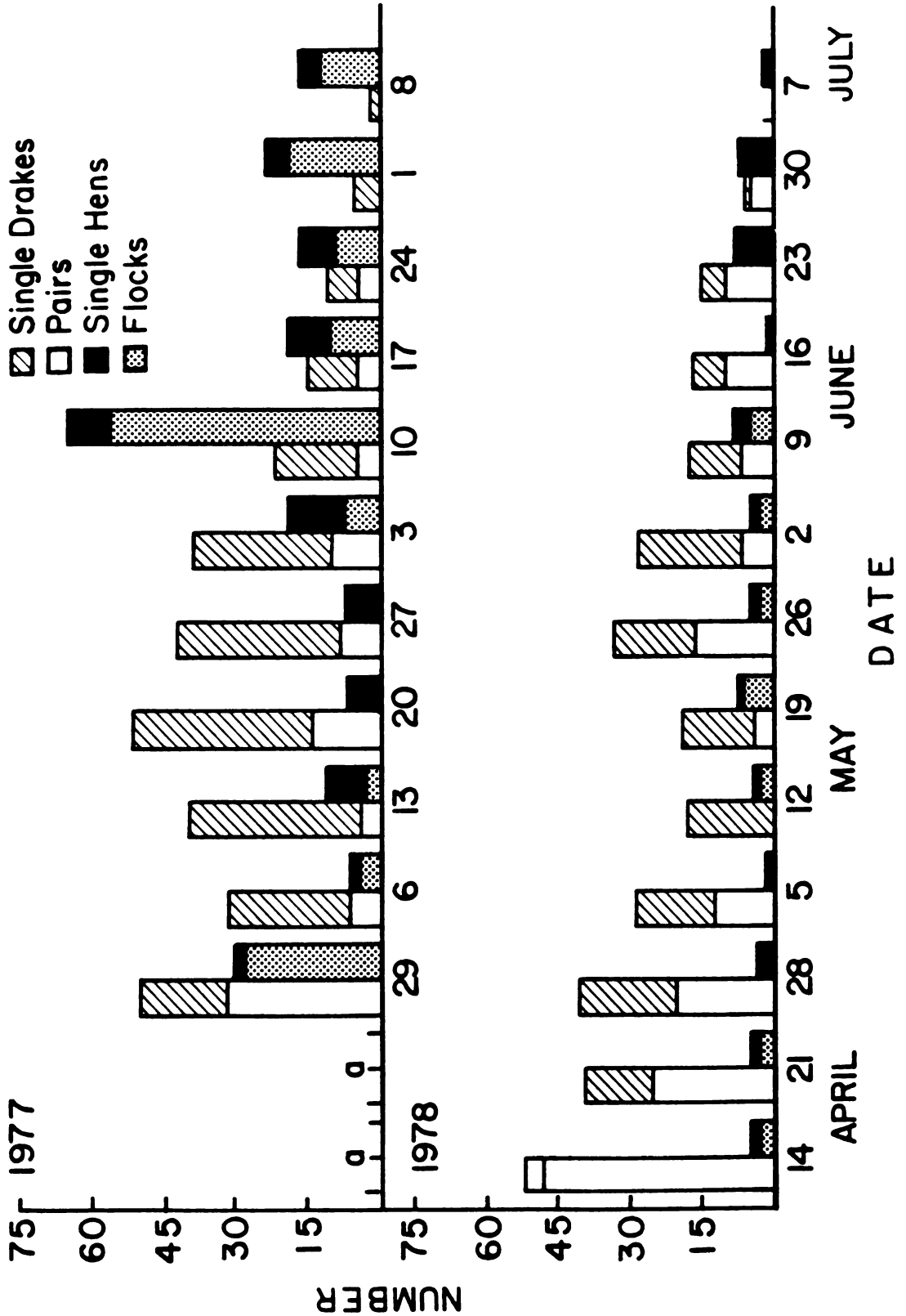
Mallards observed during ground counts were categorized into one of four groups: single drakes, pairs, single hens, or flocks (Figure 3). The combined number of pairs and single drakes have traditionally been used as an estimate of the breeding numbers (indicated pairs) on an area. While birds in flocks and single hens have been considered as estimates of the nonbreeding segment of the population (Hammond 1959).

The mean number of pairs observed per ground count was not significantly different between years ($t = 0.99$, 22 df, $P > 0.05$). The number of single drakes was correlated by date between years ($r = 0.84$, 9 df, $P < 0.01$). During the major portion of the breeding season, 29 April-17 June, 65 percent more single drakes were observed in 1977 which was significantly more than in 1978 ($t = 3.3$, 7 df, $P < 0.05$).

Single hens were observed on all ground counts in both years. In 1977, 2-12 single hens were observed during each ground count and 42 more hens were counted during 28 April-8 July 1977 than in 1978.

Large flocks of mixed species of waterfowl were present on Zirbel Slough between 15-22 April 1977. Accurate counts were difficult and attempts to categorize the status of the mallards observed were limited to estimates. Approximately 75 percent of the 200 and 100 mallards counted on 15 April and 22 April, respectively were in flocks (3 or more birds). Between 29 April-8 July, 148 mallards were observed in flocks in 1977 compared to 20 in 1978. Both the sex ratio and distribution by date of the flocks were different. During 1977, 42 percent (62) of the flocks were hens while in 1978, 10 percent (2) were hens. Chronologically, in 1977, flocks occurred during 15 April-13 May and 3 June-8 July while in 1978 small flocks of drakes were present between

Figure 3. The number of mallards as single drakes, pairs (divide by 2 for number of pairs), single hens and flocks observed during ground counts on Zirbel Slough in 1977 and 1978. (a) Categorization on these counts was limited to estimates and therefore not included.


Single Drakes
Pairs
Single Hens
Flocks
1977
1978
NUMBER
75
60
45
30
15
0
0
APRIL
MAY
JUNE
JULY
DATE
14
21
28
5
12
19
26
2
9
16
23
30
7
29
6
13
20
27
3
10
17
24
1
8

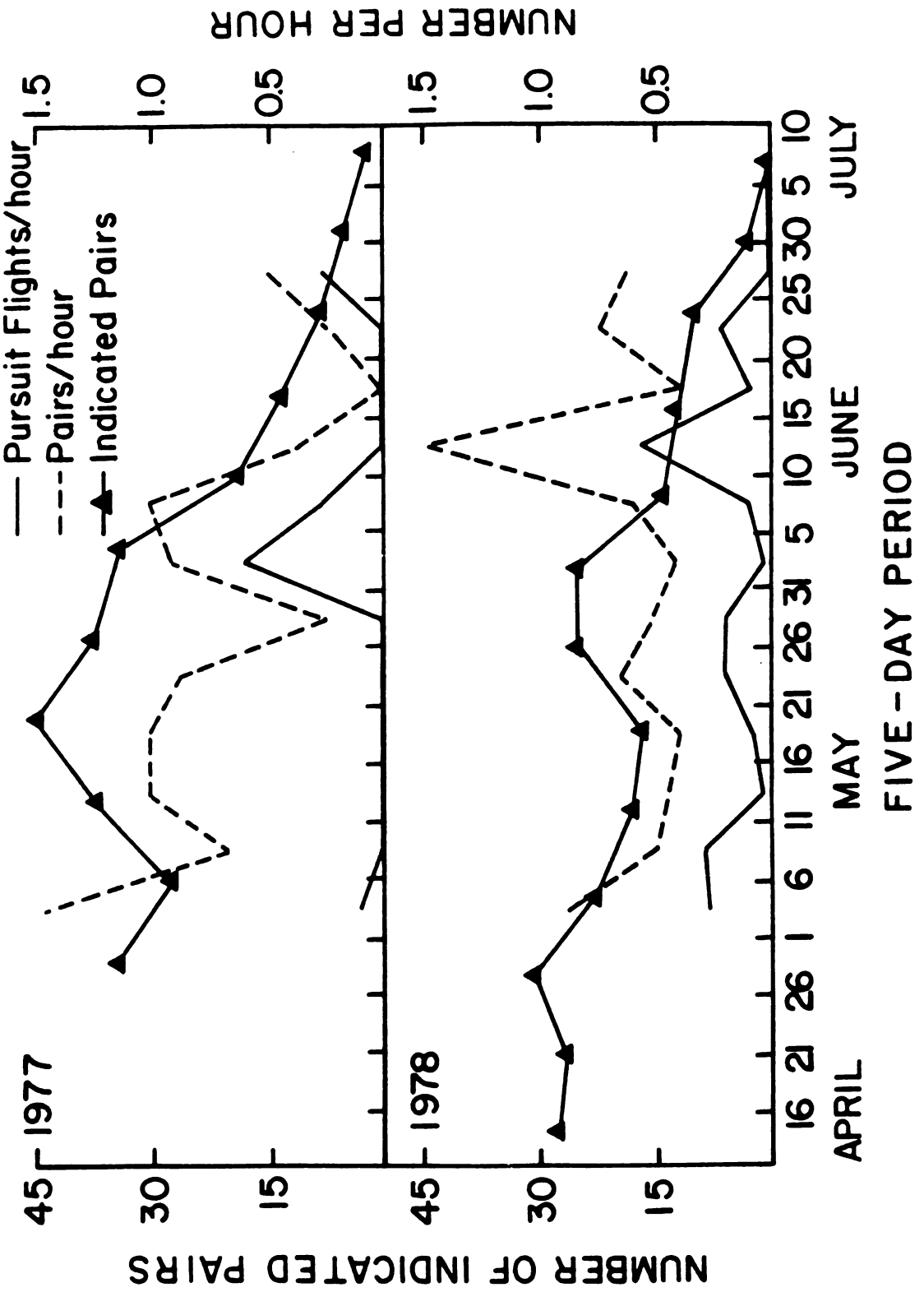
12 May-9 June.

Data from ground counts were used to obtain an indication of the number of pairs utilizing the study area as breeding habitat. The number of indicated pairs using the area (Figure 4) was significantly correlated by date of census between years ($r = 0.84$, 9 df, $P < 0.01$). The total number of indicated pairs using the area was similar between years except during 3 counts made between 12 May-26 May 1977, in which 106 percent, 165 percent, and 52 percent increases were noted, respectively.

Pairs per hour per five-day period observed during fixed-point observations were not significantly correlated between years ($r = 0.08$, 10 df, $P > 0.05$) nor was the mean number of pairs observed per hour per five-day period significantly different between years ($t = 0.38$, 22 df, $P > 0.05$). In 1977, .69 ± .42 ($\bar{x} \pm SD$) pairs per hour per five-day period were observed during the fixed-point observations while in 1978, .63 ± .30 were observed.

Pursuit flights, except for trace occurrences in early May and late June 1977, were observed for a 21 day period between 26 May-15 June in 1977 and for a 56 day period between 1 May-25 June in 1978. Although there was not a relationship between the number of pairs observed per hour per five-day period and number of pursuit flights per hour per five day period in 1977, they were significantly correlated in 1978 ($r = 0.85$, 10 df, $P < 0.01$). Within each year when the total number of mallards observed per hour per five-day period increased the number of pursuit flights observed per hour per five-day period increased (1977, $r = 0.63$, 10 df, $P < 0.05$; 1978, $r = 0.83$, 10 df, $P < 0.05$).

Figure 4. Number of pursuit flights and pairs observed per hour per five-day period during fixed-point observations and the number of indicated pairs observed during ground counts on Zirble Slough in 1977 and 1978.


NUMBER OF INDICATED PAIRS
NUMBER PER HOUR
Pursuit Flights/hour
Pairs/hour
Indicated Pairs
1977
1978
45
30
15
1.5
1.0
0.5
16 21 26 1 6 11 16 21 26 31 5 10 15 20 25 30 5 10
APRIL
MAY
JUNE
JULY
FIVE-DAY PERIOD

Trapping and Marking

During the two years 234 drakes and 34 hens were captured in the clover-leaf traps (Table 2). The mean capture rate was 3.05 ducks per day for 56 days in 1977 (616 trap days, 0.28 ducks/trap day) and 1.84 ducks per day for 51 days in 1978 (561 trap days, 0.17 ducks/trap day). Daily capture rate of drakes on Zirbel Slough ranged from 0 to 8/day and averaged 0.25 and 0.15 drakes/trap day for 1977 and 1978, respectively. Twenty-four percent (36) of the drakes in 1977 and thirty-seven percent (31) in 1978 were recaptured at least once.

Cumulative capture of drakes during both years increased steadily until late May and early June (Figure 5). Trapping was terminated during the first week of June in both years due to the drastically reduced trap success.

Capture rate of drakes show a seasonal trend, being highest during mid-April-early May. Mean capture rate of drakes per five-day period was significantly higher in 1977 than in 1978 ($t = 4.6$, 9 df, $P < 0.05$).

The percent of marked birds observed per ground count after 1 May was significantly lower in 1977 than in 1978 ($t = 2.73$, 18 df, $P < 0.02$). However, the percentage of marked birds observed on the counts was significantly correlated by date between years ($r = 0.72$, 8 df, $P < 0.05$) and the peak percentage of marked birds occurred during mid-May in both years.

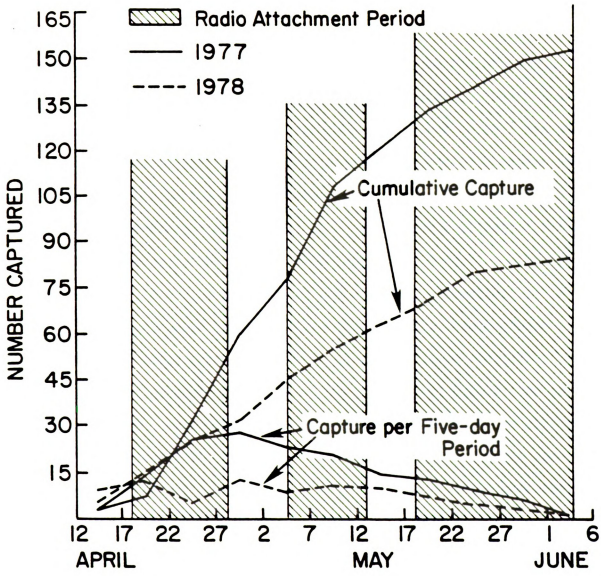
Drake Observations

During fixed-point observations and ground counts the highest percentage of drakes occurred during mid-May. The percentage of drakes

Table 2. Number of mallards captured and marked with a nasal saddle or nasal saddle and radio transmitter and the trapping statistics on Zirbel Slough in 1977 and 1978.

Category	Year	
	1977	1978
Number of males captured	151	83
Number of females captured	22	12
Number of males fitted with a transmitter	20	22
Number of females fitted with a transmitter	11	2
Number of different males recaptured	36	31
Total number of male recaptures	64	58
Number of traps used	11	11
Number of days trapped	56	51
Number of trap days	616	561
Trap success (ducks/trap day)	0.28	0.17
Males captured/trap day	0.25	0.15

Figure 5. Cumulative number of drake mallards captured and the number of drake mallards captured per five-day period on Zirbel Slough in 1977 and 1978 with the shaded zones denoting time intervals when radio transmitters were placed on drakes.


Radio Attachment Period
1977
1978
Cumulative Capture
Capture per Five-day Period
NUMBER CAPTURED
165
150
135
120
105
90
75
60
45
30
15
12
17
22
27
2
7
12
17
22
27
1
6
APRIL
MAY
JUNE

observed during the fixed-point observations was significantly correlated with the percentage of drakes observed during the ground counts for both years (1977, $r = 0.89$, 6 df, $P < 0.01$; 1978, $r = 0.89$, 8 df, $P < 0.01$). The percent of drakes observed initially was just over 50 percent, increased to 90 percent during early May, then gradually declined to 5 percent in early July.

Visual observations of marked drakes throughout the breeding season provide an indication of the reproductive status of each drake. Reproductive status of 146 and 80 drakes was obtained in 1977 and 1978, respectively (Table 3). Twenty percent of the drakes with radios and 14 percent of the marked drakes without radios were observed with a hen in 1977. These percentages are not significantly different from the number observed with a hen in 1978 ($X^2 = 2.0$, 1 df, $P > 0.05$ and $X^2 = 2.9$, 1 df, $P > 0.05$ with radios and without, respectively). Although a similar number of drakes were observed with hens between years, there were 2.3 times more drakes observed without a hen in 1977.

Twenty-one percent (47) of the total 226 drakes established an association with a hen. Of the drakes observed with a hen in 1977, 86 percent (19) had established their association prior to 15 May compared with 56 percent (14) in 1978. For 42 drakes that were marked with nasal saddles and radios during three time periods, none of the 1977 drakes established an association with a hen after the late April trapping period (Table 4). This can be compared to 1978 when drakes marked during each trapping period subsequently were observed with a hen.

The status (with or without a drake) of 34 marked hens, 22 in 1977 and 12 in 1978 was also obtained. In 1977, 9 (41 percent) of the hens

Table 3. The number (%) of drake mallards marked with nasal saddles or nasal saddles and radio transmitters that were subsequently observed with or not with a hen after capture on Zirbel Slough during 1977 and 1978.

Type of marker	1977			1978		
	With a hen	Not with a hen	Total	With a hen	Not with a hen	Total
Drakes with radios	4 (20.0)	16 (80.0)	20	10 (45.5)	12 (54.5)	22
Drakes without radios	18 (14.3)	108 (85.7)	126	15 (25.9)	43 (74.1)	58
Total	22 (15.1)	124 (84.9)	146	25 (31.3)	55 (68.7)	80

Table 4. Number of drake mallards marked during three periods with nasal saddles and radio transmitters that were subsequently observed after capture with or not with a hen on Zirbel Slough in 1977 and 1978.

1977			1978		
Capture date	With a hen	Not with hen	Capture date	With a hen	Not with hen
19-22 April	4	2	19-28 April	2	5
5-12 May	0	6	9-13 May	5	2
24 May - 4 June	0	8	18 May - 1 June	3	5
Total	4	16	Total	10	12

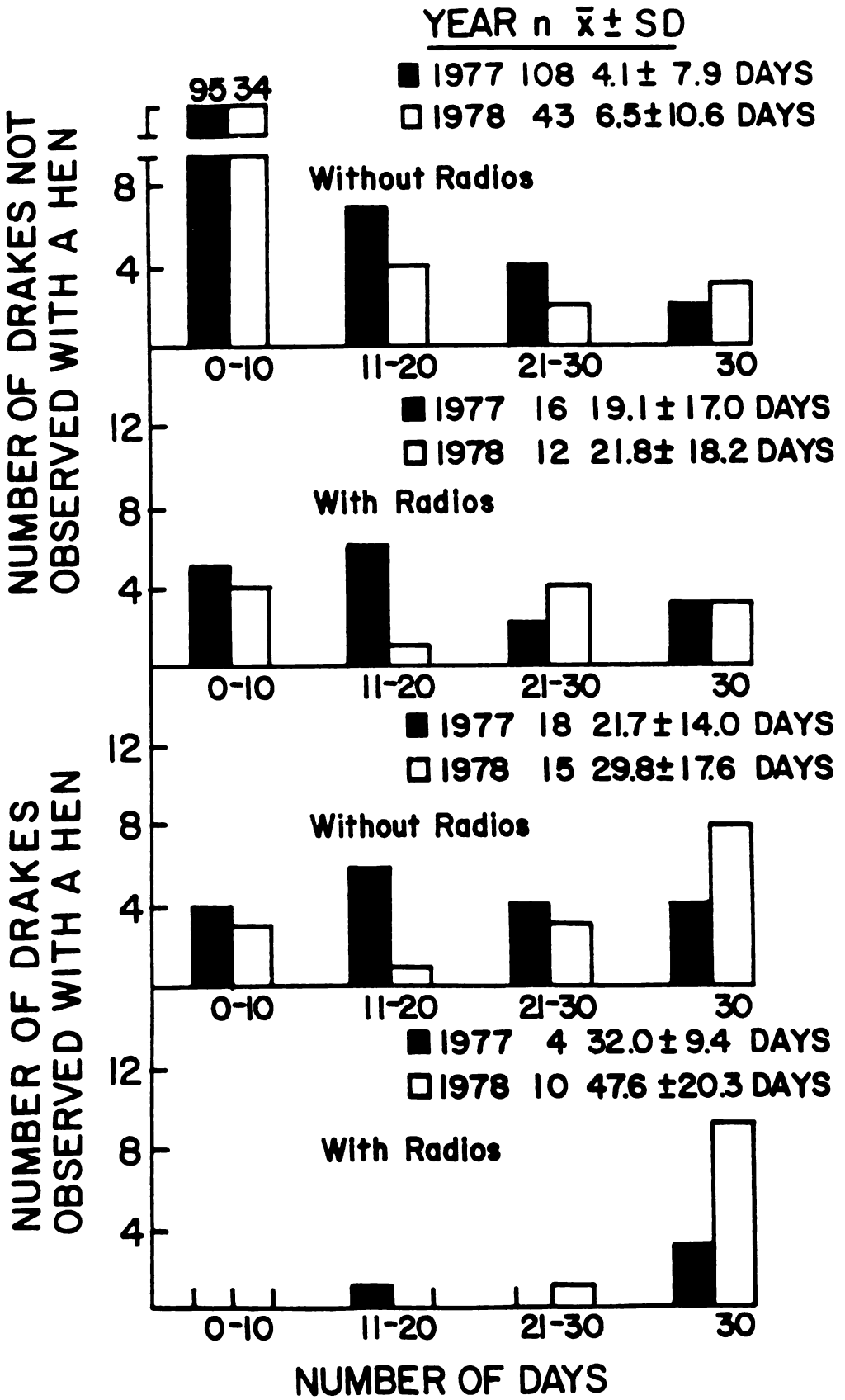
were observed with a drake compared to 6 (50 percent) in 1978, values which were not significantly different (X^2 = 0.02, P > 0.05).

The number of days that drakes spent on the area (Figure 6) was significantly influenced by three factors: the status (with or without a hen), the radio transmitter, and the year (three way analysis of variance F significance values = 0.001, 0.001, and 0.023, respectively). Drakes observed with a hen spent significantly more time on the study area than drakes that were not observed with a hen. The number of days that drakes, not marked with a radio and not observed with a hen, were present on the study area was similar each year and averaged 4.8 ± 8.8 days (Figure 6). Drakes not observed with a hen but marked with a radio were present on the area 20.3 ± 17.3 days, which is 4.2 times longer than for drakes not marked with a radio. The mean number of days spent on the area by drakes marked with a radio and observed with a hen (43.1 ± 18.9) is 1.7 times longer than for drakes with hens but not marked with a radio (25.4 ± 16.0 days). Regardless of status, drakes tended to be present on the study area for longer amounts of time in 1978 than in 1977 with the difference between years being greatest for drakes observed with hens.

Drake Movements

Nasal saddles and radios were placed on 42 drakes during the two years to obtain behavioral and movement data. The back mounted radio transmitters that were used had a functional life span of 80-133 days and an average range of 1.6 km (ground to ground). Aerial surveillance increased maximum range to 24 km and expanded the average range of all functioning radios to 4.0 km. Nonfunctioning radio transmitters

Figure 6. The number of days that drakes, marked with a radio transmitter or not marked with a radio transmitter and observed with a hen or not observed with a hen, were present on Zirbel Slough in 1977 and 1978.


YEAR n x̄ ± SD
1977 108 4.1 ± 7.9 DAYS
1978 43 6.5 ± 10.6 DAYS
95 34
Without Radios
1977 16 19.1 ± 17.0 DAYS
1978 12 21.8 ± 18.2 DAYS
With Radios
1977 18 21.7 ± 14.0 DAYS
1978 15 29.8 ± 17.6 DAYS
Without Radios
1977 4 32.0 ± 9.4 DAYS
1978 10 47.6 ± 20.3 DAYS
With Radios
NUMBER OF DRAKES NOT OBSERVED WITH A HEN
NUMBER OF DRAKES OBSERVED WITH A HEN
0-10
11-20
21-30
30
4
8
12
NUMBER OF DAYS

were documented in only two cases, one in each year.

Aerial searching for birds with radio transmitters totaled 2.5 hours and 4.5 hours within and 7.5 hours and 13.3 hours outside the 800 sq km area in 1977 and 1978, respectively. During the 20.8 hours of aerial searching beyond the 800 sq km area five drakes were located, 3 in 1977 and 2 in 1978.

Daily locations obtained from the ground surveillance of each drake with a transmitter were recorded on field maps and more than one location per day per individual was uncommon. Ground surveillance within the 800 sq km area accounted for 98 percent of the 986 locations of drakes during the two field seasons. Twenty-nine of the 42 drakes had greater than 10 locations per bird and averaged 31.6 ± 17.3 locations per bird. Drakes observed with a hen were monitored for a 47.4 ± 19.0 day span and drakes not observed with a hen for a 41.5 ± 19.7 day span.

The locations obtained for the 29 drakes, 12 in 1977 and 17 in 1978, were used to calculate an "utilization area". The northwest corner of Zirbel Slough was arbitrarily chosen as the origin of a two-dimensional coordinate system. A mean X and Y coordinate point (defined as an activity center) was determined from all locations for an individual. Four standard deviations of the mean X and Y distance were plotted parallel to the X and Y coordinate axis, respectively (two on each side of the activity center). This resulted in a rectangle that contained 95 percent of the locations made for that drake.

The activity center for each drake was plotted on a map of the Zirbel Slough region and the distribution of these centers was

examined (Figure 7). In 1977, 7 (58 percent) activity centers were located within the limits of Zirbel Slough compared with 8 (47 percent) in 1978. The activity centers which occurred outside the Zirbel Slough boundaries, except for 1 of 5 in 1977 and 2 of 9 in 1978, coincide with the location of the wetland the drake occupied the most. There was no significant difference in the distance that activity centers occurred from the coordinate system origin between years or between drakes with different status (with or not with a hen) (two way analysis of variance F significance values = 0.922 and 0.823 for year and status effects, respectively). There were differences in the size of utilization areas associated with drakes using Zirbel Slough and those using satellite wetlands surrounding Zirbel Slough. The utilization area for drakes with activity centers on Zirbel Slough were significantly smaller than those on satellite wetlands ($t = 3.47$, 13 df, $P < 0.01$). As the activity center distance increases from the coordinate system origin, the utilization area size increases ($r = 0.34$, 27 df, $P < 0.1$). Although the size of the utilization areas were not significantly different between years, drakes without hens utilized greater than three times as much area as drakes with hens (Table 5) which is significant (two way analysis of variance F significance values = 0.845 and 0.097 for year effect and status effect, respectively).

Figure 7. The distribution of activity centers of drake mallards with radio transmitters that were observed with a hen or not observed with a hen on Zirbel Slough and the surrounding area in 1977 and 1978.

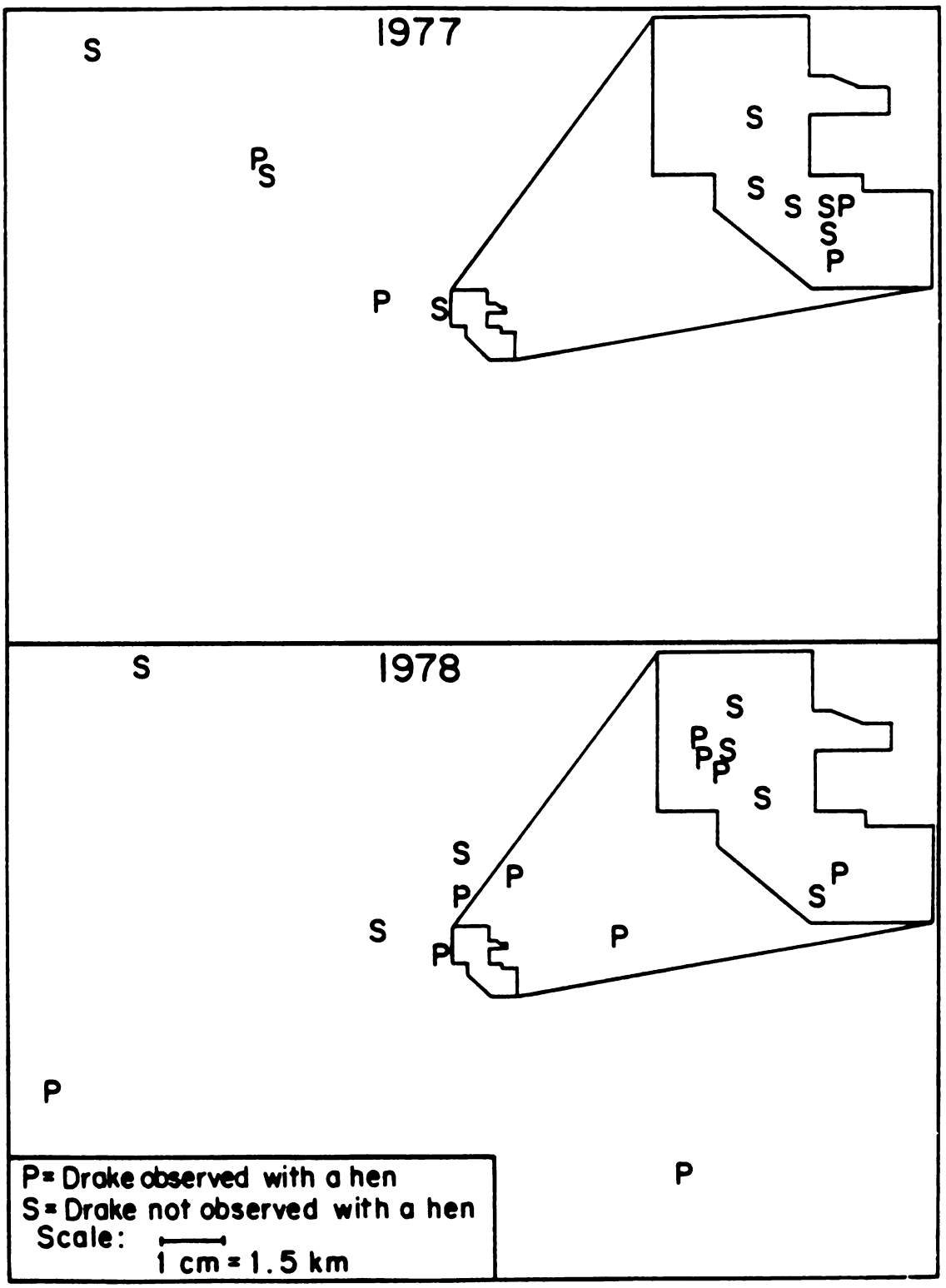

1977
1978
P= Drake observed with a hen
S= Drake not observed with a hen
Scale:
1 cm = 1.5 km

Table 5. Mean ± SD area (ha) utilized in the Zirbel Slough region by drake mallards observed with or without a hen during 1977 and 1978.

Status	Year	
	1977	1978
Drakes observed with a hen	3425 ± 5840 (4)[a]	3090 ± 3875 (10)
Drakes not observed with a hen	10230 ± 13150 (8)	12165 ± 19825 (7)

[a]Sample size.

DISCUSSION

Drought

Comparison of the mallard population levels during the two years revealed a larger number of mallards on the area and a lower proportion of breeding birds during 1977, a year of drought conditions. In 1977, nonbreeding birds, represented by single hens and flocks of hens and drakes, were present in greater numbers than in 1978. Sorensen (1978) has also observed high numbers of females occurring singly without a brood and in flocks during drought periods in Alberta. If spacing mechanisms that control upper limits on pair densities do not occur, flocked aggregations of pairs will form and short-range dispersal or long-range emigration are possible alternatives (Dzubin 1969a).

A result, using a traditional census method, that indicates higher breeding effort in 1977 is the higher number of indicated pairs. The density regulating mechanism (pursuit flights) that limits pair numbers on a breeding marsh (Dzubin 1969a) apparently does not limit numbers of single drakes using these areas. While pair numbers remained nearly equal between years the single drake component in 1977 was much higher than in 1978. Thus, single males and not pairs are responsible for the large increase of indicated pairs noted in May 1977. However, percentages of paired drakes recorded during the study, being lower in 1977, would indicate that many of these single males although counted

as pairs were actually unpaired drakes. Apparently fewer drakes establish pair bonds in a drought year and maybe more importantly pair bonds remain intact only briefly, early in the breeding period. Dissolution of pair bonds due to poor habitat conditions may account for the fact that none of the 1977 drakes marked with radios after 22 April were observed with a hen.

Therefore, during drought years, census methods that count single drakes as being indicative of a pair will overestimate breeding pairs and if production estimates are derived from these pair estimates they too will be overestimated.

Traditionally three-bird flights (TBF), attempted-rape flights (ARF), and avoidance are spacing mechanisms used by mallards to prevent crowding and to disperse pairs (Dzubin 1969a). Pursuit flights (TBF plus ARF) should then be expected to increase in frequency as densities in an unit of area increase, a result obtained during both years of this study as evidenced by the correlation between pursuit flights per hour per five-day period with the total number of mallards observed per hour per five-day period. During 1978 aggressive interactions between pairs (pursuit flights per hour per five-day period) increased with an increase in the number of pairs (pairs per hour per five-day period) present on the study area. Pursuit flights may have been important in spacing pairs and limiting pair numbers on the study area during 1978. However, during 1977 pursuit flights per hour per five-day period was not correlated with pairs per hour per five-day period. Thus during the drought pursuit flights as a regulating mechanism of pair numbers did not operate as would be expected. Also drakes in 1977 became spaced as if they were going through normal reproductive

efforts. Thus a mechanism other than behavioral actions, but yet working in unison with pursuit flights to limit numbers, must be considered.

A hen uses environmental cues to decide on her nesting activities. To be reproductively successful, she must choose a fertile mate, be physiologically prepared for egg laying, and nest in appropriate habitat. The drake, although responding to photoperiod and temperature, mainly responds to hen behavior (Weidman and Darley 1971) and does not directly respond to habitat conditions. Apparently, during 1977, pairs that returned to Zirbel Slough experienced the drought conditions and many of the hens responded by going into a non-reproductive mode similar to the description by Dzubin (1969b). The drakes were, however, physiologically ready to breed and enough breeding hens were present to perpetuate this mode. Some drakes may have been responding to live hens in the traps. Solitary drakes at a stable, but low reproductive level thus became dominant during the drought conditions and accounts for the large number of indicated pairs.

Drake Behavior

There was a significant disparate sex ratio in returning migrant flocks that used Zirbel Slough and its surrounding wetlands. The flocks averaged 55.7 percent drakes, a value emphasizing that unmated drakes exist in mallard populations. The numerous unmated drakes in this study did not significantly alter breeding attempts by pairs. A similar result was found by Humburg et al. (1978).

Disregarding the effect of the radio transmitter and the year, paired drakes spent 30.7 days on the area and unpaired drakes stayed

7.2 days. Similar results, 28.7 days for paired drakes and 7.3 days for unpaired drakes, can be calculated from Zenner's (1977) data. Humburg et al. (1978) also reported that paired drakes stay longer on the study area than unpaired drakes. However, the number of days they observed paired and unpaired drakes on their study area (17.6 days and 1.3 days for 1974, 1975, respectively) was less. This difference can be attributed to the greater success in locating a drake with a radio transmitter contrasted with drakes marked with nasal saddles only, a result that agrees with data presented by Zenner (1977).

Mallards present a problem in accurate measurement of a utilized area because of the primary use of wetlands and non-utilization of intervening uplands. The distribution of not only the wetlands but the required breeding requisites (nesting, loafing, and feeding sites) within the wetlands further complicate meaningful descriptions. Pairs operating under a system which has an upper limit on space availability have only a few options: they may crowd onto an area by reducing their utilized area (Titman 1973, Zenner 1977), they may use nonsynchronous breeding, i.e., temporal spacing of the same area as suggested by Batt and Prince (1979), they can move to less desirable habitat, they can abandon attempts to nest, or combinations of the above. Utilization areas established by drakes within Zirbel Slough each year were the same. Apparently nonbreeding by pairs in the crowded conditions of 1977 was responsible for no changes being observed in the utilization areas. As might be expected drakes with established activity centers beyond Zirbel Slough had an increased utilization area size. These drakes may have been lacking all the required requisites at their activity centers and used Zirbel Slough to supplement their activity

center provisions. Paired drakes were site tenacious and consequently the utilization area was smaller than those for unpaired drakes. An important activity of the unpaired drake during the breeding period appears to be one of movement as evidenced by the 28 percent that were transient and never observed after they were marked. Unpaired drakes that remained on the area rarely occurred at the same location consistently and ranged over larger areas than paired drakes.

Numerous estimates of home range (utilization area) and activity centers have been published for mallards (Dzubin 1955, Titman 1973, Zenner 1977). However, inconsistencies of area determination and variations in procedures of obtaining observations leave little confidence in comparisons of these measurements. In all cases the estimates obtained in this study are considerably larger than presented elsewhere. The distribution of wetlands surrounding Zirbel Slough appears to affect the size of the utilization area. Even though upland habitats are not used directly by mallards, they should be included in an estimate of their utilization area to obtain an accurate reflection on energetic demands. With an increase in the distance of the activity center from Zirbel Slough, a concomitant increase occurs in the amount of energy required to travel between the two areas. The impact of the increased size of the utilization area as a function of habitat distribution needs further study, especially if similar energetic demands are placed on the female during reproduction.

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