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The habitat use, movements, and behavioral energetics of unsuccessfully breeding female canvasbacks (*Aythya valisineria*) were examined during the preflightless period in southern Manitoba during 1989-90. Following breeding attempts, unsuccessful females generally expanded their home range on the breeding area, remained there for up to one month, preferentially used large semipermanent and permanent wetlands, and were gregarious. Nocturnal shifts in habitat use were apparent and may be an adaptation to avoid predation by mink. Unsuccessful females depart the breeding area to participate in a moult migration of up to 300 km independent of the departure of males. Wetlands approximately 40 km north of the breeding area appear to serve as staging wetlands for the moult migration. Both Swan Lake and Dauphin Lake in central Manitoba appear to be important moulting waters for unsuccessful females. Time spent on the breeding area and on staging wetlands may be required to replenish fat reserves for the moult migration, the moult itself, and upcoming fall migration. During the preflightless period, females spend approximately 40% of their diurnal energy budget feeding and their daily energy expenditure is approximately 1200-1300 kJ. The cost of the moult migration from the breeding area to Swan Lake is estimated to be between 1700 and 3100 kJ requiring between 40 and 80 g of stored body fat. This study underscores the importance of breeding, staging and moulting habitats to female canvasback populations in Manitoba.

HABITAT USE, MOVEMENTS, AND BEHAVIOR OF POSTBREEDING FEMALE CANVASBACKS IN MANITOBA

by

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CHAPTER II.

HABITAT USE, MOVEMENTS, AND BEHAVIOR OF POSTBREEDING FEMALE CANVASBACKS IN MANITOBA

INTRODUCTION

The breeding biology and breeding habitat requirements of canvasbacks (Aythya valisineria) in the prairie pothole environment have received much attention (Olson 1964, Sugden 1978, Stoudt 1982, Anderson 1985), but the postbreeding-premigrational ecology of females is less well known. The discovery by Haramis et al. (1986) that canvasbacks arriving on the wintering area with the greatest body mass are most likely to survive the winter and subsequent breeding season underscores the importance of this period. Female canvasbacks are the limiting sex in the continental population due to highly skewed sex ratios (2.3M:1F; Trauger 1974) and they may maintain local breeding populations due to strong breeding site philopatry (Anderson 1985). More information is needed on the use and requirements of space, time and energy by unsuccessful females during the postbreeding period to protect local and continental populations.

Two distinct classes of female are produced by the breeding season; those that successfully hatch and raise a brood and those that are unsuccessful in this attempt. The ecology of females with broods has received attention in many cases as they generally remain on the breeding area with the brood (Talent et al. 1982, Leonard 1989). Unsuccessful females usually depart the immediate breeding area earlier than successful females (Gilmer et al. 1977), thus precluding the gathering of similar data for these females. This segment of the population is undoubtably under much different time and energy constraints having been released from further parental investment. For example, Leafloor and Ankney (1991) found that unsuccessful female mallards (Anas platyrhynchos) may undergo the wing moult earlier than successful females. Given typically low nest success in many prairie breeding waterfowl and variable breeding habitat conditions (Higgins 1977, Cowardin et al. 1985, Greenwood et al. 1987), the majority of females may be unsuccessful in any given year despite renesting effort. This is especially true in drought years when nest success and breeding effort are suppressed (Rogers 1964, Sugden 1978).

With this in mind, the objectives of my research were to focus on unsuccessful female canvasbacks to determine; 1) habitat use patterns during the postbreeding-premoult period, 2) the chronology and distance of premoult movements, 3) possible moulting areas, and 4) time and energy budgets during this period. Information of this type will help to elucidate factors critical to population management.

The following thesis is presented in two chapters. In Chapter 1, I present data on the selection of breeding area habitat by female canvasbacks that are ultimately unsuccessful. Home range estimates of radioed females are given and compared for both the breeding and postbreeding period of residency. Use of habitats is examined in relation to diurnal and nocturnal time periods and date. In addition, the chronology and distance of the female moult migration is documented for several females. Findings are discussed in the light of current knowledge of these aspects of postbreeding biology.

In Chapter 2, I provide data on the time budgets of unsuccessful females during the preflightless period. The effects of year, time-of-day, location and marking are investigated. I also estimate the energy budgets of unsuccessful females during this period and provide estimates of moult migration cost. The importance of this data to local population management is discussed.

CHAPTER I. HOME RANGE, HABITAT USE AND MOVEMENTS OF UNSUCCESSFUL FEMALE CANVASBACKS

INTRODUCTION

Highly philopatric species such as the canvasback (Aythya valisineria) provide the best opportunity for intensive population management. To manage intensively requires detailed knowledge of the spatial and temporal requirements for all segments of the population. The breeding biology of canvasbacks in the Minnedosa area of Manitoba has been intensely studied for many years (Olson 1964, Stoudt 1982, Anderson 1985) and management to increase the local population has been successful (Anderson unpubl. data).

In many years, particularly in drought years, however, a substantial portion of the female population may be unsuccessful due to nest depredation or abandonment. Other females, especially yearlings, may not even attempt to breed. These unsuccessful females generally depart the breeding area and are lost from further observation. The habitat requirements and patterns of use during the period following nest loss have been described for mallard and wood ducks (Aix sponsa) in Minnesota (Gilmer et al. 1977), but similar information is unavailable for pothole nesting canvasbacks.

All North American waterfowl undergo a moult of body and flight feathers following breeding. During this period the remiges are simultaneously lost and the bird becomes flightless until new remiges grow in (Salomonsen 1968). Movements to secure moulting areas up to thousands of kilometres from the breeding area have been recorded (Salomonsen 1968). In diving ducks, virtually all males make this 'moult migration' earlier and in greater numbers than females (Salomonsen 1968). Postbreeding males from the Minnedosa population undergo a northerly moult migration, presumably to several large lakes identified by Hochbaum (1944), Bergman (1973) and Bailey (1983). Several band returns from summer banded females recovered just north of Minnedosa suggest a northward movement also for females (M.G. Anderson, Delta Waterfowl Research Station, pers. com.), however, the extent of this movement and the ultimate location of moult for females is unknown.

Objectives of this study were to examine postbreeding ecology of unsuccessful female canvasbacks relative to: (1) home range, habitat use, and movements prior to departure from the breeding area, and (2) movements and habitats used following departure from the breeding area.

STUDY AREA

I examined the movements and habitat use of postbreeding females intensively on a 15.4 km^2 study area approximately 5 km south of Minnedosa, Manitoba (Figure 1). Movements were examined extensively in southern Manitoba

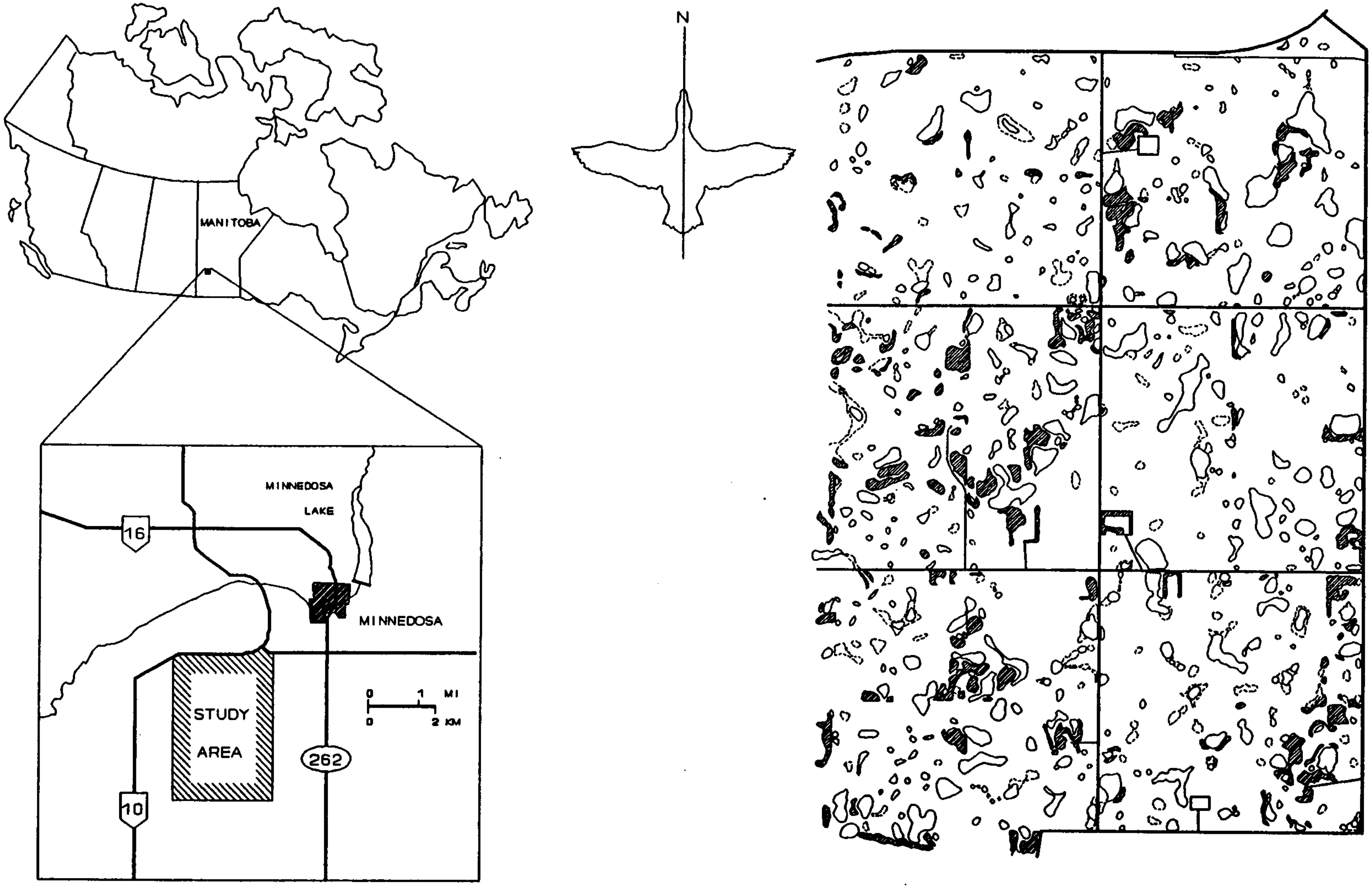

Figure 1. Location and detail of study area used in southern Manitoba, 1989-90. Detail of study area shows wetland basins (open polygons), aspen groves (hatched polygons), and roads (bold solid lines).

from Minnedosa north to The Pas and east to Lake Manitoba and the Delta Marsh (Figure 2). Research was conducted from April through late August in 1989 and 1990. Prior to my study, a marked population of female canvasbacks existed on the study area from research conducted by Sorenson (1990).

The Minnedosa study site is within the 7149 km^2 Newdale Plain Subregion of the Parkland Ecoregion as identified by Poston et al. (1990). This subregion is ranked as a regionally important breeding area for migratory waterfowl (Poston et al. 1990). Near Minnedosa, wetland density averages 26 wetlands/km^2 (Stoudt 1982) with all permanency classes (Stewart and Kantrud 1971) represented. Average wetland area is 0.45 ha and canvasback breeding densities are typically 2-4 pairs/km^2 (Stoudt 1982) although densities of 7.7 pairs/km^2 have been reported (Sorenson 1990).

Waterfowl research in the Minnedosa area has been ongoing since the early 1950's (Evans et al. 1952, Olson 1964, Kiel et al. 1972, Stoudt 1982, Anderson 1985, Rotella 1990, Sorenson 1990). For the years 1962 to 1972 average canvasback nest success was 45% (apparent) and hen success was 56% adjusted for renesting (Stoudt 1982). Stoudt (1982) attributed the majority of canvasback nest loss to predation by raccoons (Procyon lotor). Nest success estimates for canvasbacks on my study area from 1986-88 were 57, 68, and 28% respectively (apparent) (Sorenson 1990). A reduction in available secure breeding habitat due to prairie-wide

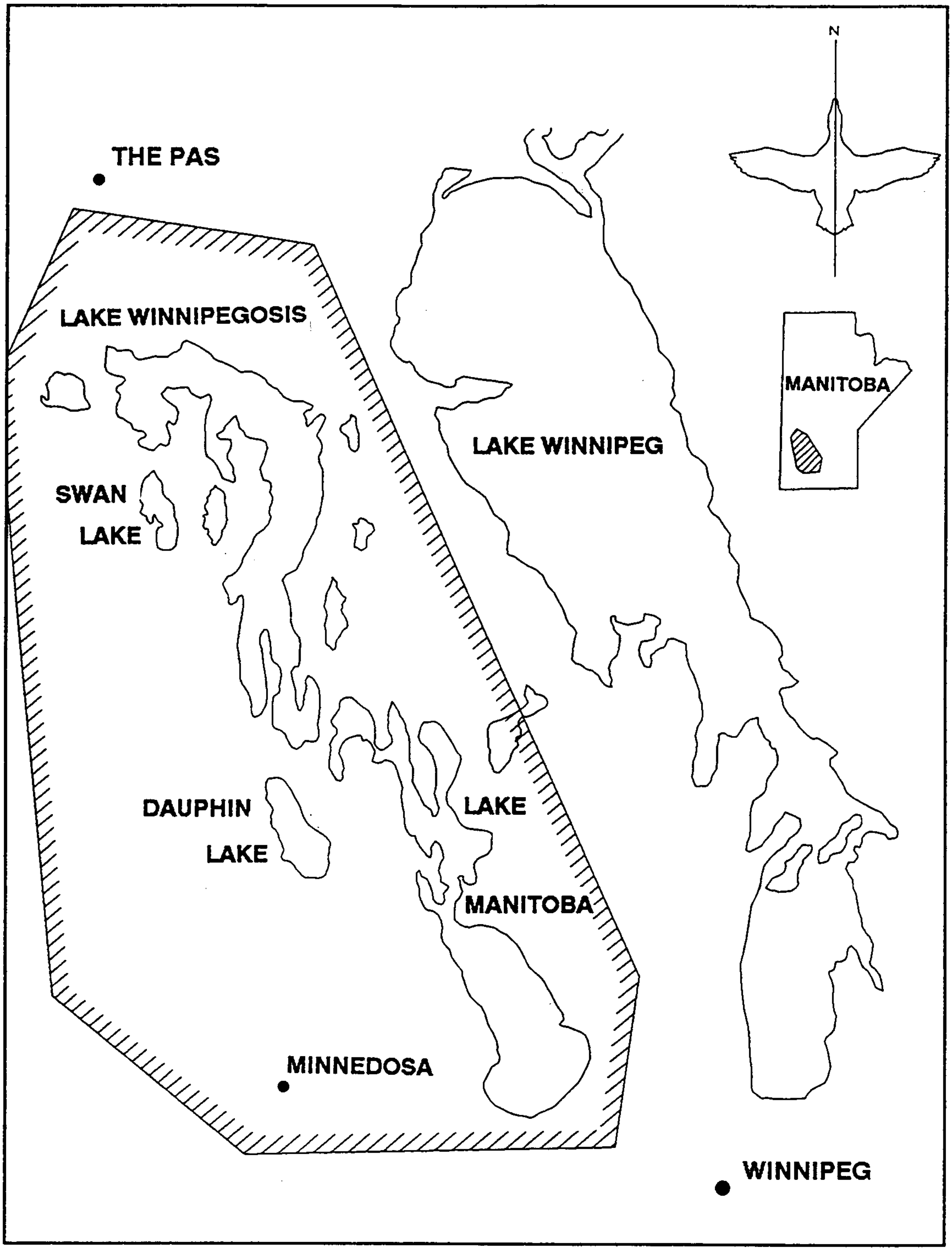

Figure 2. Area in which aerial radio-tracking occurred following the departure of postbreeding females from the study area during the summers of 1989-90.

drought conditions in 1988 was responsible for low nest success that year. The drought continued through the first year of this study producing the second lowest prairie wetland index on record in southern Manitoba (Didiuk and Caswell 1989) and reducing canvasback pair densities (Figure 3).

Native aspen parkland on the study area has been replaced by intensive agricultural land use, primarily devoted to small grain farming and cattle production. Further descriptions of the area with respect to physiography, climate, vegetation, and land use are provided by Kiel et al. (1972) and Stoudt (1982). Access was provided by a network of gravel 'grid' roads that criss-crossed the study area in N-S and E-W directions every 1.6 km.

Radio-tracking of postbreeding movements involved a wider area of southern Manitoba primarily north and east of Minnedosa (Figure 2). This effort concentrated on large wetlands and small lakes 30-60 km north of Minnedosa and just south of Riding Mountain National Park. Detailed descriptions of wetlands in this area are provided in Fedoruk (1971) and Sunde and Barcia (1975). Several large lakes further north and east identified as attracting large concentrations of moulting diving ducks (Hochbaum 1944, Bergman 1973, Bailey 1981) were also searched for radio-marked females.

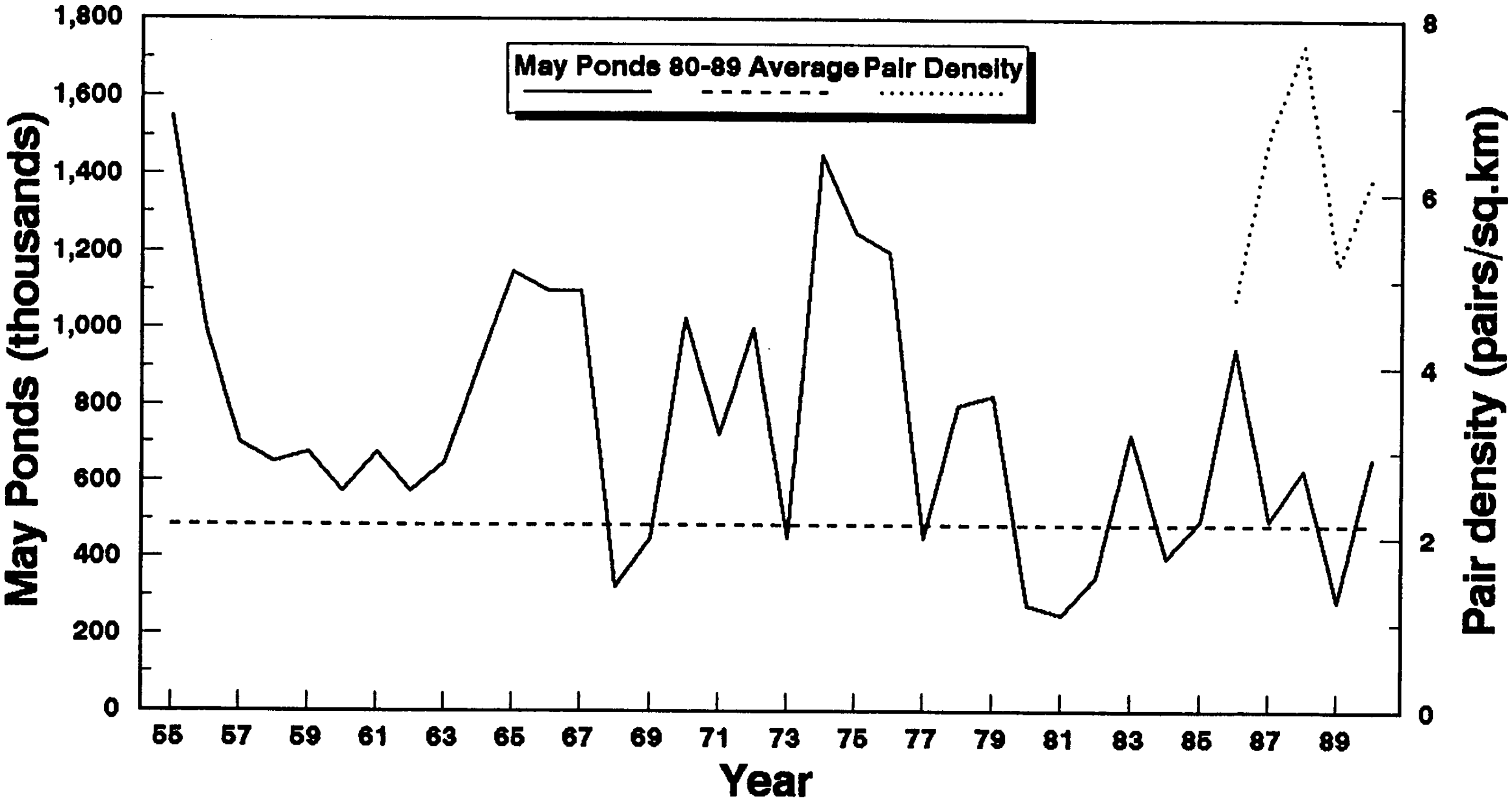

Figure 3. May pond counts in southwestern Manitoba (strata 36-40), 1955-1990, and canvasback pair density on the Minnedosa study area, 1986-1990. (Sources: Didiuk and Caswell 1989, Reynolds et al. 1990, Sorenson 1990, this study).

METHODS

Home Range and Habitat Use

I assessed the home range, habitat use and movements of unsuccessful female canvasbacks with the use of 21 g abdominally implanted radio transmitters (Telonics, Mesa, AZ). Transmitters were implanted as described by Olsen et al. (1990). Following surgery, all females were held at least 1 hour (in a well ventilated holding box) prior to release to allow recovery from the procedure. All females were released at their capture site. I implanted radios in decoy-trapped prelaying females (Anderson et al. 1980) and in nest trapped hens during incubation (Weller 1957). Females were also banded (USFWS leg band) and marked with individually identifiable nasal discs (Lokemoen and Sharp 1985) for visual identification. Only decoy trapped females that had been banded or marked on the study area in previous years were radioed to increase the likelihood that they were residents of the study area. All females captured were therefore at least 2 years old. Prior to surgery, females were weighed (nearest 10 g) with a Pesola® 1500 g spring scale and bill length, bill width and tarsus were measured (nearest 0.5 mm) with callipers.

Reproductive success of radioed hens was determined by tracking females during morning hours when egg-laying occurs. Repeated locations on a wetland several mornings in a row indicated a potentially nesting hen. Emergent vegetation was then searched to locate the nest. In the one case where the nest was not destroyed by predators, I collected the eggs to simulate predation. In cases where nesting was not detected, the female was considered unsuccessful when she was observed on 3 consecutive occasions unaccompanied by a brood or drake.

I used weekly counts over a 25 km roadside transect (Sauder et al. 1971; Anderson and Emery 1990) as a means of indexing the canvasback population on the study area and determining breeding season chronology. Of specific interest was the chronology of pair dissolution and the concurrent increase in unpaired females. Roadside transects, systematic searches for nasal marked females, and incidental sightings during other activities provided supplemental information about pair status of marked individuals.

For the purpose of estimating home range and habitat use, radioed females were tracked from the ground with a vehicle-mounted null antenna array using twin 5-element yagi antenna (Kenward 1987). Ground range of transmitters was approximately 0.8 to 1.0 km. Radioed females were located twice daily for as long as they remained on the study area; once during the morning (0600-1200 hrs) and once either in the afternoon (1200-1700 hrs) or evening (1700-2200 hrs), according to a random schedule. Estimated locations were plotted on digitized aerial photographs from which location coordinates were derived. Date and time were recorded for each location. In addition, I obtained nocturnal locations at least once per week during the period 2400-0200 hrs. Home range of breeding females was determined from 400 locations of 9 decoy trapped hens. Postbreeding home range was determined from 455 locations of these 9 hens and an additional 3 nest trapped females. Home range estimates were obtained in 1990 only because radios were not implanted in prelaying hens in 1989 and the sample size of nest-trapped females was small. I calculated three home range estimates from location coordinates; 50% and 95% harmonic mean-use contours (Dixon and Chapman 1980) and a Minimum Convex Polygon (MCP) area (Hayne 1949). I included the MCP estimate to provide a measure of the area over which a female ranged and to compare to other published estimates. Calculations were performed using the home range program McPAAL (version 1.2, Stuwe 1987). A 680 m^2 grid cell was used for the harmonic means estimate. All home range estimates are based on 23 to 48 locations per female. Postbreeding home range was based on radio locations after a hen had been classed as unsuccessful.

Accuracy of the tracking system was checked periodically by pinpointing the location of a radioed female and then immediately checking the wetland visually to confirm the location. I also "zeroed" the null antenna array periodically by placing a dummy transmitter at a known bearing (plotted on an aerial photograph) from the tracking vehicle. In addition, when triangulation indicated roadside ponds, visual confirmation of the location was obtained. All triangulations were made at distances of ≤0.8 km as 'grid' roads were located every 1.6 km. The flat to rolling topography of the study area and few trees made it ideal for telemetry (Hupp and Ratti 1983).

Records of movement between wetlands both diurnally and nocturnally were obtained using a Rustrak chart recorder set up near wetlands occupied by a radioed female and left for up to 24 hours. Time of movement to and away from the wetland were recorded on the strip chart by the presence/absence of the radio signal, similar to the system of Ringelman et al. (1982).

Habitat Availability

All wetland basins in the study area were visited in June to assess availability and to classify habitat. Wetlands containing water at that time were assumed available for use by postbreeding females. Wetland availability over the entire study area was assumed to reflect wetland availability for each female. Wetland habitats were classified as seasonal or semipermanent/permanent and assigned a cover type (1,2 or 3) according to the system of Stewart and Kantrud (1971). Semipermanent and permanent wetland categories were combined as they are indistinguishable without a bottom sample from the deepest portion of the wetland (Stewart and Kantrud 1971). Dominant emergent vegetation was recorded as cattail (Typha sp.), bulrush (Scirpus sp.), or whitetop (Scolochloa festucacea). Area of each wetland was measured from 1:10,000 scale aerial photographs with a digitizing polar planimeter. A fourth habitat measure was created based on a combination of permanency class and size. These were; small seasonal and semipermanent (<2100 m^2), large seasonal (>2100 m^2), medium semipermanent (2100 to 8096 m^2), and large semipermanent (>8096 m^2). Proportions of wetlands in each of these categories were then calculated.

Analysis

Breeding vs. postbreeding home range size was compared using the Wilcoxon signed rank procedure for paired data (Sokal and Rohlf 1981) on all 3 home range estimates. Nocturnal locations were included in overall home range size comparison. Nocturnal locations in relation to diurnal locations, however, were examined by excluding nocturnal locations, computing 50% and 95% use contours for diurnal locations and using these as an expected model for nocturnal locations. The number of observed and expected locations outside these contours was examined by Chi square analysis (Sokal and Rohlf 1981). Spearman rank correlation procedures were used to determine if home range size was dependent on the number of locations.

The Neu et al. (1974) method was used to examine the null hypothesis that habitat categories were used in proportion to their availability. According to Alldredge and Ratti (1986), this method should work well in controlling Type I and II errors for the number of habitats and locations I used. The average of expected values over all categories was 6 or more and I used a significance level of 0.01 for these tests (Roscoe and Byers 1971). Wetland habitat categories examined were permanency, cover type, dominant emergent vegetation, and size. In addition, use of these categories was examined for independence of time (0600-2300 hrs vs. 2300-0200 hrs) and date (< 20 June vs. >20 June) by contingency table analysis. Where analysis indicated disproportionate habitat use, individual habitat use was compared to availability using Bonferroni multiple comparison tests. Unless otherwise stated, significance level of all statistical inference is 0.05. All means reported are followed by ±1 standard error(SE).

Postbreeding Movements

Following the departure of several radioed hens from the study area, weekly aerial searches using a fixed-wing aircraft (Cessna 172) were carried out at 1000-1500 m above ground level following the procedures of Gilmer et al.(1981). Based on anecdotal late summer sightings of marked canvasbacks and several band returns (M.G. Anderson, Delta Waterfowl Research Station, pers. com.), initial searches concentrated on large wetlands approximately 40 km north of the study area. When females left this area flights were made further north over lakes known to attract large concentrations of postbreeding male diving ducks (Bergman 1973, Bailey 1983, Bailey and Titman 1984).

RESULTS

Home Range

Fourteen previously marked/banded females were radioed in 1990, of which 12 provided usable data for breeding and postbreeding home range estimates. Nine decoy trapped females provided both breeding and postbreeding home range estimates, while an additional 3 nest trapped hens provided postbreeding estimates only. Two decoy trapped hens were excluded from analysis; one female departed the study area shortly after marking and one was paired to an injured (flightless) drake and showed very reduced inter-wetland movement.

Postbreeding female canvasbacks used larger areas (at $\alpha=0.10$) than breeding females at the 50% contour level (Wilcoxon signed ranks test, $P=0.0371$), the 95% contour level ($P=0.082$), and for the Minimum Convex Polygon estimate ($P=0.0098$) (Table 1). Spearman rank correlations indicated breeding (BR) and postbreeding (PB) home range estimates were unrelated to the number of radio locations for the 50%

Table 1. Home range area (km^2) of female canvasbacks during the breeding and postbreeding periods near Minnedosa, Manitoba, May-July 1990. The postbreeding period was defined by either known nest failure or multiple sightings unaccompanied by a mate or brood.

		Home Range Estimate		
Period	n	50% contour	95% contour	MCP
Breeding	9	0.09 (0.02)	1.04 (0.26)	1.10 (0.24)
		*	+	*
Postbreeding	12	0.28 (0.11)	2.86 (1.06)	1.94 (0.45)

*P ≤ 0.05 (Wilcoxon signed ranks test).
+P ≤ 0.10 (Wilcoxon signed ranks test).

contour level (BR: r=0.115, P=0.730; PB: r=0.481, P=0.096), the 95% contour level (BR: r=0.054, P=0.870; PB: r=0.376, P=0.193), and for the MCP estimate (BR: r=0.139, P=0.676; PB: r=0.166, P=0.566). Breeding females used a mean of 11.7 ±1.0 ponds within the home range while postbreeding females used 13.0 ±1.6 ponds, but the difference was not significant (paired t=1.33, P=0.41). Spearman rank correlations indicated that number of ponds used was independent of the number of radio locations (> 23 locations) for breeding (r=0.278, P=0.431) and postbreeding (r=0.350, P=0.245) estimates.

Too few nocturnal locations were obtained during the postbreeding period to determine nocturnal home range, however, a greater than expected number of nocturnal locations were outside the 95% contour (23.7%, X^2=42.5, 1 df, P<0.00001) and 50% contour (66.1%, X^2=6.12, 1 df, P=0.013) levels of diurnal home ranges (APPENDIX). This result suggests a movement away from diurnal core activity areas at night. Wetlands used at night (1.12 ha ± 0.17) tended to be smaller than wetlands used during the day (1.35 ha ± 0.14) but the difference was not significant (Z=0.725, P=0.234).

Postbreeding females shifted to a greater use of larger wetlands as date progressed (F=2.72, P<0.00001) (Figure 4). In addition, the number of wetlands used (8.2 ± 0.78) within the postbreeding home range prior to the median date of

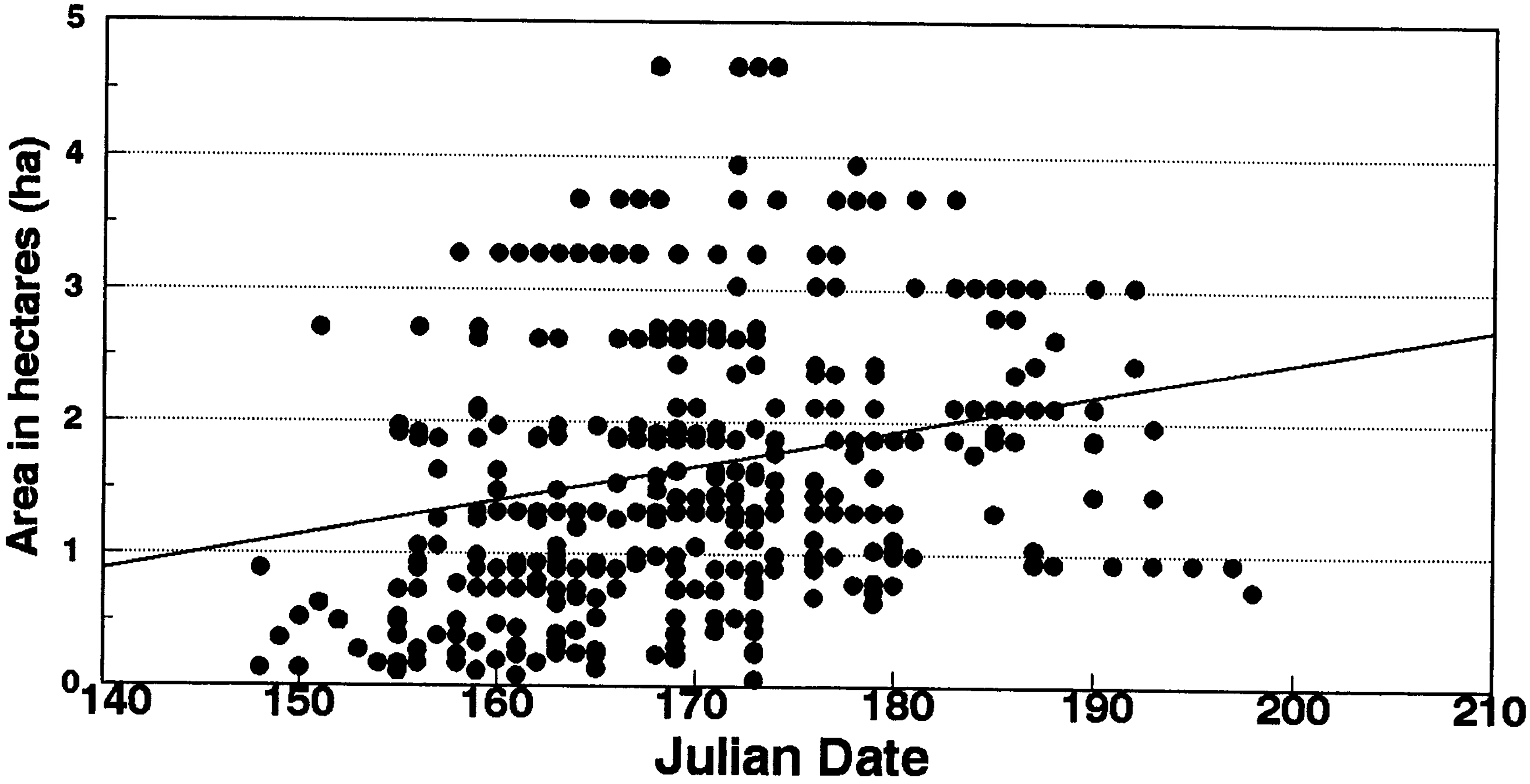

Figure 4. Area of wetlands used by postbreeding female canvasbacks in 1990 regressed on Julian date (Julian Date 180 = June 29).

postbreeding residency for each female was greater than the mean number (6.7 ± 0.84) used after the median date (paired t= 1.78, P=0.050). Thus by late in the postbreeding period, females restricted themselves to a few, large wetlands.

Habitat Use

Both time of day and date affected use of wetland class, dominant emergent vegetation, and size category. During daylight hours (0500-2300), use was independent of time for wetland class (X^2=0.96, 2 df, P=0.619), dominant emergent vegetation (X^2=3.89, 4 df, P=0.421), and size category (X^2=9.67, 8 df, P=0.289). Cover type use was independent of time (X^2=10.33, 6 df, P=0.111).

The median date of postbreeding residency on the study area (June 20) was used to divide residency into early and late periods to examine date effects on habitat use. Use was independent of date for wetland class (X^2=2.74, 1 df, P=0.098), cover type (X^2=5.06, 2 df, P=0.080), and dominant emergent vegetation (X^2=8.10, 2 df, P=0.017). Use of size categories was not independent of date, however, (X^2=36.11, 4 df, P<0.0001) and therefore was investigated separately before and after 20 June.

The Neu et al. (1974) method indicated proportional use of semipermanent wetlands by postbreeding females was significantly greater than availability during diurnal hours. This preference was not seen at night, however, when seasonal and semipermanent wetlands were used in proportion to their availability (Table 2). Similar results were observed for dominant emergent vegetation use. During diurnal hours, wetlands dominated by bulrush were highly preferred habitats over those dominated by cattail and whitetop, but this preference disappeared at night when all types received use in proportion to availability (Table 2). Cover type 3 was preferred at all times over cover types 1 and 2 (X^2=143.15, 2 df, $P<0.0001$). Postbreeding females showed a strong preference for large semipermanent wetlands ($\geq$ 8096 m^2) during diurnal and nocturnal hours. Seasonal, as well as small and medium semipermanent wetlands were avoided during the day. A shift occurred at night, however, when large seasonal and medium semipermanent wetlands were used in proportion to availability. Small seasonal and small semipermanent wetlands were avoided at all times by postbreeding unsuccessful females.

Prior to the median date of residency for postbreeding hens, seasonal and small semipermanent wetlands were avoided, medium semipermanent wetlands were used in proportion to availability, and large semipermanent wetlands were preferred. During the latter half of residency, all wetlands other than large semipermanent ones were avoided (Table 2).

Strip chart recorders were used to record arrival and departure of radioed females from wetlands. Frequency of

Table 2. Comparison of habitat availability to habitat use by time and date for postbreeding female canvasbacks near Minnedosa, Manitoba, May-July 1990 using Neu's Chi-square statistic (Neu et al. 1974). The Chi-square statistic tests the null hypothesis that all habitats are used in proportion to their availability. Confidence intervals on % use are Bonferroni multiple comparison intervals at $\alpha=0.05$.

		95% Confidence intervals on % use			
		Time (hrs)		Date	
Habitat variable	% available	0500-2300	2300-0500	<20 June	>20 June
Class					
Seasonal	25.6	(1.0 - 4.6)	(5.9 - 27.5)		
Semipermanent	74.4	(95.3 - 99.1)	(72.5 - 94.1)		
Chi-square		107.82	2.55	-	
P value		0.000	0.110		
Dominant Emergent					
Scirpus sp.	20.7	(49.2 - 61.2)	(15.9 - 44.1)		
Scolochloa sp.	22.9	(0.8 - 4.8)	(5.2 - 28.2)		
Typha sp.	53.3	(36.1 - 47.9)	(37.9 - 68.7)	-	
Chi square		305.92	3.53		
P value		0.000	0.171		
Size					
Sm. seasonal & semipermanents	37.0	(2.5 - 8.1)	(0.0 - 12.0)	(4.3 - 13.7)	(0.0 - 3.4)
Lg. seasonal	12.8	(0.4 - 4.2)	(3.5 - 26.5)	(1.8 - 9.4)	(0.0 - 4.8)
Med. semipermanents	25.1	(7.0 - 14.8)	(15.2 - 44.8)	(12.8 - 25.6)	(2.9 - 11.5)
Lg. semipermanents	25.1	(76.6 - 86.4)	(33.9 - 66.1)	(58.5 - 73.9)	(83.9 - 94.3)
Chi square		676.57	32.13	219.23	478.00
P value		0.000	<0.0001	0.000	0.000

arrivals and departures indicated that postbreeding females were undergoing crepuscular movements (Figure 5). Early morning movements peaked from 0500-0600 hrs while evening movements peaked from 2200-2300 hrs. Relatively few movements were recorded between 1000 and 1900 hrs and no moves were recorded between 2400 and 0400 hrs or between 1100 and 1600 hrs. In addition, radio location data indicated that 88% of nocturnal locations (n=60) were on different wetlands than those occupied the previous day and 93% of locations the following morning were on different wetlands than those occupied that night. These movements correspond to the apparent shift in habitat use observed.

Roadside surveys in 1989 and 1990 provided indices to the number of pairs and to the total number (paired and unpaired) of canvasbacks on the study area. In 1989, a year of severe drought, the number of females observed closely tracked the number of males throughout the summer, diverging only slightly in June as a few postbreeding females remained on the study area longer than males (Figure 6). An expected decrease in the number of females relative to the number of males during the nesting period in May (females on nests) did not occur. Of those hens that did attempt to breed on the study area (apart from the 5 nests I collected) none successfully hatched a brood. Mean date of departure for radioed hens in 1989 was 19 June (n=6).

A different pattern was observed in 1990 (Figure 7), a

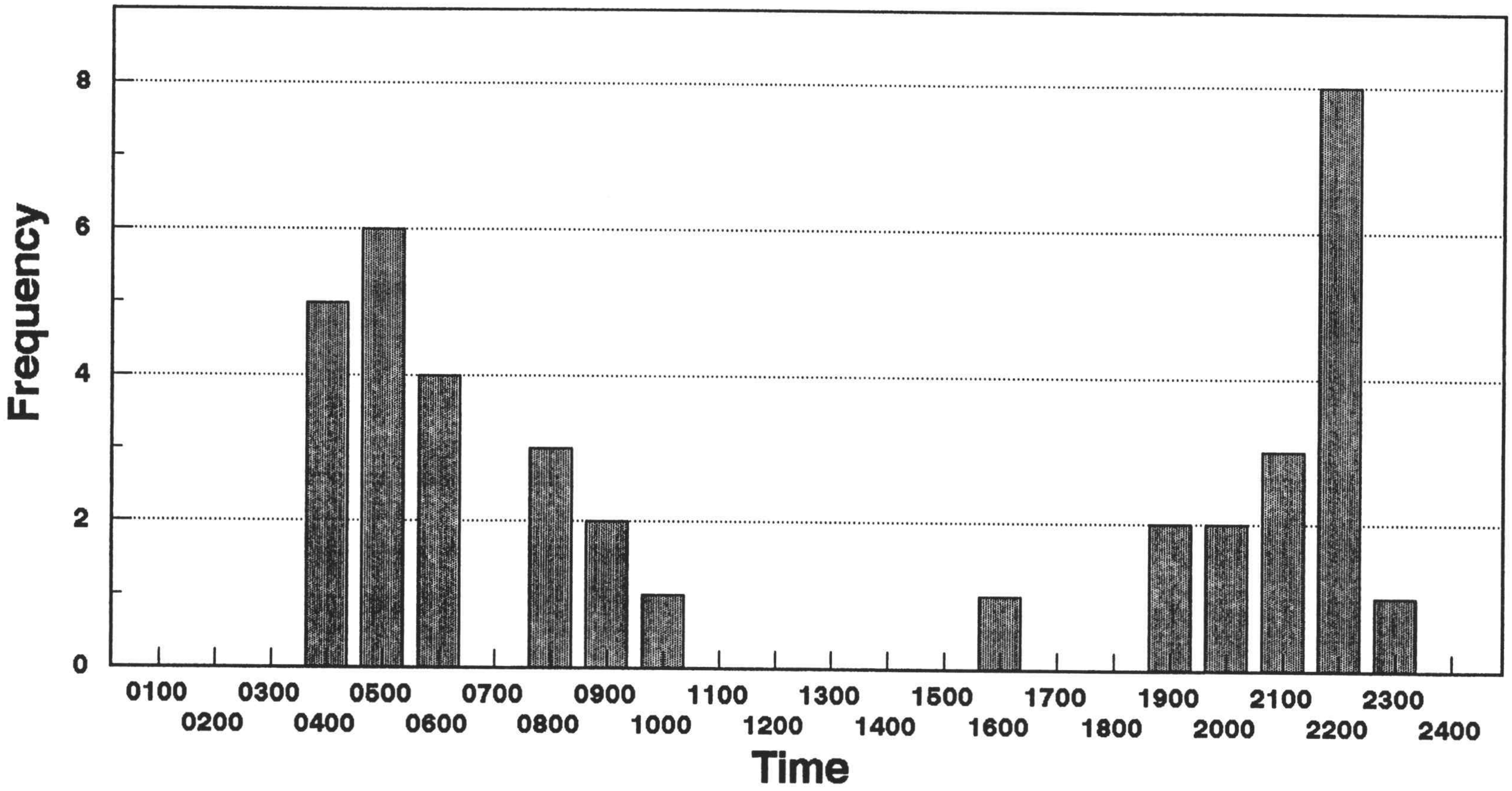

Figure 5. Frequency of inter-wetland movements by time-of-day. Data from chart recordings of radioed postbreeding females during June and July, 1989-1990.

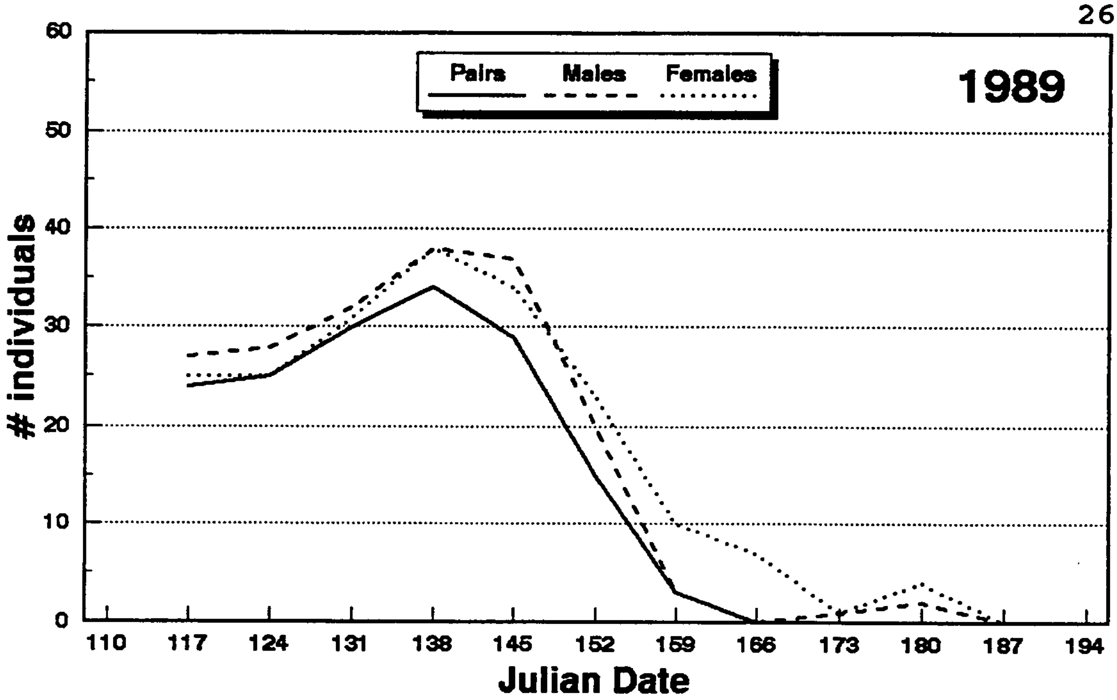

Figure 6. Number of Pairs, Males, and Females seen on weekly roadside censuses from April through July, 1989.

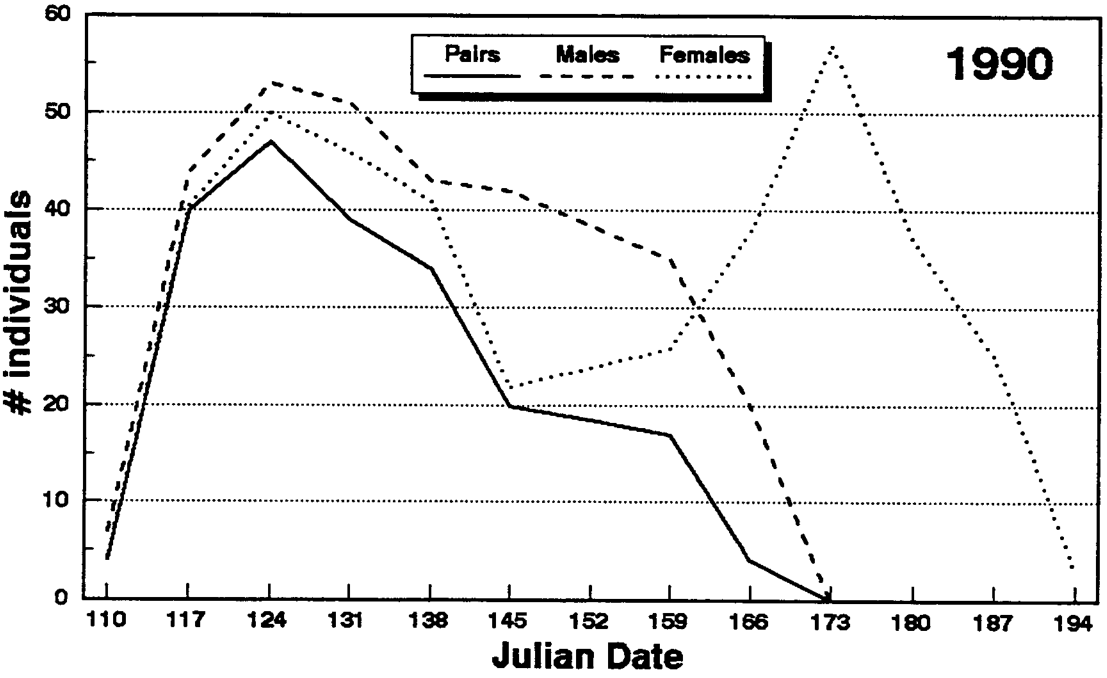

Figure 7. Number of Pairs, Males, and Females seen on weekly roadside censuses from April through July, 1990.

year with improved water levels and precipitation. The canvasback population on the study area peaked earlier and at a higher level than in 1989. In addition, the expected disparity in observed males and females concurrent with nesting occurred in mid-to-late May. Males remained on the study area 1-2 weeks longer, while females remained approximately 1 week longer than in 1989. The peak in female numbers observed on June 22 is probably due to a combination of the appearance of females from failed nests on the study area and the congregation of females on large wetlands visible from the road. Females began to group on the study area in June and flock size increased throughout the month. In late June, flocks of up to 27 females were observed on the large wetlands of my study area while on a wetland adjacent to my study area, I observed a flock of 72 females (13 marked). Females began departing the study area in late June and nearly all females were gone by mid-July (Figure 7). Mean date of departure for radioed females in 1990 was July 1 (n=13).

Postbreeding Movements

All unsuccessful females left the study area prior to the flightless period. In 1989, 3 radioed hens were successfully tracked after they departed the study area (Figure 8). Similar moves were observed in 1990 for six of ten successfully tracked females (Figure 9). Flock counts of

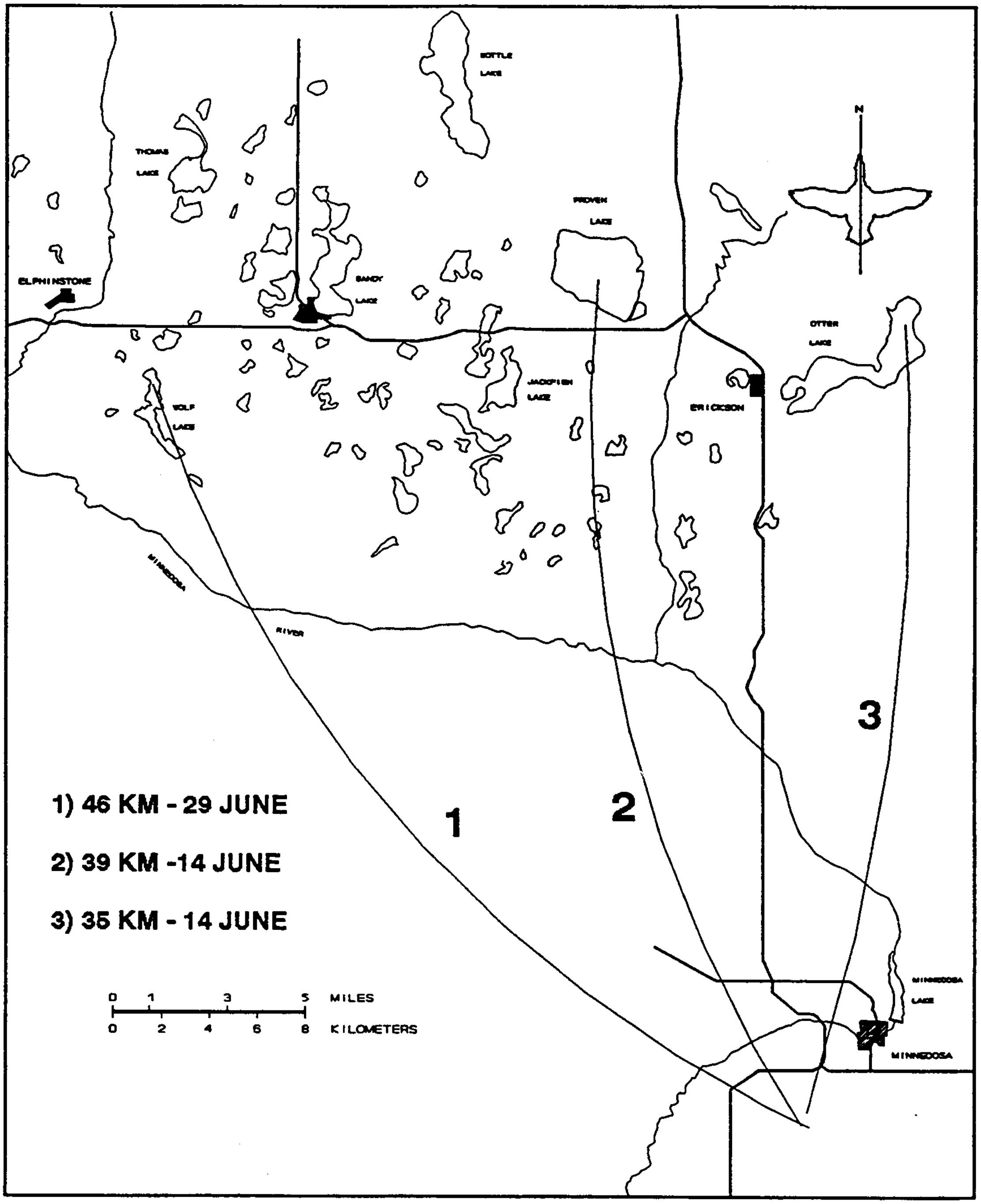

Figure 8. Initial movements of 3 radioed postbreeding females following their departure from the study area in 1989.

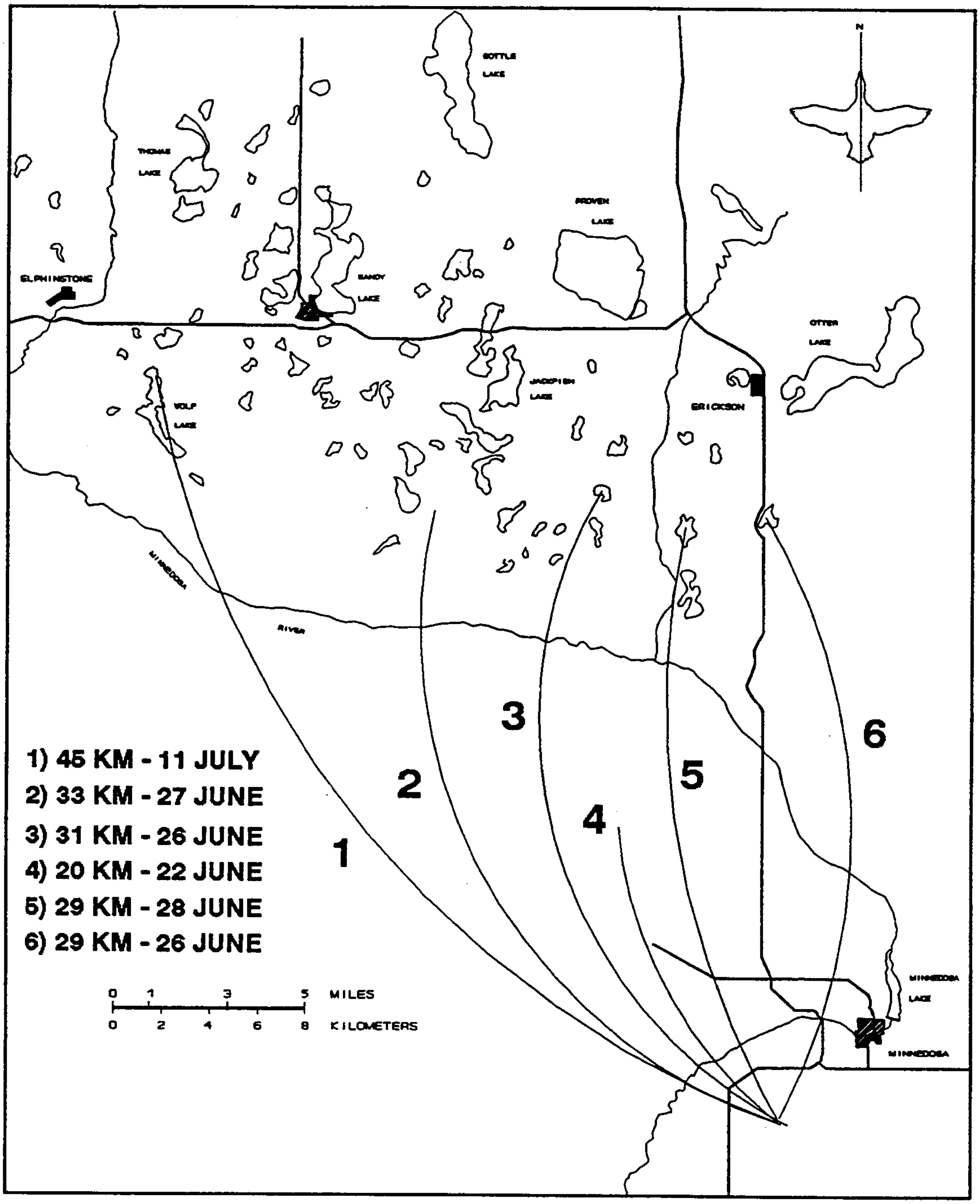

Figure 9. Initial movements of 6 radioed postbreeding females following their departure from the study area in 1990.

female canvasbacks on these wetlands in July ranged from 7 to 50 females (mean=25 ±3.0). Females were often associated with large mixed-sex flocks of postbreeding redheads and with smaller numbers of lesser scaup (Aythya affinis) and common goldeneyes (Bucephala clangula). These flocks were occasionally accompanied by 1-3 male canvasbacks but overall, male canvasbacks were rare. Marked female canvasbacks were occasionally observed in these flocks although most were unmarked.

Tracking of subsequent movements to suspected moulting areas was successful for 2 females in 1989 and 5 females in 1990. These hens were located in August on Dauphin Lake and Swan Lake, 140 km and 290 km north of the study area respectively (Figure 10). These lakes have been identified by previous investigators as important moulting lakes for diving ducks (Hochbaum 1944, Bergman 1973, and Bailey 1983). However, expected transmitter life did not extend into September and actual moulting of these females was not confirmed. Most females apparently took several weeks to make the movement to Dauphin and Swan Lakes, but 1 female in 1990 departed the study area on 9 July and was located on Swan Lake 8 days later. No locations were obtained on Lake Winnipegosis, a well known moulting area for diving ducks, despite intensive aerial searches in both 1989 and 1990.

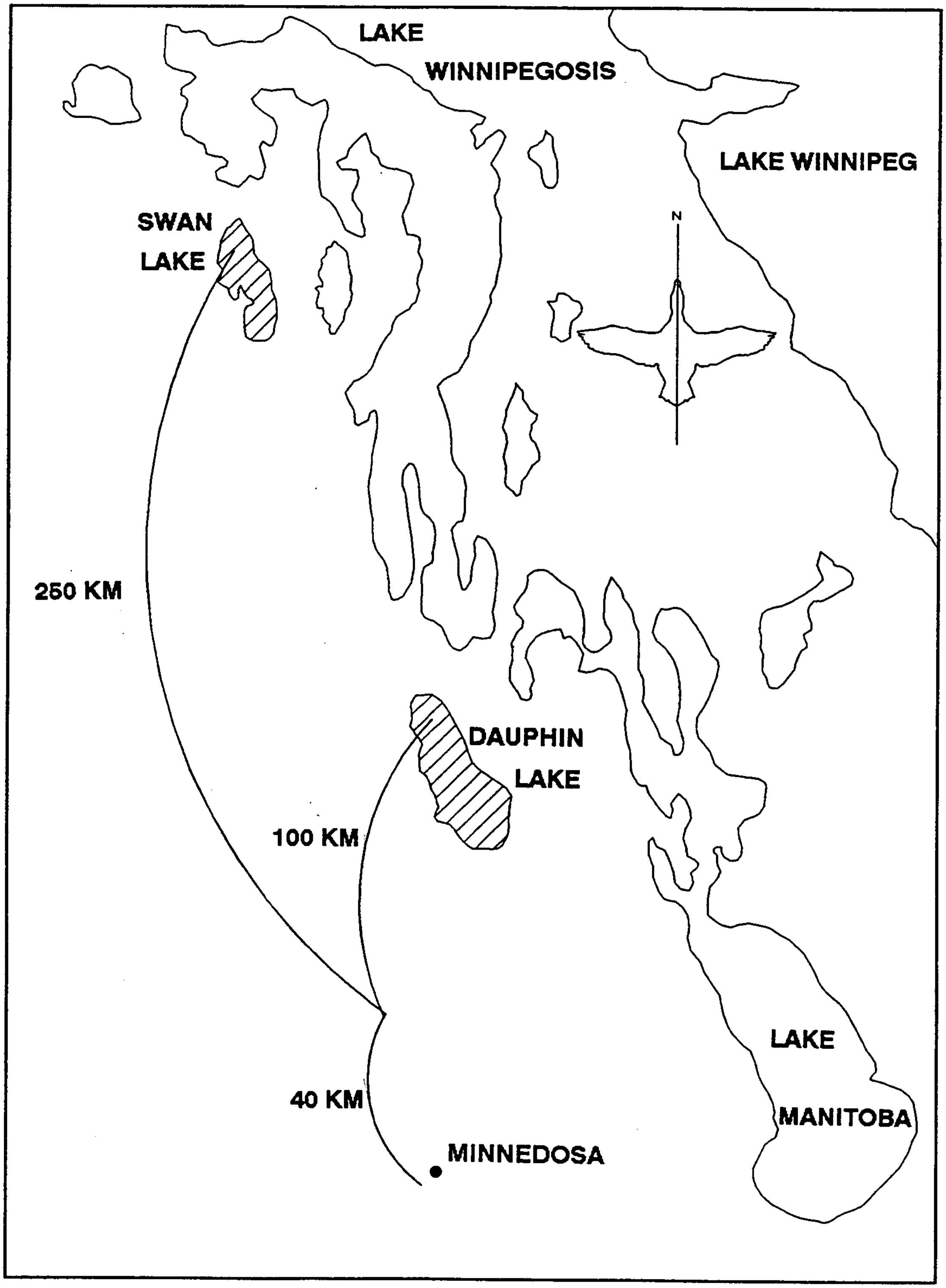

Figure 10. Map showing the distance of the moult migration performed by unsuccessful female canvasbacks and the location of suspected moulting lakes identified by this study.

DISCUSSION

The attachment of radio transmitters, especially surgical implants, to investigate movements and habitat use requires the assumption that the attachment does not affect subsequent behavior. With proper placement in the abdomen, Korschgen et al. (1984) concluded that transmitters had little or no effect on the reproductive performance of mallards or on behavior in goldeneye (Bucephala clangula) and ring-necked ducks (Aythya collaris). These conclusions have been supported by ongoing research with wild breeding canvasbacks in Minnesota (Korschgen pers. com.), by recent research with wild breeding mallards in Alberta (Rotella et al. in press), and by this study (see CH. 2). Of 6 hens implanted with radios in 1989, all 6 were sighted on the study area in 1990 suggesting no lethal effects of the radio package.

My data indicate that unpaired females that have abandoned breeding attempts remain on the breeding area longer than their mates and increase their range of movements. Dzubin (1955) and Anderson (1985) have previously reported estimates of the breeding home range (MCP) for canvasbacks to be 2.8 and 1.4 km^2 respectively. Both Dzubin (1955) and Anderson (1985) determined home range from resightings of marked non-radioed individuals within 5 miles of my study area. My MCP breeding home range estimates averaged 1.1 km^2 (range:0.28-2.33 km^2).

Following cessation of breeding, females ranged over a significantly larger area. Small wetlands typically used by nesting females were used relatively little by postbreeding females. Wetland use during the postbreeding period is more similar to wetland use during the post-arrival period described by Anderson (1985)(i.e. large semipermanent and permanent wetlands). During postbreeding residency, semipermanent and permanent wetlands in excess of 0.8 ha and dominated by bulrush receive preferential use as females begin to congregate in small flocks of up to 70 individuals.

I recorded a surprising redistribution of female canvasbacks at night, however, when permanency and dominant emergent vegetation classes were used in proportion to availability. This apparent redistribution is supported by records of late evening and early morning movements to and away from nocturnally used wetlands.

The fact that a greater than expected number of nocturnally used wetlands lie outside of diurnal centers of activity may suggest a predator avoidance mechanism. Avian prey may be more vulnerable to predators during nocturnal periods (Kruuk 1964) and timing of habitat use has been suggested as a predator avoidance mechanism for the Antarctic Whale Bird (Pachyptila desolata) (Murphy 1936). Whale Birds come ashore at night to dig a nest burrow and care for their young while skuas and other predators are inactive. I propose that the nocturnal shift in habitat use by female canvasbacks may be an example of a temporal mechanism to avoid predation by mink (Mustela vison). Mink forage extensively in wetland basins (Eberhardt and Sargeant 1977, Arnold 1986) and show a preference for semipermanent and permanent wetlands used diurnally by diving ducks, especially canvasbacks, redheads (Aythya americana) and ruddy ducks (Oxyura jamaicensis) (Arnold 1986). Mink forage most during the nocturnal and crepuscular periods and subsist primarily on waterfowl during the latter part of the summer (Arnold 1986). In fact, it has been suggested by Eberhardt and Sargeant (1977) that mink predation on female diving ducks may significantly contribute to the highly disparate sex ratios observed in these waterfowl. Nocturnal redistribution may be a strategy to avoid this predation risk.

The effects of severe drought on breeding chronology (Figure 6) and intensity has been observed previously for breeding canvasbacks (Stoudt 1971, Sugden 1978) and lesser scaup (Rogers 1964) and was probably the major factor determining timing of departure of postbreeding females in 1989. Many of the females seemingly abandoned breeding attempts and may have accompanied their mates directly to the moulting lakes. With better wetland conditions in 1990, the breeding population remained longer on the study area during the breeding period (Figure 7) and all radioed females remained on the study area well past the departure of their mates regardless of whether they attempted to nest. The purpose of this delay may have been to build reserves for moult from known food resources on the home range. Alternatively, females may use this period to assess sago pondweed production in home range wetlands. Anderson (1985) suggested that familiarity with local food resources was an important selective force in the highly traditional use of breeding wetlands by canvasback females. Sago pondweed is a patchily distributed food resource in wetlands on the study area and most breeding females show significant yearly variation in preferred feeding sites within ponds (Anderson 1985). Knowledge gained during postbreeding movements on the breeding area could conceivably confer an advantage in selecting a home range with abundant food resources the following year.

The independent northward movement of unsuccessful female canvasbacks to lakes traditionally used by drakes represents a true moult migration and is a significant finding in 2 respects. First, this is a considerable move in distance for females, some of which have expended large amounts of energy on egg production and incubation. Second, it underscores the importance of these lakes to the welfare of local breeding populations further south. This finding contrasts sharply with Hochbaum (1944) who concluded that unlike males, most females did not undergo a moult migration but remained on or near the breeding area to undergo the moult. He also concluded that females were not gregarious during the wing moult and scattered widely on breeding marshes. In fact, a more recent survey of these lakes (Bergman 1973:163) indicated an influx of females in August "presumably ... adult females that had completed or abandoned nesting and brood rearing". Similarly, Gilmer et al. (1977) reported that the majority of unsuccessful hen mallards left their study area in small flocks but did not join the males. Salomonsen (1968), reviewing moult migration literature from Europe, reported that unlike dabbling ducks, the moult migration of diving ducks is characterized by the participation of a segment of the female population. Participation by females apparently occurs for the Pochard (Aythya ferina) and Tufted Duck (Aythya fuligula) (Lebret 1950, van der Wal and Zomerdijk 1979) and the Red-crested Pochard (Netta rufina) (Bezzel 1964; cited in Salomonsen 1968).

While female diving ducks are known to follow males to the moulting waters, only a small fraction of the female population are thought to participate (Salomonsen 1968). Data from my study indicate participation in the moult migration by females may be largely dependent on the reproductive success of females. In years of drought and/or high nest losses, virtually the entire female population may participate in a moult migration. Both Swan Lake and Dauphin Lake appear to be important moulting lakes for females from the Minnedosa area and probably much of southern Manitoba.

Apart from an adequate food supply, isolation from predators and human disturbance have been suggested as important factors in the selection of moulting habitat by waterfowl (Salomonsen 1968, Bergman 1973). Bergman (1973) noted that Swan Lake received much heavier use by moulting canvasbacks than Dauphin Lake and attributed the difference to level of recreational use. Swan Lake receives little or no use whereas Dauphin Lake is actively used by recreational boaters and fishermen during the summer. Bailey (1983) concluded that Swan Lake was unique in the boreal forest region of Manitoba in attracting large numbers of moulting and staging canvasbacks. Evidence from this study underscores that conclusion and stresses the importance of Swan Lake to breeding populations in southern Manitoba.

CHAPTER II. BEHAVIOR AND BIOENERGETICS OF UNSUCCESSFUL FEMALE CANVASBACKS

INTRODUCTION

Prince (1979) stated that an analysis of both time and energy allocation is needed to understand the requirements of the postbreeding stages of the life cycle. Several recent studies have addressed this need in migratory and wintering canvasbacks (Takekawa 1987, Hohman and Rave 1990, and Howerter 1990). Energy requirements in relation to habitat use are mediated through time-activity budgets (Paulus 1988). Relationships between time and energy allocation, and energy intake outlined by Takekawa (1987) have provided important information for restoration and management of canvasback fall staging habitat (Kahl 1991a). Information of this type is needed for the canvasback to elucidate habitat-energy requirements during the postbreeding-premoult period.

In addition, most female anatids enter the postbreeding period in relatively poor body condition (Korschgen 1977, Raveling 1979, Reinecke et al. 1982). The period between cessation of breeding attempts and the initiation of moult therefore may be extremely important in determining condition prior to fall migration, a period of high energy demand.

Information on postbreeding movements indicates that most unsuccessful female canvasbacks remain on the breeding area up to one month after breeding attempts and then perform a northward moult migration of several hundred kilometers including staging areas along the way (CH.1). Knowledge of time and energy allocation during this period is essential in understanding and interpreting patterns of habitat use. The objective of this study was to examine the postbreeding ecology of unsuccessful female canvasbacks relative to time and energy budgets during the preflightless period.

STUDY AREA

I studied the behavior of unsuccessful female canvasbacks on a 15.4 km^2 breeding area approximately 5 km south of Minnedosa, Manitoba (Figure 1) and on lakes near Erickson, Manitoba (Figure 11).

High wetland density and ideal aquatic vegetational communities in the Minnedosa area attract breeding densities of up to 7.7 canvasback pairs/km^2 (Sorenson 1990); some of the highest in North America (Bellrose 1980). A population of female canvasbacks marked from 1986 to 1990 by Sorenson (1990) and myself were resident on the breeding area in both years of this study. Six marked females in 1989 and 14 in 1990 also carried abdominally implanted radio transmitters.

Native aspen parkland in the study area has been largely replaced by intensive agricultural practices devoted to small grain farming and cattle production. Further

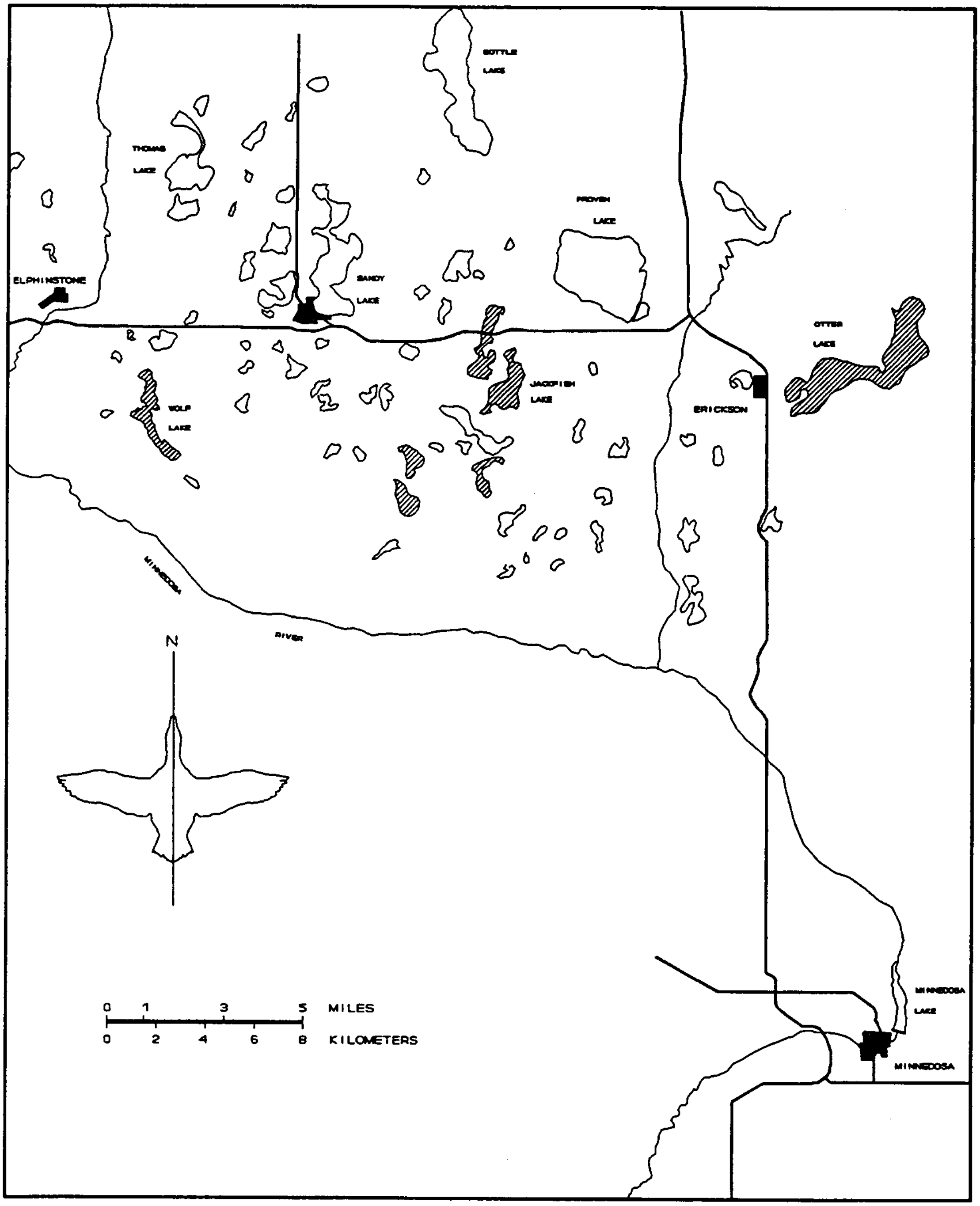

Figure 11. Lakes near Erickson, Manitoba where behavioral observaions were conducted on flocks of preflightless female canvasbacks during July and August, 1989-90. The majority of time budgets were collected on the cross-hatched wetlands in the above figure.

description of the area with respect to physiography, climate, vegetation, and land use are provided by Kiel et al. (1972) and Stoudt (1982). Access was provided by a series of 'grid' roads that criss-crossed the study area in N-S and E-W directions every 1.6 km.

Tracking of postbreeding movements of unsuccessful females from the breeding area in June and July indicated that large wetlands near Erickson, Manitoba were important stopover points in a northward movement to moulting areas (CH. I). While only 40 km N of Minnedosa, this area lies in a different Subregion of the Parkland Ecoregion (Poston et al. 1990). Wetlands in this area are considerably larger than those near Minnedosa (Sunde and Barcia 1975). Many contain sago pondweed (Sunde and Barcia 1975), an important food resource for canvasbacks (Bartonek and Hickey 1969). Extensive descriptions of the area are provided by Fedoruk (1971) and Sunde and Barcia (1975).

METHODS

Time Budgets

I used focal individual observations (Altmann 1974) to quantify the diurnal behavior of unsuccessful female canvasbacks on the breeding area (Minnedosa) and in aggregations of preflightless females on lakes north of the breeding area (Erickson). Breeding area observations were conducted on known and suspected unsuccessful breeders in

June and July and on preflightless aggregations in July and August of 1989 and 1990. Assistants and I made observations using a 15-45X spotting scope from either a vehicle or a hidden location overlooking the wetland. Each focal individual was observed for 1 hour and instantaneous behaviors were recorded every 15 seconds using a metronome (Wiens et al. 1970). Behaviors were recorded on a Tandy 102 laptop computer using the program TIMBUD (Taylor 1986). If our approach appeared to disturb individuals we allowed 5-10 minutes prior to the initiation of observation to allow birds to resume normal behavior.

Analysis of behavior was based on the following behavioral categories; Feeding - all dives, dive pauses, surface feeding, dabbling, and manipulation of food items on the surface; Resting - females inactive with head positioned low on the chest or sleeping with eyes closed and head under wing; Comfort - behavior associated with body maintenance such as preening, bathing, wing flapping, stretching and scratching (Mckinney 1965); Locomotion -deliberate movement between points by swimming or flying if not immediately associated with another defined activity; Social - interspecific and intraspecific agonistic encounters (eg. bill thrusts, chases, etc.); Alert - head held erect with neck extended (usually in response to disturbance). Similar categories have been used by Anderson (1985), Lovvorn (1987), and Perry et al. (1989). Date, time, pond, marker identity, presence of a transmitter, and weather were recorded for each observation period. Only observation periods lasting the full 1 hour were included in analysis.

Behavior was recorded throughout 3 diurnal periods; early (0600-1100 hrs), midday (1100-1700 hrs), and late (1700-2100 hrs). On the breeding area, either known or suspected unsuccessful (observed on 3 consecutive occasions unaccompanied by brood or drake) marked individuals were randomly chosen for observation in each period/day and assigned an observation time. If that female could not be found, alternative females were randomly chosen. Unmarked females were also observed for comparison to marked individuals. In preflightless aggregations near Erickson, unmarked individuals were randomly selected by directing the spotting scope toward the flock and choosing the bird closest to the center of the field of view. Observation periods were stratified to obtain a representative sample in all 3 diurnal time periods.

Foraging Time

In addition to recording behavior, I recorded the number and time under water for all foraging dives observed during most focal observations on the breeding area. Dive duration was recorded using a stopwatch and was recorded on the laptop computer. If a dive time was missed due to stopwatch malfunction, a missed dive was recorded. This allowed an estimation of proportion of total foraging time under water and in the dive- pause (period between dives during a foraging bout). Rustrak chart recorders provided limited data on nocturnal (2200-0600 hrs) foraging by recording intermittent signal loss when females dove under water.

Analysis

For statistical analyses, proportion of time spent in each behavior was normalized using the arcsine square root transformation (Zar 1974). A multivariate analysis of variance (Proc GLM:MANOVA, SAS Institute 1987) was used to determine if time spent in various behaviors differed with year (1989 vs. 1990), time-of-day (early vs. midday vs. late), presence or absence of a mark or radio, or location (Minnedosa vs. Erickson). Partial correlation coefficients were determined within the MANOVA procedure to reveal significant relationships among behaviors. Individual behaviors were then tested in a multiway ANOVA (Proc GLM:ANOVA, SAS Institute 1987) to determine which behaviors differed with the independent factors. Only independent factors that were significant in explaining variability in the MANOVA test were used in the multiway ANOVA procedure. Time budgets were calculated by back-transforming means reported for each behavior in the MANOVA procedure. Dive times were compared using t-statistics (Sokal and Rohlf

1981).

Unless otherwise stated, significance level for all statistical inference is 0.05. All means reported are followed by ±1 standard error (SE).

Energy Budget

I used energy coefficients reported for waterfowl by Prange and Schmidt-Nielsen (1970), Wooley and Owen (1978), and Takekawa (1987)(Table 3) to develop an energy budget for unsuccessful females. Those coefficients reported by Wooley and Owen (1978) were multiplied by 1.24 to convert from resting metabolic rate (RMR) to basal metabolic rate (BMR) (King 1974). All coefficients used here are in multiples of basal metabolic rate (BMR). BMR for canvasbacks was estimated using the formula of Calder (1974) for nonpasserines:

$$M = 15.477\ W^{0.73}$$

M = BMR energy in kJ/hr
W = Body mass in kg

Hourly energy expenditure (HEE) was calculated as follows:

$$HEE = \Sigma\ (m_b \times BMR \times p_b)$$

m_b = multiple of BMR for a given behavior b
p_b = proportion of time spent in a behavior b
b = behavior (1-6)

Energy expended in feeding was corrected for different energy expense in the dive and dive-pause portions of a

Table 3. Activities and applicable multiples of BMR used in the estimation of Hourly Energy Expenditure (HEE).

Activity	x BMR	Reference
Feeding		
dive	7.7	Takekawa (1987)
dive-pause	2.9	Takekawa (1987)
Swimming	4.0	Prange and Schmidt-Nielson (1970)
Rest	2.0	Takekawa (1987)
Alert	2.6	Wooley and Owen (1978)
Social	3.0	Wooley and Owen (1978)
Comfort	2.2	Wooley and Owen (1978)

feeding bout by partitioning the time spent feeding based on dive/dive-pause ratios and multiplying each by respective multiples of BMR defined by Takekawa (1987). Additional costs of thermoregulation were not factored into HEE as daily temperatures in July and August are generally well above 10°C and therefore considered thermoneutral (Wooley and Owen 1977).

Moult Migration Cost

Flight costs and estimates of flight range for moult migration were derived from BASIC programs provided in Pennycuick (1989). These programs were used in preference to the standard 12-15X BMR estimate (Tucker 1973) as flight costs do not behave as simple multiples of BMR (Castro and Myers 1988, Pennycuick 1989). Flight costs were estimated for an 1100g female flying at 70 km/h airspeed (velocity for maximum range [Pennycuick 1989], Tucker and Schmidt-Koenig 1971, Bellrose and Crompton 1981). Fat reserves were estimated as 9.5% of body mass based on values reported by Thompson (1992) for preflightless male canvasbacks.

RESULTS

Time Budget

Time budgets were determined from 43 and 159 hours of focal individual observation in 1989 and 1990 respectively. During the period between cessation of breeding attempts and moulting, unsuccessful female canvasbacks spent most of their time feeding, resting, and preening (Figure 12). Movement, alert and social behaviors accounted for less than 14% of the diurnal time budget.

Partial correlation coefficients indicate that several behaviors were correlated (Table 4). Feeding, the most common activity overall, was negatively correlated with rest, social, and comfort and unrelated to movement and alert. The magnitude of correlation coefficients indicates that increases in foraging time are apparently at the expense of rest and to a lesser extent comfort and social activities. Social interactions were rare overall and rarely occurred during foraging bouts. Resting was also negatively correlated with movement and comfort activities but unrelated to alert and social interactions. Movement was positively correlated with both comfort and alert behaviors. Disturbed females generally assumed the alert posture and moved either toward or away from the disturbance stimulus, rarely flying. All correlations except the negative feed-rest correlation are low ($r < 0.30$).

The diurnal time budget was affected by several of the tested factors. A multivariate analysis of variance (MANOVA) indicated that year ($P<0.001$), time-of-day ($P<0.001$), location ($P=0.002$), and the year by time-of-day interaction ($P=0.030$) were significant in explaining variability of time spent in various activities. Neither marking ($P=0.471$) nor

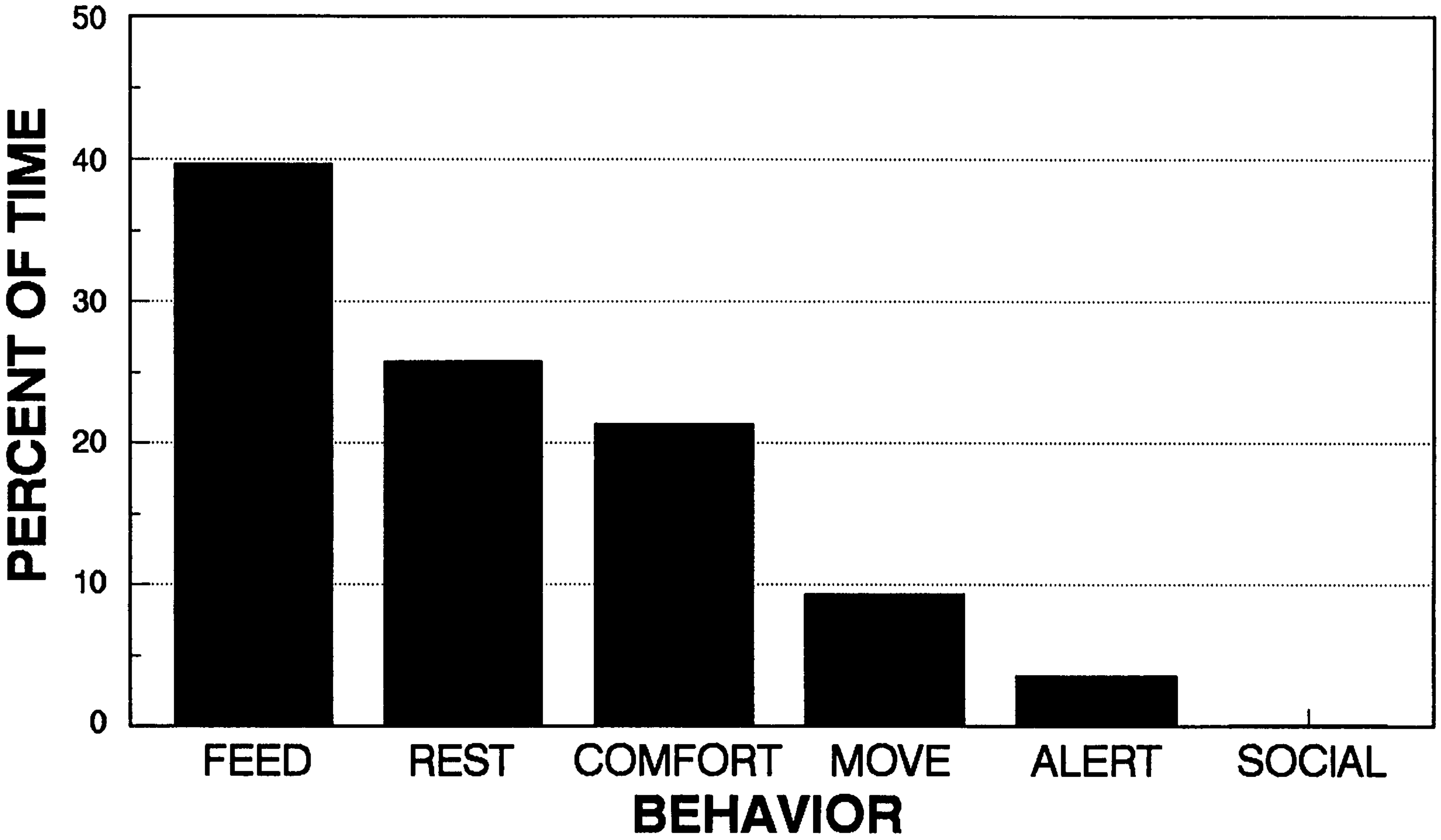

Figure 12. Overall time-activity budget of preflightless female canvasbacks combining year, and location.

Table 4. MANOVA Partial correlation coefficients for all behaviors exhibited by postbreeding female canvasbacks in southwestern Manitoba, June-August, 1989-90. Coefficients indicate whether the amount of time spent in a behavior is positively or negatively correlated with the amount of time in other behaviors.

Behavior	FEED	REST	COMFORT	MOVE	ALERT
REST	-0.80 ***				
COMFORT	-0.23 **	-0.20 **			
MOVE	0.07	-0.30 ***	0.23 **		
ALERT	-0.12	-0.04	0.05	0.20 **	
SOCIAL	-0.16 *	0.09	0.15 *	0.11	-0.13

*$P \leq 0.05$.
**$P \leq 0.01$.
***$P \leq 0.001$.

presence of a radio (P=0.229) significantly affected behavior. Closer examination of the year by time-of-day interaction indicated that time-of-day was only significant due to a low sample size (n=2) of focal observations in the late time period of 1989. For this reason, only year, location, and nest status were used in the analysis of individual behaviors by ANOVA (Table 5).

Female canvasbacks in 1989 and 1990 differed in behavior only in the amount of time spent in alert behavior (ANOVA F=22.76, P=0.0001)(Figure 13). Behaviors also differed with location (Figure 14). Females on larger wetlands near Erickson in July and August spent 8% more time swimming (F=14.36, P=0.0002), 7% more time in comfort activities (F=8.20, P=0.0046) and 3 % less time in alert (F=17.17, P=0.0001) than those on the breeding area in June and July. Proportion of time in other behaviors remained unchanged. The analysis of movement was confounded by a significant year by location interaction (F=7.43, P=0.007) indicating the response depended on year. While the trend was the same in both years, the difference was only significant in 1990. In both 1989 and 1990, a trend toward less time spent resting at Erickson vs. Minnedosa was observed, but the difference was not significant (F=2.17, P=0.1423).

Table 5. ANOVA results for factors YEAR and LOCATION identified by MANOVA as significantly affecting the overall time budget of postbreeding female canvasbacks in southwestern Manitoba,June-August, 1989-1990.

	FEED	REST	COMFORT	MOVE	ALERT	SOCIAL
YEAR	0.132[b]	0.018	0.013	0.000	0.267	0.004
Wilks' Lambda[a]=0.892						
F=3.70; 6,183 df; P=0.0017	.2701[c]	.6890	.4904	.9312	.0001	.1605
LOCATION	0.016	0.244	0.232	0.219	0.201	0.000
Wilks' Lambda=0.895						
F=3.66; 6,183 df; P=0.0019	.6984	.1423	.0046	.0002	.0001	.7739
YEAR*LOCATION	0.000	0.008	0.001	0.113	0.000	0.002
Wilks' Lambda=0.983						
F=0.54; 6,183 df; P=0.7795	.9580	.7841	.8859	.0070	.9554	.3164
MS ERROR	0.108	0.113	0.028	0.015	0.012	0.002

[a] Wilks' Lambda, F statistic, df, and P value from MANOVA test of behavior proportions distributed over year, location, and interaction term.

[b] Mean square from ANOVA models by behavior.

[c] Probability that F(critical) > F(calculated).

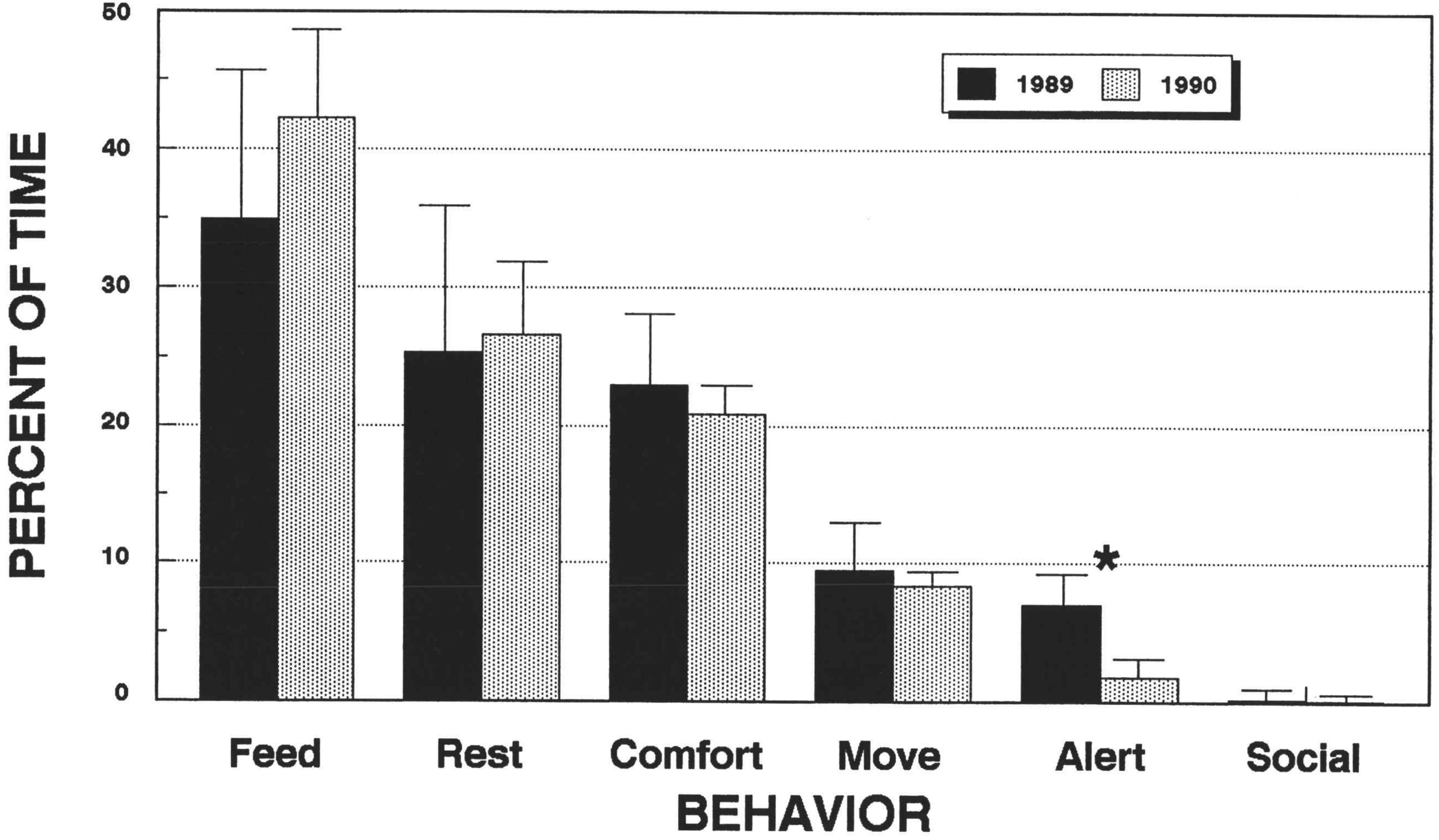

Figure 13. Time-activity budget of preflightless female canvasbacks in 1989 vs. 1990. Standard error bars are +2xSE. Asterisk indicates significant difference ($P \leq 0.05$) in proportion of time spent in behavior by year.

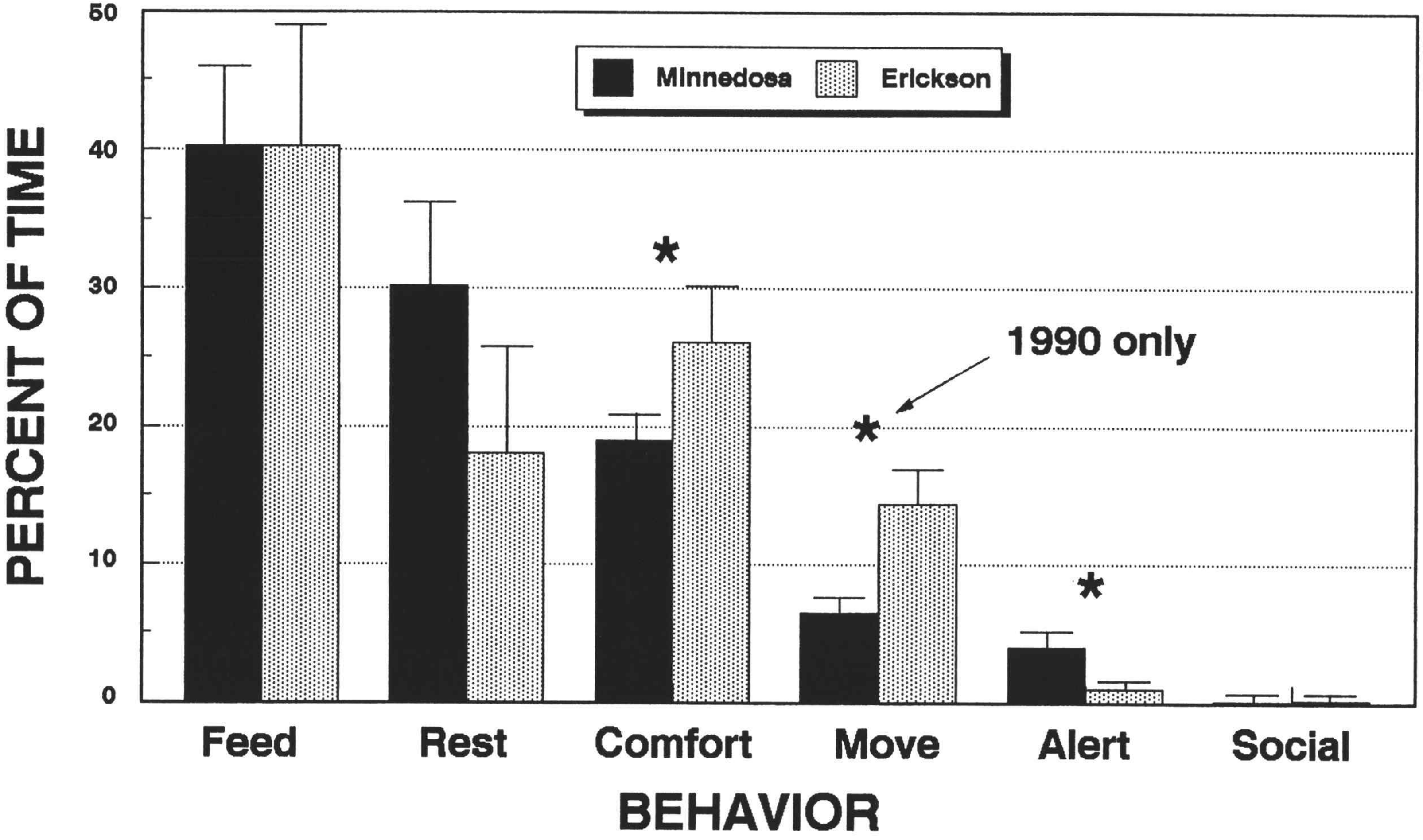

Figure 14. Time-activity budget of preflightless female canvasbacks near Minnedosa (June-July) vs. Erickson (July-August). Standard error bars are +2xSE. Asterisks indicate significant differences ($P \leq 0.05$) in proportion of time spent in behaviors by location.

Foraging Time

The average time spent underwater by canvasbacks in foraging dives on wetlands near Minnedosa was significantly less than that of foraging dives in the larger and presumably deeper wetlands near Erickson ($t=3.52$, $P=0.002$)(Table 6). The percent of the foraging bout spent underwater (or dive/dive-pause ratio), however, remained constant indicating that an increase in dive duration was accompanied by an increase in the dive-pause between dives (Table 6). Spearman rank correlation indicated that the number of dives/minute was negatively correlated with average dive time ($r=-0.87$, $P=0.014$).

Energy Budget

The above time budgets were translated into energy budgets by weighting each behavior by appropriate multiples of basal metabolic rate (Table 3). Estimates of energy expenditure are based on the basal metabolic rate of a 1000 g (±11.0 g; n=9 nest trapped females) female for Minnedosa time budgets and for an 1100 g female for Erickson time budgets. No data is available on weights of postbreeding females in July or August and therefore the 1100 g is an assumption. Weight gain during this period is expected to replenish reserves lost during reproductive efforts (egg laying, incubation)(Reinecke et al. 1982).

Hourly energy expenditure (HEE: kJ/bird/hr) of females

Table 6. Comparison of dive and dive-pauses (mean ± SE) for preflightless female canvasbacks near Minnedosa and Erickson, Manitoba, June-August 1990.

	Minnedosa		Erickson
Dive Duration (sec)	14.0 ± 1.1	**	19.4 ± 1.0
Dive-pause (sec)	10.1 ± 0.6	*	12.8 ± 0.7
Dive/dive-pause Ratio	1.46 ± 0.10	NS	1.56 ± 0.10

*$P \leq 0.05$.
**$P \leq 0.01$.
NS-difference not significant.

on the breeding area near Minnedosa was 6.6 kJ/bird/hr less than that spent by females on larger wetlands in the Erickson area (Table 7). The average of HEE in these two areas (60.6 KJ/bird/hr) may be used as an estimate of energy expenditure by unsuccessful females during the preflightless period assuming half the postbreeding-premoult period is spent on the breeding area. Total energy expenditure during the observed period 0600-2100 hrs would then be 909 kJ. Nocturnal behavior was not observed although on 3 occasions when signals were recorded on chart recorders at night, no feeding (as indicated by intermittent signal loss) was recorded between 2200 and 0400 hrs. If this is true, energy expenditure during the remainder of the 24 hour period may be substantially less. Assuming the remaining 9 hours are spent resting at 2.0 x BMR, total nocturnal energy expenditure would be 298 kJ. Daily energy expenditure (DEE) would therefore be approximately 1200 kJ. This energy budget undoubtedly underestimates energy expenditure as estimates of daily flight time are not available. Except for crepuscular flights between wetlands, daily flights of marked and radioed individuals among wetlands near Minnedosa were uncommon (CH. 1).

Moult Migrational Costs

Tracking data (CH.1) indicated that unsuccessful females perform a moult migration of up to 300 km North of

Table 7. Hourly energy expenditure (HEE in kJ/bird/hr) by behavior for preflightless female canvasbacks near Minnedosa and Erickson, Manitoba, June-August 1989-90.

		Feed[a]								
		Dive	D.pause	Rest	Comfort	Move	Alert	Social	TOTAL	AVERAGE
		7.7[b]	2.9	2.0	2.2	4.0	2.6	3.0		
MINNEDOSA	proportion[c]	.240	.160	.300	.190	.065	.040	.001	1.000	
	HEE[d]	28.61	7.18	9.35	6.47	4.02	1.61	0.05	57.3	60.6[e]
ERICKSON	proportion	.240	.160	.181	.261	.144	.008	.002	1.000	
	HEE	30.66	7.70	6.01	9.48	9.55	0.43	0.10	63.9	

[a] proportion of time spent feeding has been divided into proportions spent in dives and dive-pauses based on measurements of dive and dive-pause duration.

[b] multiple of BMR for each behavior.

[c] proportion of diurnal period engaged in each activity.

[d] HEE = BMR mltiple x BMR x proportion of time spent in each activity. BMR for Minnedosa females = 15.48 kJ/bird/hr. BMR for Erickson females = 16.59 kJ/bird/hr.

[e] assumes equal time spent on breeding area and staging areas prior to moult.

the breeding area. Using the flight cost programs of Pennycuick (1989), I have projected the flight costs for an 1100g female flying at an airspeed of 70 km/h for various distances with and without wind effects (Table 8). Based on these projections, the 300 km flight undertaken by unsuccessful females from the Minnedosa area to Swan Lake would require from 1700 to 3100 kJ of energy. Fat is generally regarded as the primary source of flight fuel (Blem 1976). If a gram of fat contains 39.5 kJ (Ricklefs 1974), between 40 and 80g of fat reserve would be required to cover this distance nonstop.

Total Energy Expenditure

Assuming a moulting area 300 km north of the breeding area, total energy expenditure for the period from nest loss in mid-June to arrival on the moulting area in mid-August would be 60 days x DEE + cost of moult migration. This formula yields an estimated energy requirement of 74,200 kJ for the period.

DISCUSSION

Diurnal time-activity budgets of nonbreeding canvasbacks vary considerably both seasonally and geographically (Table 9)(Lovvorn 1987, Takekawa 1987, Hohman and Rave 1990, Thompson 1992, this study). I found foraging, resting, locomotion and comfort to be the most prevalent

Table 8. Estimated flight range and energy expenditure (kJ) of an 1100g female canvasback (104g fat reserve) flying various distances (airspeed = 70 km/h) under five wind conditions. Energetic costs are based on estimates provided by the BASIC programs of Pennycuick (1989) for long distance migrants.

		Distance(km)				
Wind	Range(km)	20	50	100	200	300
20 km/h tailwind	719	110	280	570	1140	1710
10 km/h tailwind	636	130	320	650	1290	1940
No Wind	559	150	370	740	1480	2220
10 km/h headwind	479	170	430	860	1710	2570
20 km/h headwind	395	210	520	1040	2080	3120

Table 9. Percent of the diurnal time period spent in common activities by nonbreeding canvasbacks (adapted from Hohman and Rave 1990).

Period Location	Activity				References
	Feed	Rest	Move	Comfort	
Preflightless					
Manitoba	40	26	9	21	This study
Alberta					
Early PF	32	35	14	19	Thompson (1992)[b]
Late PF	22	47	14	22	Thompson (1992)
Moulting					
Alberta	13	49	13	25	Thompson (1992)
Postflightless					
Alberta	35	29	9	27	Thompson (1992)
Fall Staging					
Alberta	39	38	8	15	Thompson (1992)
Fall migrating					
Wisconsin	19[a]	35	17	15	Takekawa (1987)
Wintering					
Louisiana					
Catahoula L.	13	42	29	13	Hohman & Rave (1990)
Mississippi Delta	23	42	19	9	Hohman & Rave (1990)
Chesapeake Bay	4[a]	63	10	10	Howerter (1990)
Spring-migrating					
Wisconsin	39	22	8	13	Lovvorn (1987)
Ontario	36	17	14	15	Lovvorn (1987)

[a] dive time only, dive-pause included as resting activity.
[b] male canvasbacks only.

behaviors while time spent in courtship, aggression, and alert behaviors were negligible.

Preflightless females in this study spent a similar amount of time foraging to those reported by other studies conducted during periods when nutrient acquisition is important (i.e. preflightless, staging, migrating)(Table 9). Time spent in comfort activities is also typical of periods surrounding the moult (Thompson 1992). Wintering and fall-migrating canvasbacks, on the other hand, generally spent less of the diurnal period feeding and preening and more time resting and moving than that observed in my study. Care should be taken in comparing my results to studies by Takekawa (1987) and Howerter (1990) as they classified dive-pauses as resting and therefore underestimated time spent in feeding bouts (J.Y. Takekawa pers. com.).

Several investigators have found that time budget of staging and wintering diving ducks differ between the diurnal and nocturnal periods (Pedroli 1982, Bergan et al. 1989). Pedroli (1982), Takekawa (1987) and Howerter (1990) reported that feeding behavior increased significantly at night. In my study, apparently little nocturnal feeding occurred during the preflightless period on the breeding area and hence would indicate that sometime between the preflightless period and fall migration canvasbacks may switch from being primarily diurnal feeders to being nocturnal feeders. Better data on nocturnal feeding during the preflightless and flightless period is needed to test this hypothesis.

I documented a significant difference in the time budget of unsuccessful females between those on the breeding area in June/July, and those in preflightless aggregations near Erickson in July/August. Movement, primarily swimming, and comfort activities increased between the two areas. Increased movement on the larger wetlands near Erickson may be required for the location and utilization of local food resources for several reasons. Sago pondweed is likely the most utilized food resource at this time (Bartonek and Hickey 1969) and many wetlands near Erickson contain sago pondweed (Sunde and Barcia 1975). Movement data (CH.1) indicate that members of these flocks are transitory on the area and hence may be unfamiliar with resource distribution on a fine scale. In addition, while sago is perennial and may be reliably found at a given site from year to year, the productivity of a stand may vary considerably (Anderson and Low 1976) necessitating searching behavior. Finally, feeding as a flock may deplete resource patches relatively quickly and necessitate more frequent movement in search of profitable foraging areas. An increase in comfort activity (preening, bathing, and wing-flapping) is consistent with the onset of contour feather moult in July (Austin 1987).

Several explanations are possible as to why females spent less time alert on the wetlands near Erickson. Flock size may be a factor. Abramson (1979) found that the amount of time spent by Curlews (Numenius arquata) "looking up" rather than feeding decreased as the number in a flock increased. Flocked canvasbacks on large bodies of water may feel safer from potential threats and hence show less response. The frequency and proximity of disturbance stimuli may also affect time spent alert. Many of my observations on the breeding area were made on roadside wetlands and while extremely tolerant of vehicles, female canvasbacks would generally become alert when farm machinery moved past. Canvasbacks on the large wetlands near Erickson tended to forage further from shorelines and avoided shorelines near roads.

Dive times recorded on the larger wetlands near Erickson are considerably greater than any previously reported for the canvasback (Table 10) and are assumed to be due to foraging in deeper water. Draulans (1982) showed a similar relationship between dive time and water depth in the tufted duck (Aythya fuligula). Unfortunately I have no measurement of water depth at feeding sites. Dive/dive-pause ratios remained the same as those near Minnedosa indicating that increased dive time was accompanied by a concurrent increase in dive-pause length. Based on time-budget data and dive times, females are capable of making 154 dives per foraging hour on wetlands near Minnedosa and 111 dives per foraging hour on wetlands near Erickson. Overall, time spent

Table 10. Dive durations reported for female canvasbacks.

Location	Period	Dive Duration (sec ± SE)	Reference
Manitoba			
Minnedosa	Preflightless	14.0 ± 1.1	This study
Erickson	Preflightless	19.4 ± 1.0	This study
Manitoba	Breeding	15.6 ± 1.9	Siegfried (1978)
Manitoba	Breeding	15.6 ± ?	Anderson (1985)
Wisconsin	Fall Staging	14.9 ± ?	Takekawa (1987)

feeding was the same at both sites. Whether or not the fewer dives were made up for by longer foraging time on the substrate is unknown.

Daily energy expenditure calculated is similar to that reported for post-arrival and pre-laying female canvasbacks on the breeding area (Anderson 1985)(Table 11). The estimates of Anderson (1985) are probably low, however, as he used 4.0 x BMR to estimate foraging costs rather than 7.7 x BMR as measured by Takekawa (1987). My DEE estimate is also lower than that reported for fall staging (Takekawa 1987, Korschgen et al. 1988) and wintering canvasbacks (Howerter 1990)(Table 11). My estimates will be lower than staging females partly due to lower body mass and hence lower BMR of preflightless females. Reinecke et al. (1982) report that postlaying and wintering body weights of black ducks are similar and suggest that reduction of lean weight may decrease daily energy expenditure. The estimate of Howerter (1990) for wintering canvasbacks is probably higher due to a greater amount of time spent feeding (nocturnally) and additional thermoregulation costs which I assumed were nil. In addition, daily flight costs are not accounted for in my estimate. Including 15 minutes of flight time per day would increase DEE by 130 kJ making my estimate similar to that of Takekawa (1987). Takekawa's (1987) data indicated that female canvasbacks spent approximately 4.3 hours per day foraging underwater, much of it at night. Based on my

Table 11. Estimates of daily energy expenditure (DEE) by canvasbacks during various stages of their annual cycle.

Period Location	Sex (M/F)	DEE (kJ)	Method	Reference
Breeding				
Manitoba				
Post-arrival	F	1328	Time budget	Anderson (1985)
Pre-laying	F	1360	Time budget	Anderson (1985)
Laying	F	1883	Time budget	Anderson (1985)
Preflightless				
Manitoba	F	1207	Time budget	This study
Alberta				
Early PF	M	1025	Time Budget	Thompson (1992)
Late PF	M	934	Time Budget	Thompson (1992)
Flightless	M	811	Time Budget	Thompson (1992)
Postflightless	M	1334	Time Budget	Thompson (1992)
Fall Staging				
Wisconsin	M/F	1312	Time budget	Takekawa (1987)
Wisconsin	M/F	1674	2 x Existence Energy	Korschgen (1988)
Alberta	M	1172	Time Budget	Thompson (1992)
Wintering				
Chesapeake Bay	M/F	1476	Time budget	Howerter (1990)

data, preflightless females spend 3.6 hours per day foraging underwater, primarily during daylight hours (0600-2100 hrs). DEE for preflightless female canvasbacks is apparently 20-30% greater than for preflightless males.

Submerged macrophytes, primarily the tubers of sago pondweed, comprise much of the diet of female canvasbacks in Manitoba during the nonbreeding period (Bartonek and Hickey 1969). While the gross caloric content of sago tubers has yet to be published, proximate analysis by Anderson and Low (1976) reveals its nutrient composition and hence caloric content to be very similar to that of wildcelery (<u>Valisineria americana</u>) winter buds, the preferred food on staging areas (Takekawa 1987). Wildcelery winter buds contain approximately 16.8 kJ/g dry weight (Takekawa 1987). True metabolizable energy (TME) of sago tubers has been measured at 85% (J.P. Ball, University of Guelph, pers. com.) and assuming similar energy content to wildcelery would yield 14.3 kJ/g dry weight. TME is used in preference to apparent metabolizable energy (AME) as energy budgets were calculated from multiples of BMR (Millar and Reinecke 1984). Given the above DEE, a preflightless female canvasback would have to ingest at least 85 g dry weight of sago tubers per day to maintain an energy balance. An estimated 5.2 kg dry weight of sago tubers per female is therefore required to satisfy the total energy demand of the preflightless period (74,200 kJ) including costs of the moult migration.

Consumption higher than this is expected as females probably gain weight during the preflightless period. Takekawa (1987) and Korschgen et al. (1988) have estimated the consumption of wildcelery winter buds at 102 and 125 g dry weight/day respectively.

I have estimated an additional 1700 to 3100 kJ from 40 to 80 g of catabolized fat reserve is required to fuel a 300 km moult migration. Barzen and Serie (1990) reported that incubating females (mean body mass = 1117 g ±147[SD]) carried a mean fat mass of only 39 g. Females abandoning reproductive attempts at or near these average body weights would be stressed to make a 300 km moult migration nonstop. Furthermore, seven of 14 unsuccessful females captured and weighed in June of 1989 and 1990 weighed between 930 and 990 g (unpubl. data). Using the regression provided by Barzen and Serie (1990)(-102.4 + 0.12[body mass], r^2=0.80) to estimate fat mass of incubating females, a 950 g female would have only 12 g of fat in reserve. This is only enough for a 73 km flight (Pennycuick 1989). Females staging on wetlands near Erickson spend approximately 99 kJ (6.6 kJ x 15 hrs) more daily energy diurnally than those on the breeding area. The amount of foraging activity between the two areas does not appear to increase, however. Females may therefore be able to replenish reserves faster on the breeding area and account, in part, for their delayed departure. Serie and Sharp (1989) reported canvasbacks staging on Pools 7,8, and 19 of the Mississippi River gained 2.5 to 3.3 g of body weight per day (primarily fat). Whether preflightless females can replenish fat reserves at this rate is unknown.

For those females with sufficient reserves, social factors related to flock formation rather than energetic constraints may regulate female departure from the breeding area. Leafloor and Ankney (1991) reported that unsuccessfully nesting captive mallard females showed late, asynchronous wing moult when moulting solitarily, but an early, synchronous moult when placed together during the preflightless period. Late moulting females may undergo higher energetic costs when weather is cooler (Young and Boag 1981, Wishart 1985) and may have less time for weight gain prior to migration (Hohman et al. 1992). During the 2-3 week flightless period, moulting females may reduce the amount of time spent feeding (J. Devries , unpubl. data) as do male canvasbacks (Thompson 1992). Owen (1970) reported a possible inhibitory effect of moult on fat deposition and nocturnal activity. Brood females and unsuccessful females entering the preflightless period with low body weight may find themselves in an 'energy pit' where the energetic cost of maintenance and fat deposition delays their departure from the breeding ground in preflightless aggregations. This may result in late solitary moulting on or near the breeding area and account for the dispersed and solitary postbreeding females described by Hochbaum (1944).

The cost of low body weight may be even higher. Late moulting waterfowl show higher hunting mortality (Gilmer et al. 1977, Clark et al. 1988) in part due to poor body condition (Hepp et al. 1986, Greenwood et al. 1986). In addition, Haramis et al. (1986) reported that based on mass and recapture histories of 6000 canvasbacks, those with higher body weights upon arrival on the wintering area are more likely to survive the winter and the following breeding season. The greater time and energy constraints placed on females relative to males in reproduction (i.e. egg laying, incubation, brood rearing) places them at a condition disadvantage late in the summer. This disparity in condition between males and females, if not corrected by postbreeding female activities, may be one factor leading to male biased sex ratios in canvasback. Further investigations of female canvasback condition, foraging efficiency, and fat storage during the preflightless and flightless periods is required to understand the importance of these periods. Carrying capacity and dynamics of habitats used in relation to the time and energy demands identified in this study are also of interest.

Several authors have documented the effects of disturbance, especially boating, on the time budget and energy expenditure of staging and wintering diving ducks

(Thornburg 1973, Pedroli 1982, Korschgen et al. 1985, Howerter 1990, Kahl 1991b). Wetlands near Erickson appear to function as staging areas for females on moult migration during late summer (CH.1) and may be important foraging sites to build reserves for the upcoming moult. Several lakes in this area currently receive heavy use by recreational anglers and stocking of rainbow trout in several lakes has occurred (Sunde and Barcia 1975). Expansion of a recreational fishery in this area may reduce the suitability of these wetlands for staging purposes.

CONCLUSIONS AND MANAGEMENT IMPLICATIONS

Immediately following unsuccessful breeding attempts, female canvasbacks range over a wider area of the breeding habitat and preferentially use large semipermanent and permanent wetlands dominated by bulrush. Much of their diurnal activity during this period is devoted to feeding (40%) presumably on tubers of sago pondweed. A shift in habitat use at night is apparent and may be an adaptation to avoid predation by mink. Assuming preferred feeding sites are occupied during the day, movement off these wetlands at night would indicate that little nocturnal feeding may occur. This is supported by limited chart recorder data.

Unsuccessful females may remain on the breeding area up to one month following the cessation of breeding and the departure of their mates on moult migration. Delay of departure may serve as a reserve replenishing period or be required to allow social factors within female flocks to synchronize the upcoming moult. Individual females begin to congregate in small flocks on the breeding area in June. Flocks of up to 70 individuals may be seen on larger wetlands late in June or early in July prior to their departure from the breeding area on a moult migration of up to 300 km. Many if not all females from the Minnedosa breeding population begin the moult migration by making an initial movement approximately 40 km north to lakes and large potholes south of Riding Mountain National Park.

Females on these wetlands are often accompanied by a few to several hundred redheads with lesser numbers of scaup and goldeneyes mixed in. Feeding is also the most prominent activity in this area, again occupying approximately 40% of the diurnal time period. More time was spent swimming and in comfort activities than on the breeding area. How long a given female remains on these wetlands is unknown, but is probably related to the condition of the female and food availability in the area. These wetlands apparently serve as staging areas for females on moult migration and are generally devoid of female canvasbacks by mid-August. Subsequent movement to large southern boreal forest lakes occupied by moulting drakes occurs in late July and August. Swan Lake and Dauphin Lake appear to be important moulting sites for unsuccessful females. The moult migration of unsuccessful females is independent of the male moult migration and may be limited in distance by a females ability to replenish fat reserves.

The findings of my study indicate the importance of large wetlands near Erickson, Manitoba, and underscore the importance of Swan and Dauphin Lakes as moulting habitats by linking them to breeding areas in southern Manitoba. Highly skewed sex ratios in the continental canvasback population highlight the importance of females in determining effective breeding population size. Given the highly philopatric nature of canvasback females, factors affecting the quality of habitats used during the preflightless period and on moulting areas may have direct effects on local breeding populations in southern Manitoba. Effective population management should incorporate some level of protection from disturbance for these areas during critical periods. Of special concern are levels of recreational use during summer and any developments that may affect natural water levels or water quality.

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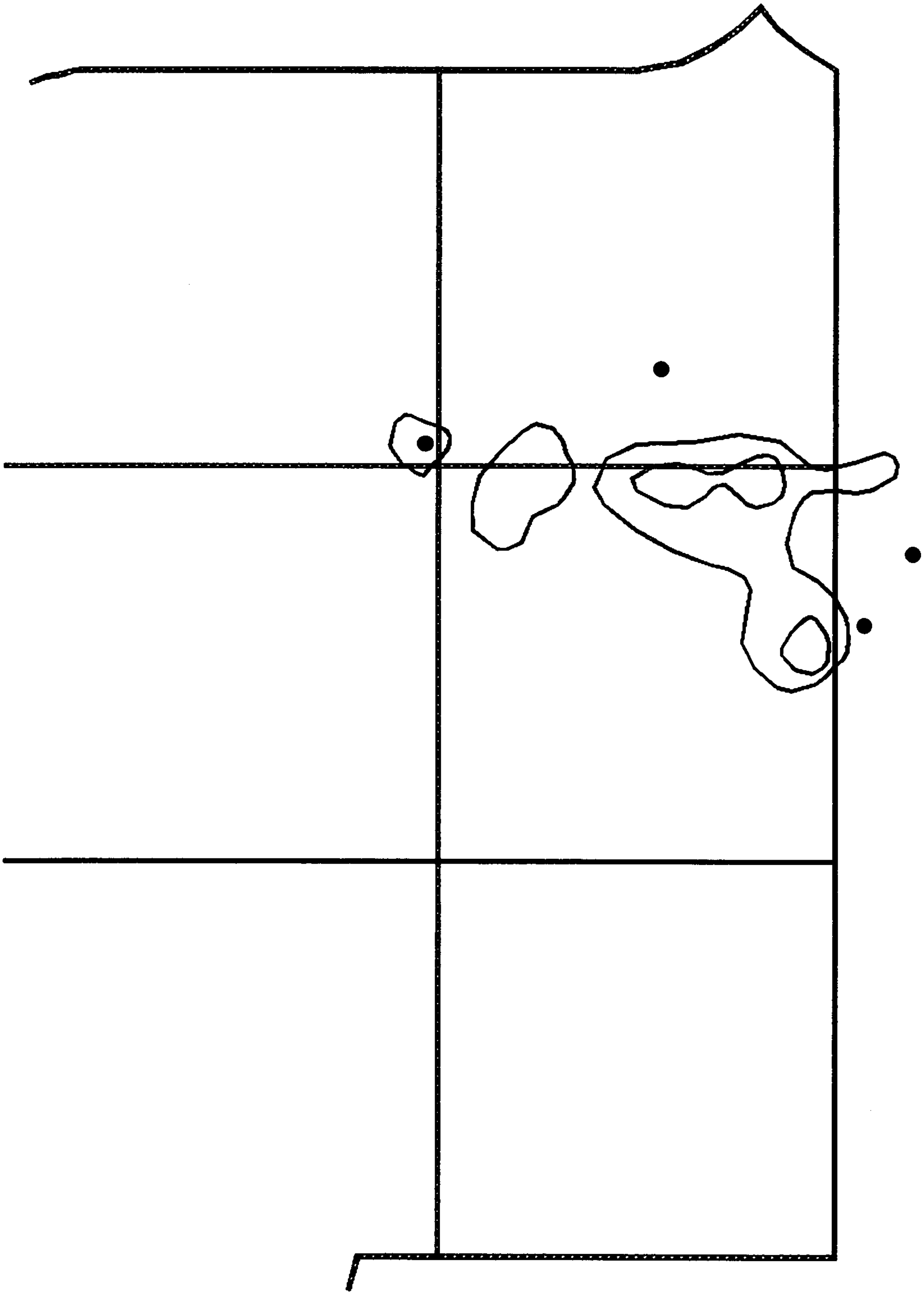
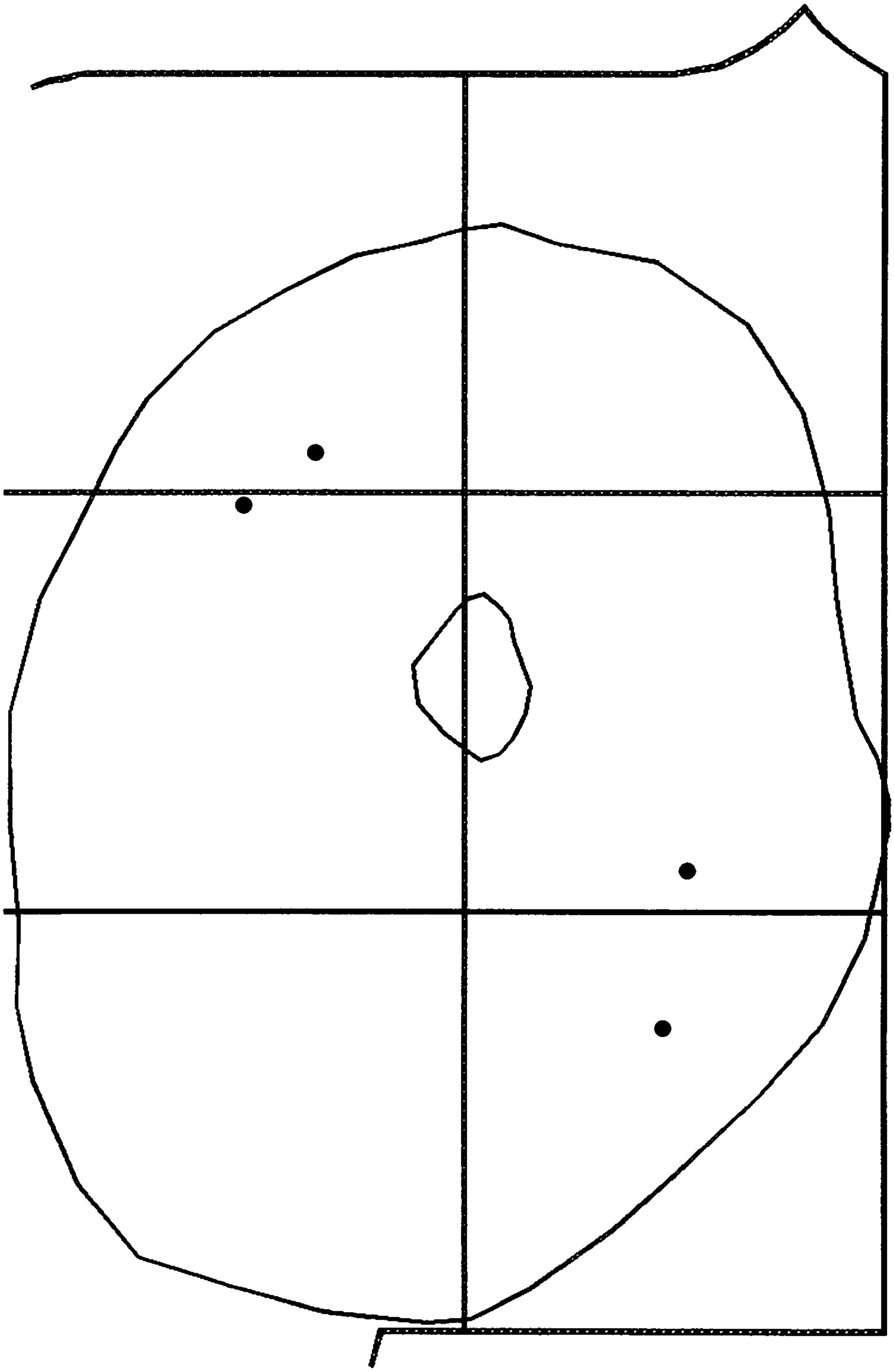
APPENDIX

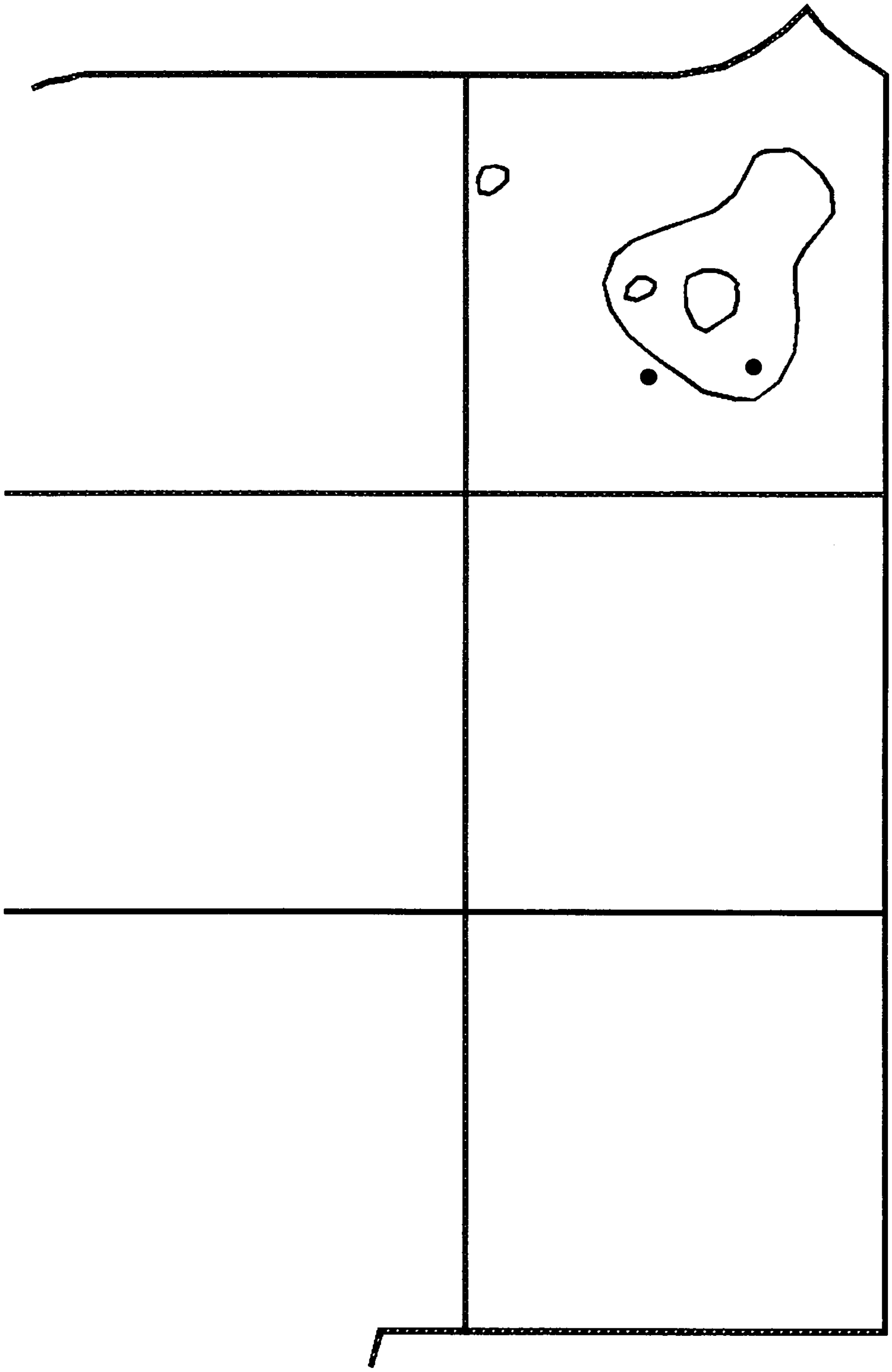
50 and 95% isopeths of the diurnal postbreeding home range of 12 radioed females in 1990. Straight lines correspond to grid roads as they appear in Figure 1. Filled dots indicate the location of nocturnally used wetlands in relation to the home range isopeths. Labels identify female by radio frequency and the number of locations used to define isopeths.



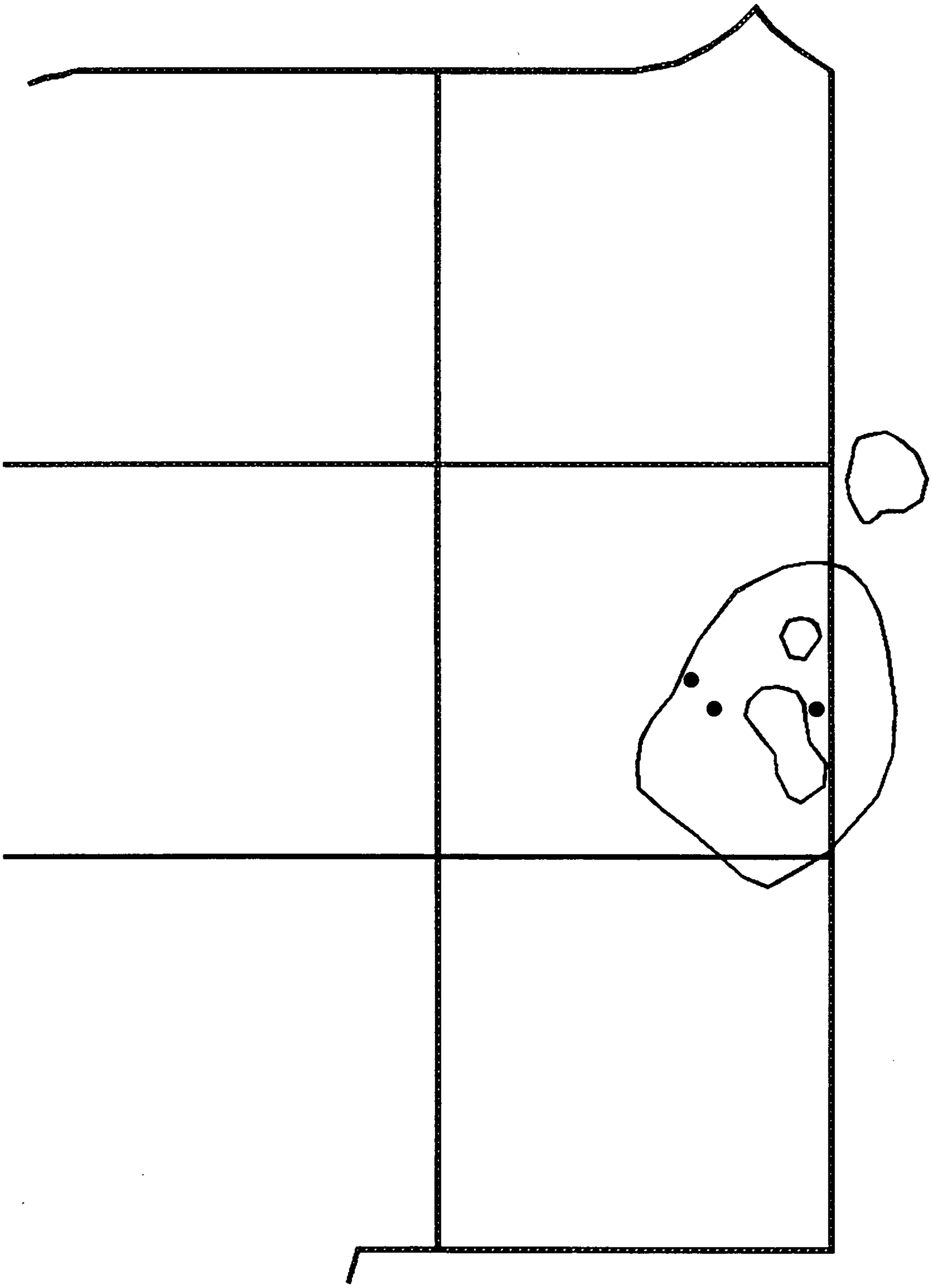
Female 4.010. Number of locations = 48



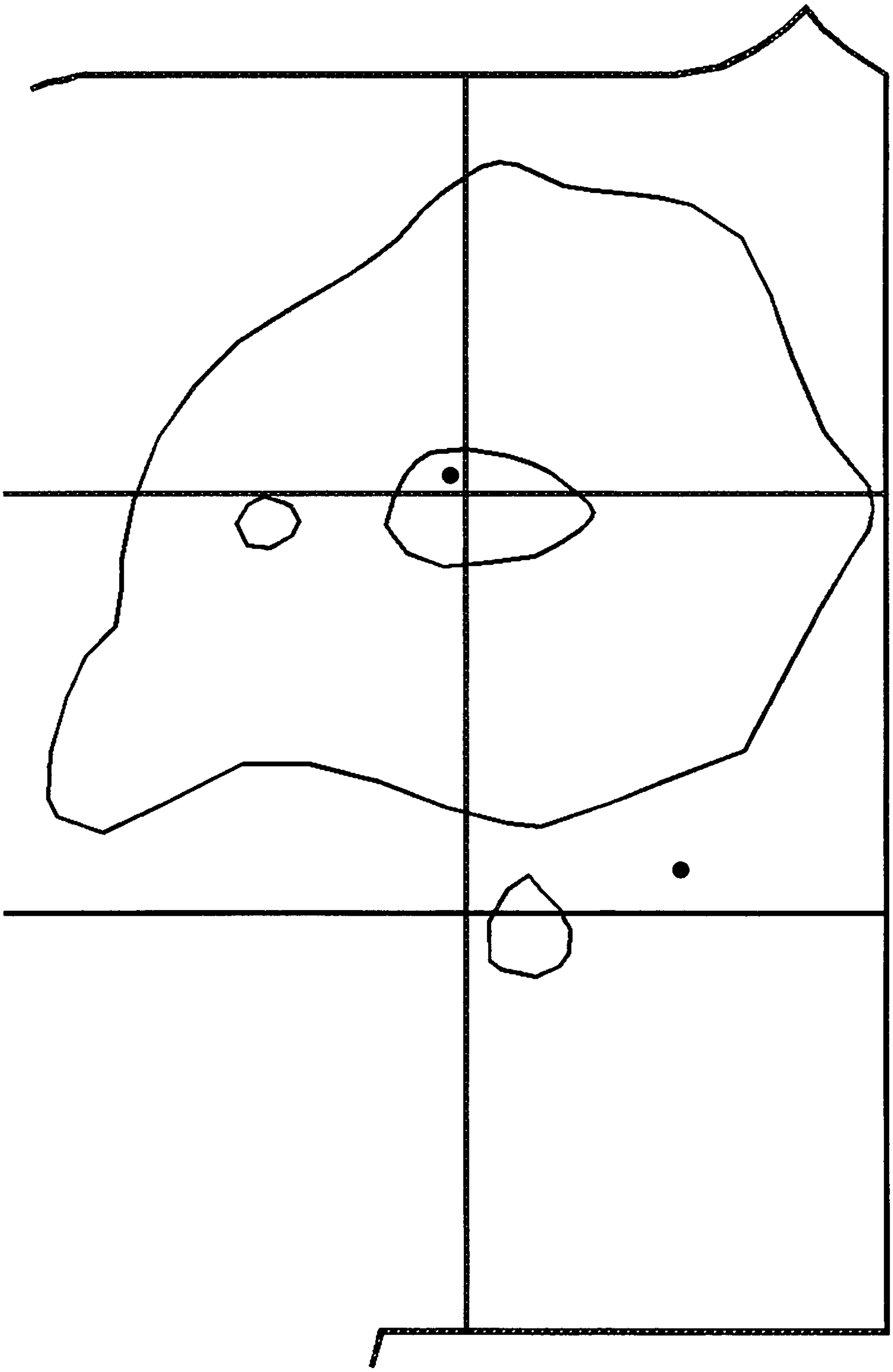
Female 4.030. Number of locations = 47



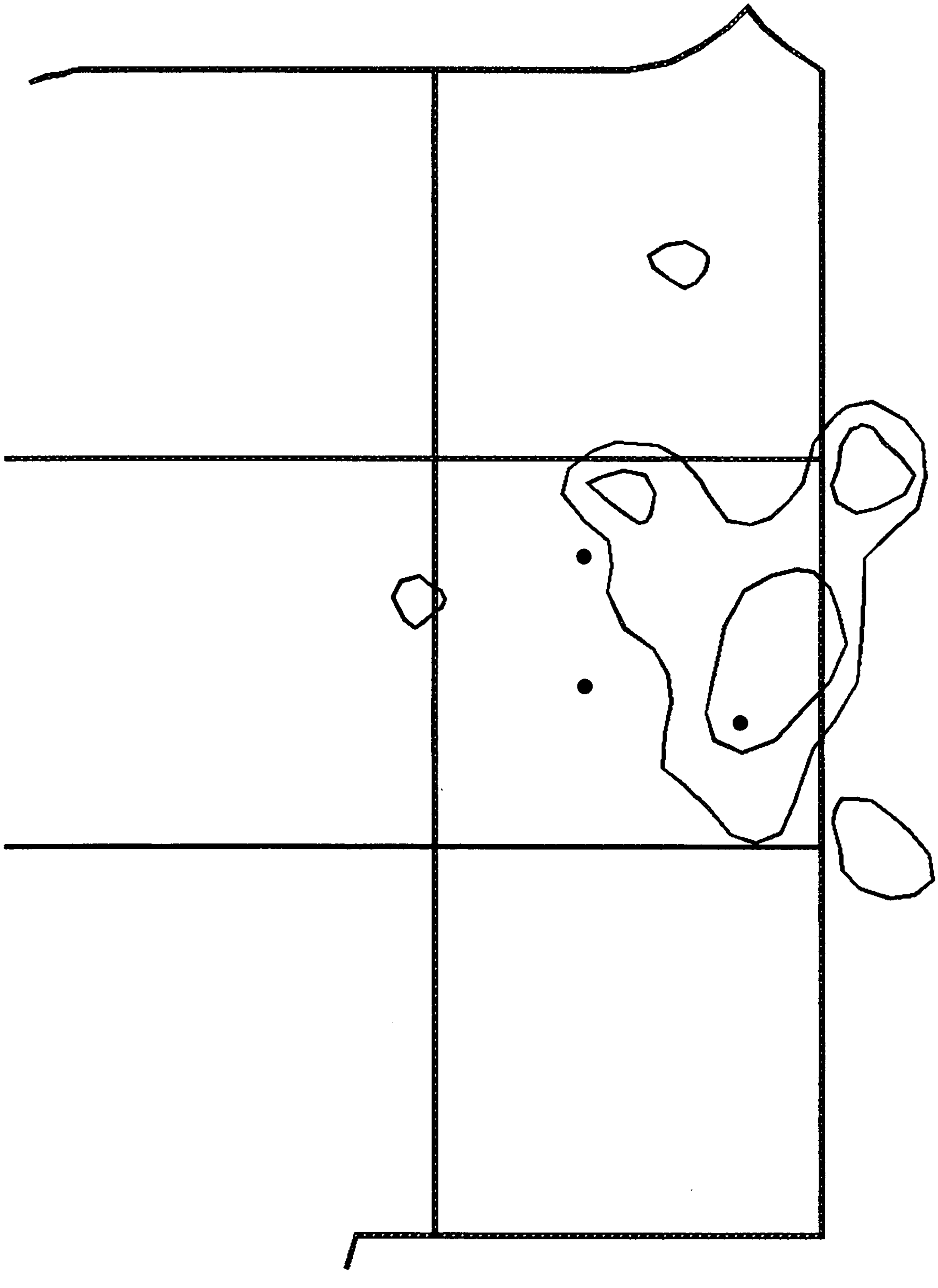
Female 4.080. Number of locations = 24



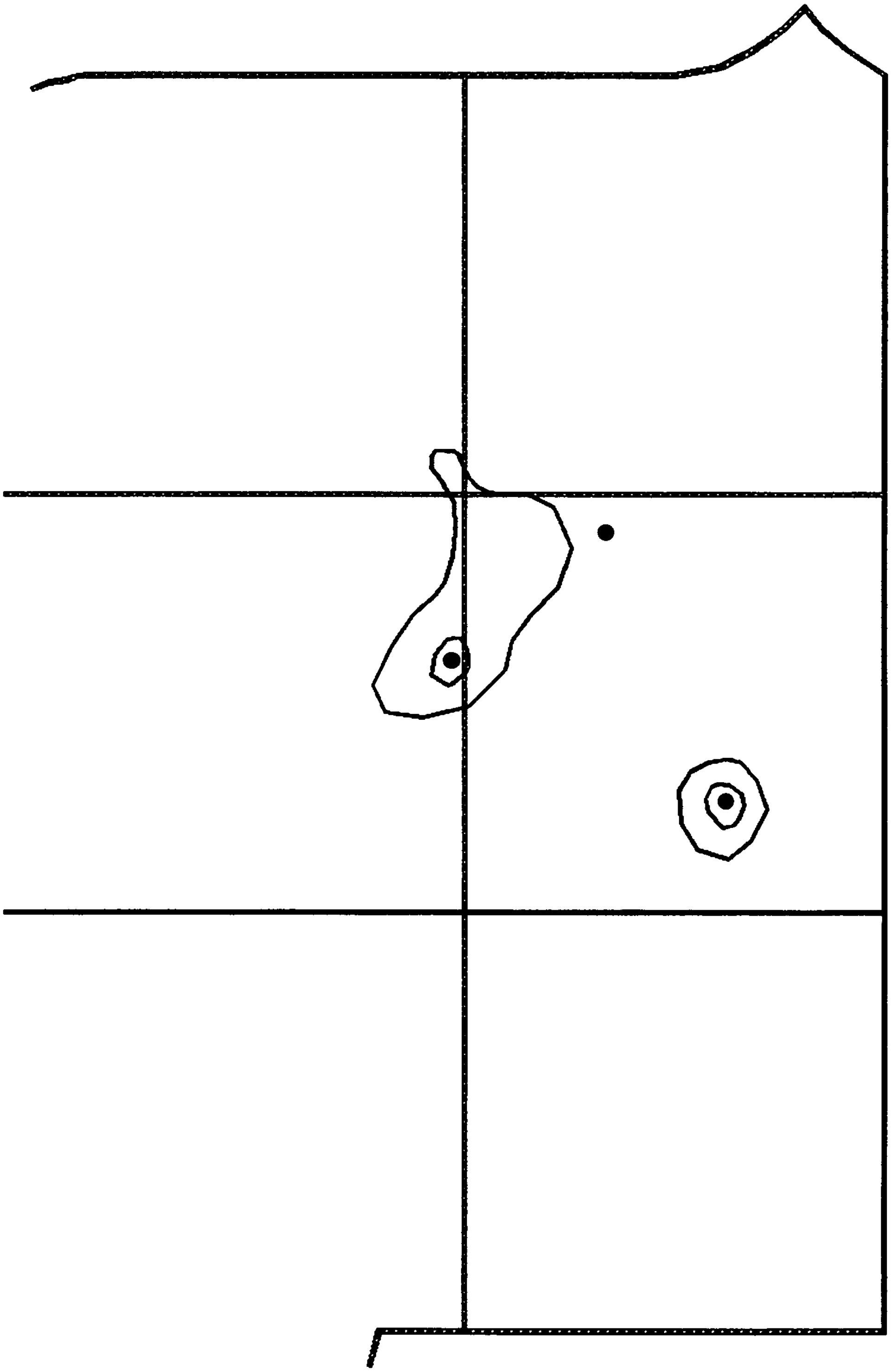
Female 4.100. Number of locations = 31



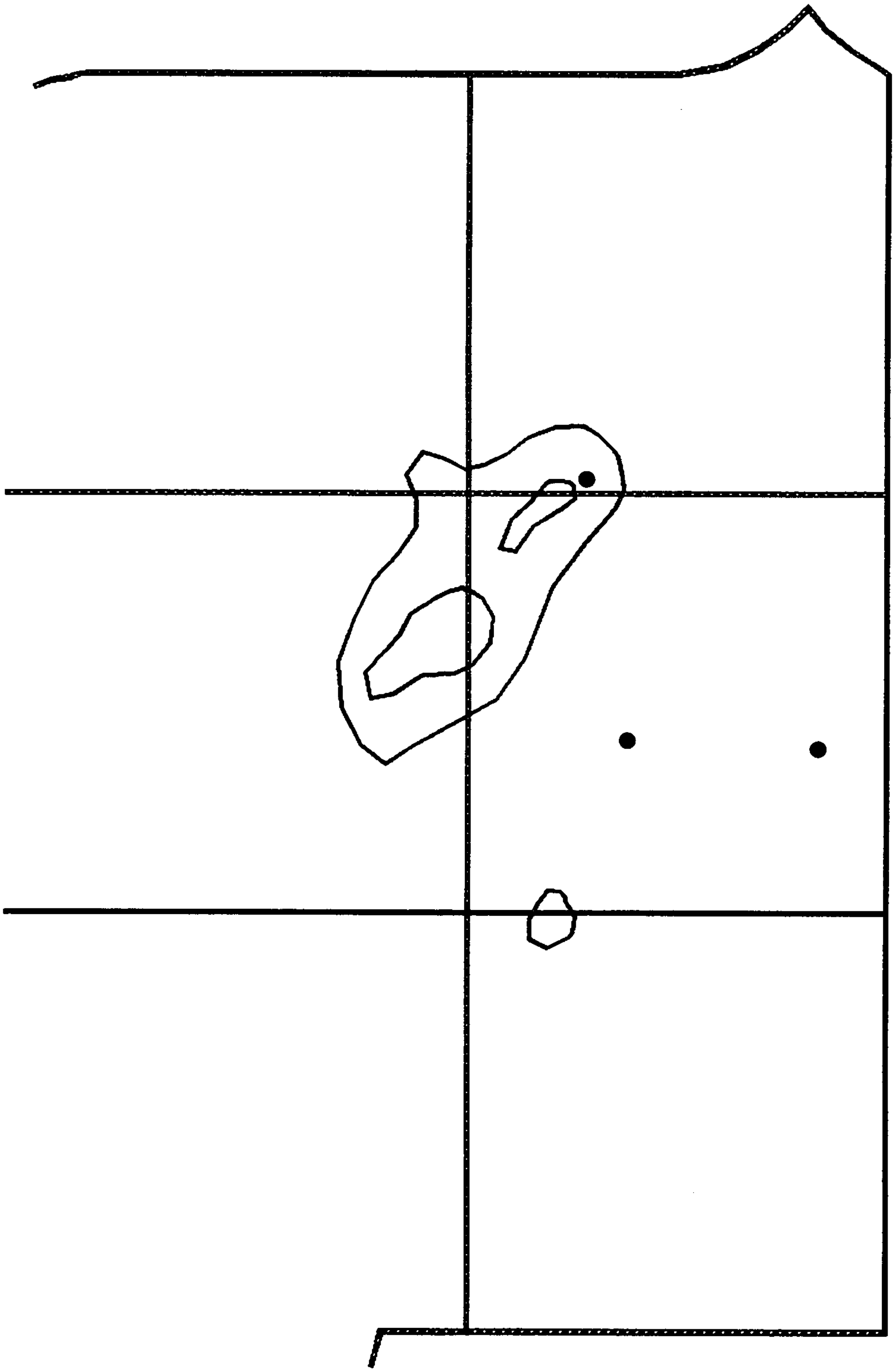
Female 4.359. Number of locations = 44



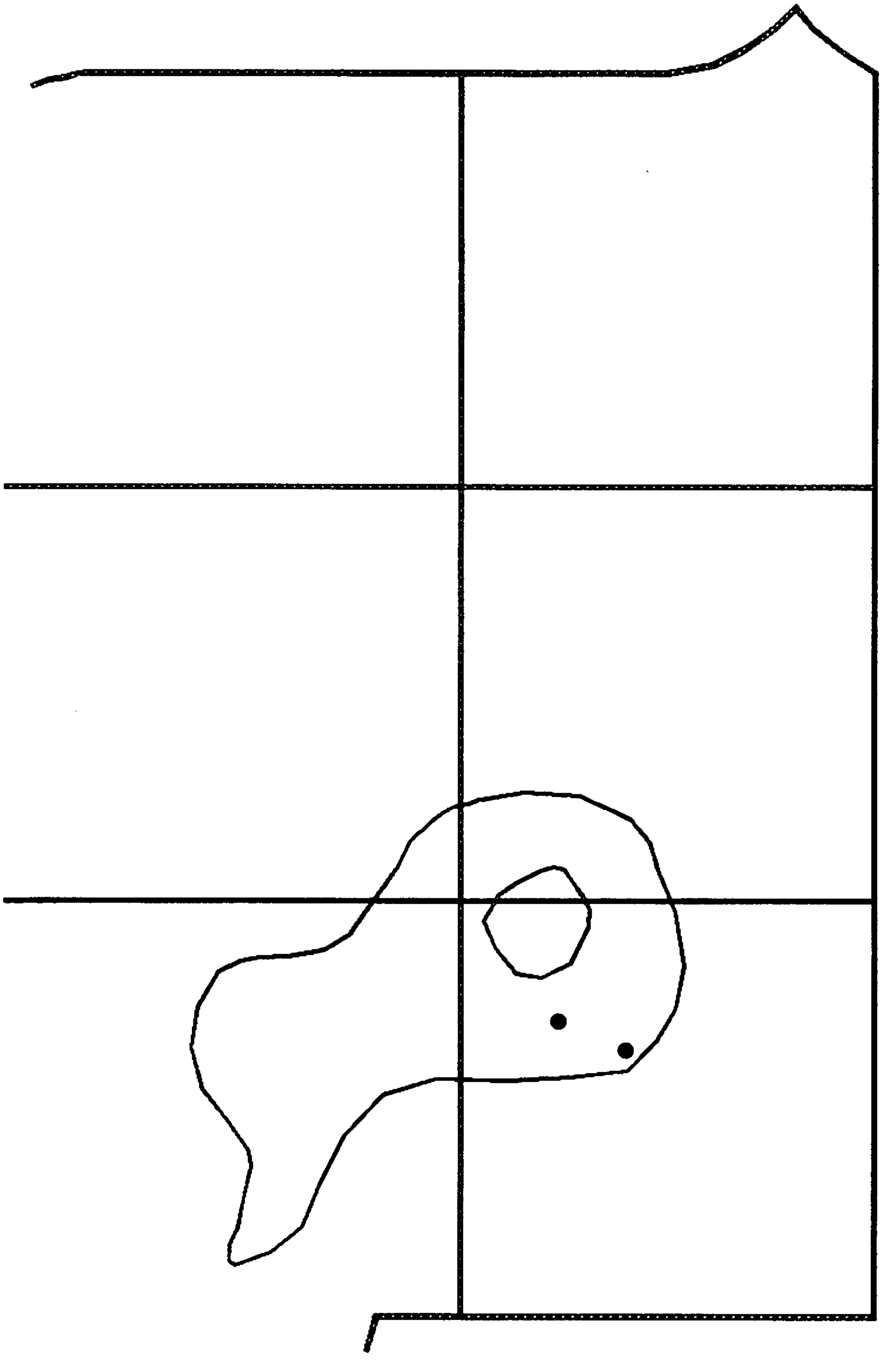
Female 4.460. Number of locations = 35



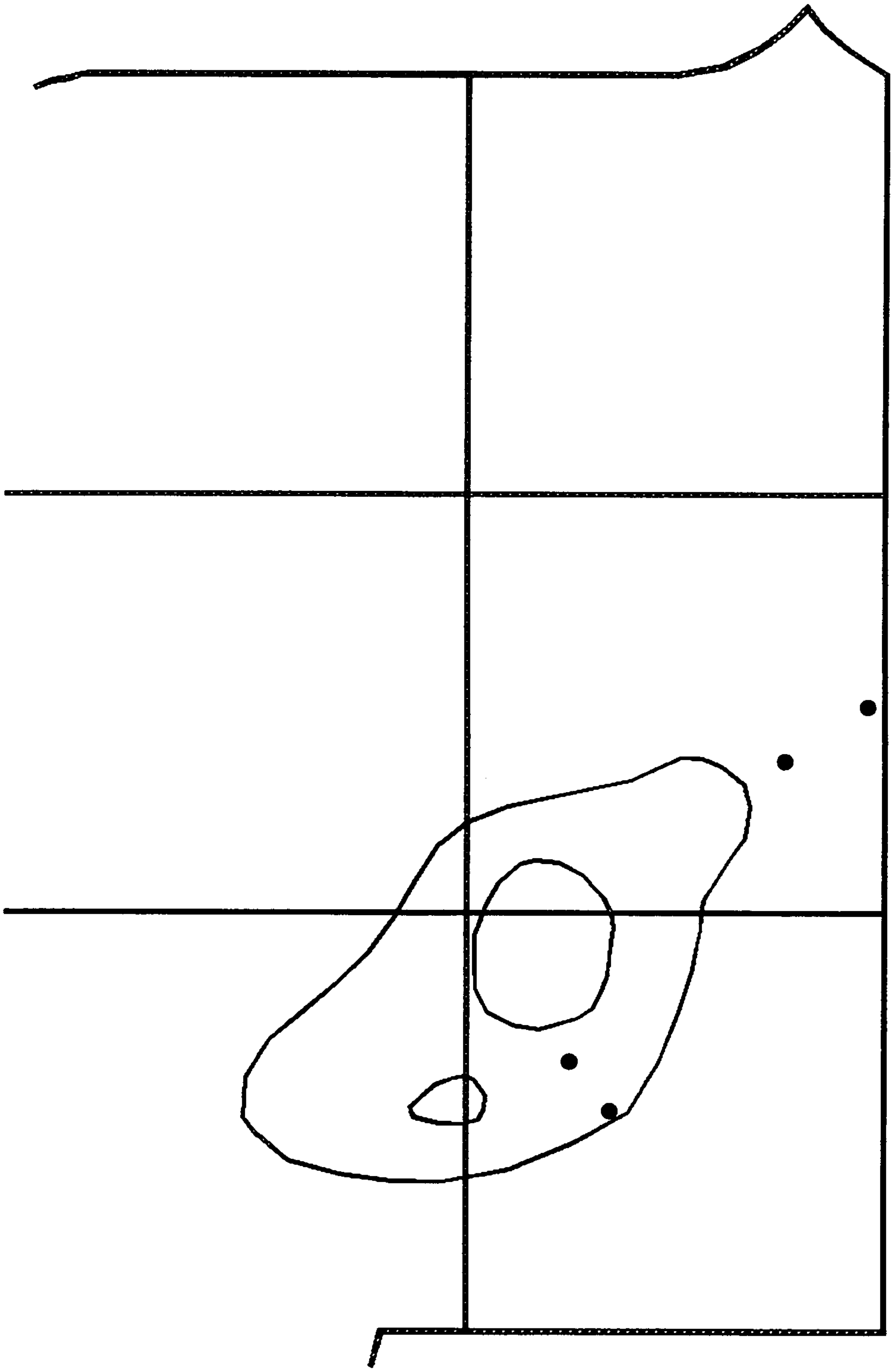
Female 4.685. Number of locations = 39



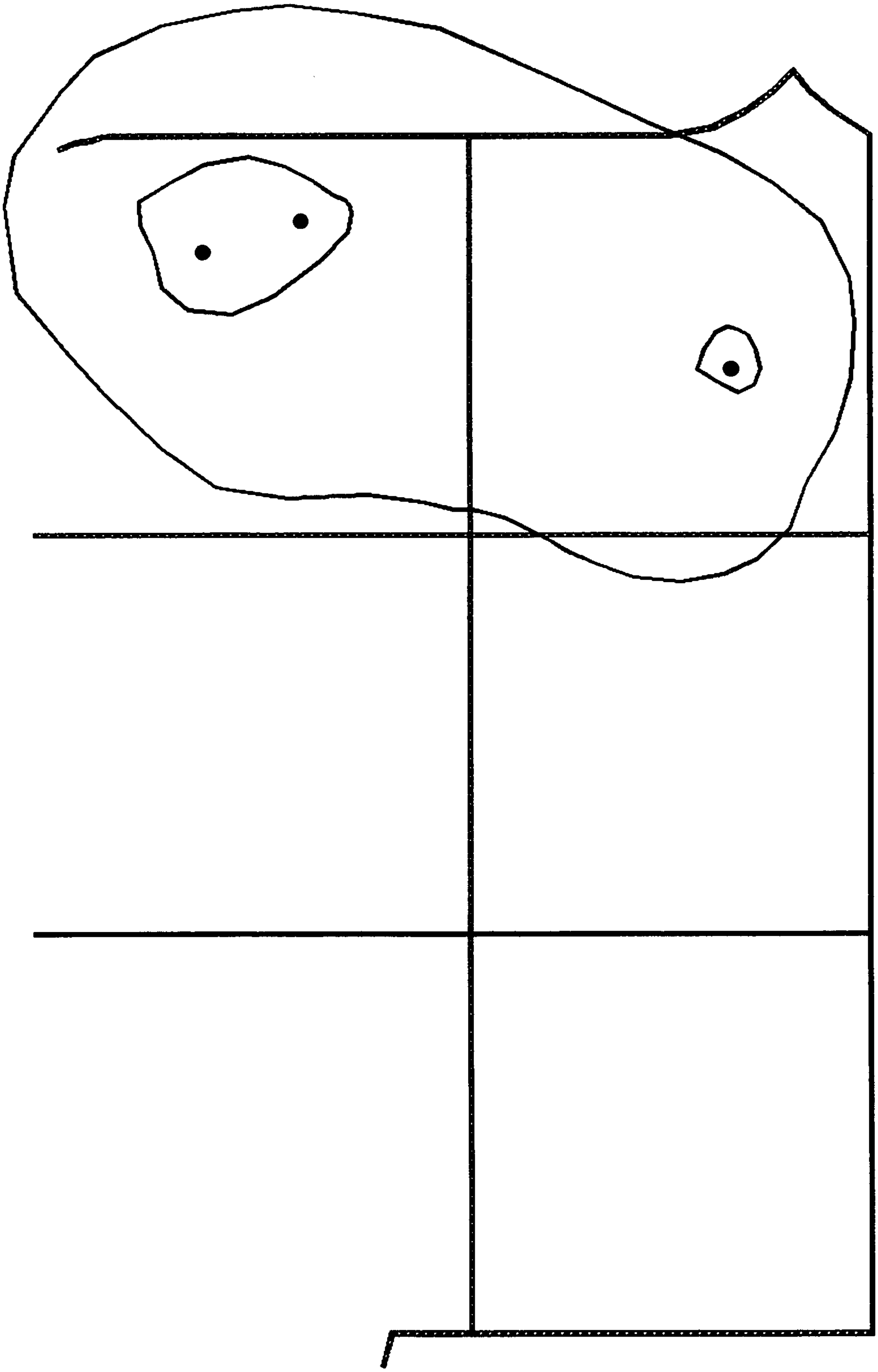
Female 4.796. Number of locations = 30



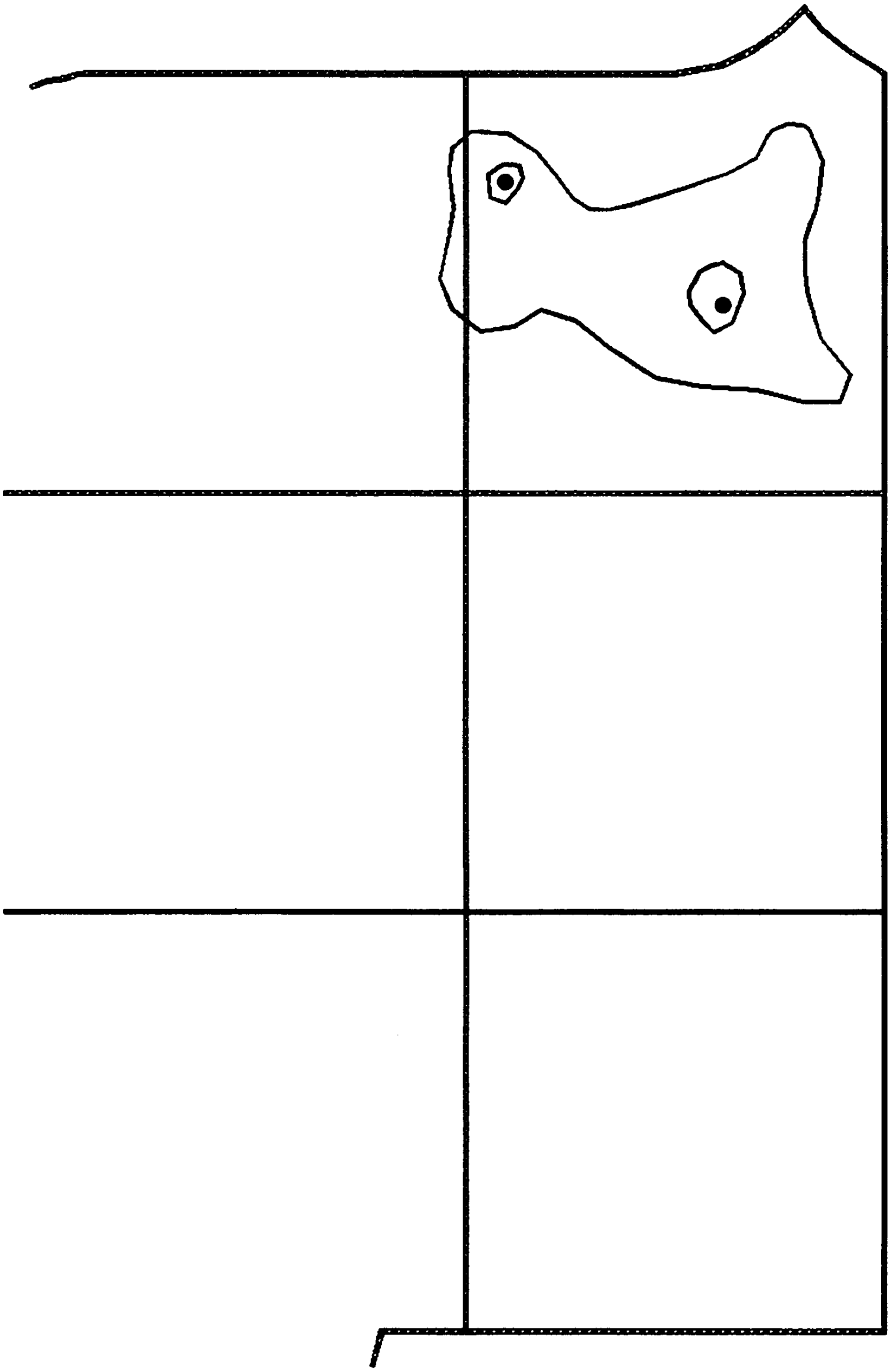
Female 4.656. Number of locations = 42



Female 5.200. Number of locations = 38



Female 5.563. Number of locations = 26



Female 5.639. Number of locations = 26