The Influence of Rain on the Behavior of Muskrats (*Ondatra zibethicus*), Other Small Mammals and Their Predators

by

©

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ABSTRACT

It is hypothesized that an increased level of activity has evolved in nocturnal small mammals in response to a reduction of predation pressure during rainfall. To test this hypothesis, the behavior of muskrats (Ondatra zibethicus) and a few predators was investigated. Freeze-branding and radio-pack implantation were used on muskrats. 1053 hours of visual observations in addition to sand-tracking data, indicated that muskrats travel, explore, disperse, and forage farther during evening hours on rainy days. Consequently, more territorial boundary crossings, territorial defenses and changes of den sites occurred during rainy days. Matings and movements related to an emergency were not influenced by rainfall.

Marsh hawks (Circus cyaneus) and short-eared owls (Asio flammeus) did not hunt during rainfall. The daily level of activity of the mink (Mustela vison), ermine (M. erminea), and feral cat (Felis catus) did not differ between rainy and non-rainy days. It is argued that their activity decreased during rainfall.

ABREGE

Il est suggéré qu'une augmentation du niveau d'activité a évolué chez les petits mammifères nocturnes suite à une réduction de la pression exercée par les prédateurs au cours des pluies. Afin de tester cette hypothèse, le comportement du rat musqué (<u>Ondatra zibethicus</u>) et de certains prédateurs a été étudié. Le marquage à froid et l'implantation de radio ont été essayés sur le rat musqué. 1053 heures d'observation visuelle en plus de quelques données de piste de sable indiquent que les rats musqués voyagent, explorent, se dispersent et fourragent plus loin durant les heures du soir des jours pluvieux. Conséquemment, les limites des territoires sont outrepassées et défendues plus souvent et les changements de gîte sont plus fréquents durant ces jours. Les accouplements et les mouvements relatif aux urgences ne sont pas influencés par la pluie.

Les busards des marais (<u>Circus cyaneus</u>) et les hiboux de marais (<u>Asio flammeus</u>) ne chassent pas pendant la pluie. Les niveaux journaliers de l'activité du vison (<u>Mustela vison</u>), de l'ermine (<u>M. erminea</u>) et du chat haret (<u>Felis catus</u>) ne sont pas différents entre les jours pluvieux et sans pluie. Il est argumenté que leur activité décroit durant les périodes de pluie.

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INTRODUCTION

Since 1940, nocturnal small mammals of the temperate regions have been known to become more active during periods of rainfall (Burt 1940). Several authors have come to the same conclusion using different techniques. These include trapping (Sidorowicz 1960), sand-tracking (Bider 1968), and photographic recording (Pearson 1960). However, all these techniques record only the presence of an animal at a specific time and place and rarely give information on the individual's actual behavior. Few satisfactory explanations for this increased small mammal activity have been put forward (Bramwell 1980; Doucet and Bider 1974; Getz 1968; Mystkowska and Sidorowicz 1961; Vickery and Bider 1981), and none have been substantiated. To gain a better understanding of the influence of rain on small mammal behavior, muskrats (Ondatra zibethicus) and a few avian and mammalian predators were visually observed or studied using sand-tracking data from Lac Carré and Mirabel.

The behavior of the muskrat was investigated because this small mammal is influenced by rainfall (Stewart and Bider 1977), it is large enough to be seen at a distance, and its population biology is well known (Errington 1963). It was hypothesized that exploration and territorial defense occur on rainy days and that not all aspects of the muskrat's behavior, such as matings and movement related to an emergency (i.e. drought), are influenced by rain. This part of my study is in the second chapter of this thesis.

To undertake this study, it was necessary to employ techniques which permitted individual recognition at a distance. Two of these techniques, freeze-branding and radio-pack implantation, have been described in the first chapter.

Bramwell (1980) and Vickery and Bider (1981) suggested that the activity of predators, or at least their efficiency, decreases with the occurrence of rainfall, and that small mammals take advantage of this reduction in predation pressure to increase their activity. This hypothesis is discussed in the third chapter.

The 3 chapters of this thesis have been submitted to journals. Because of this, some repetition occurs in the introduction and discussion of the second and third chapters.

CHAPTER 1

COMMENTS ON FREEZE-BRANDING AND RADIO-PACK IMPLANTATION IN THE MUSKRAT*

* Submitted to the Journal of Wildlife Management

When undertaking a behavioral research project on an animal, it is desirable to be able to identify every individual. To attain this goal, freeze-branding and radio-pack implantation were attempted on ditch-dwelling muskrats. The limitations and applications of these 2 techniques are described.

INTRODUCTION

Field research on behavior often requires that the individual animal be located and indentified at a distance. Many techniques to attain that goal are available (Stonehouse 1978). However, the number describing the marking of several free-living muskrats for individual identification is limited. Back-tagging should not be performed on individuals of more than 4 weeks of age, since adults can remove their tags (Errington and Errington 1937). Tail banding becomes useless when the animal is in the water because only the dorsal part of the body is visible. Ear tags are too small to be recognized at a distance (Aldous 1946). Dyes are ineffective on dark fur (Taber and Cowan 1971). Two other techniques, freeze-branding and radio-tracking showed promise and were tried on some ditch-dwelling muskrats during the summer of 1980. The utilization of either technique on muskrats has not been described in the literature.

FREEZE-BRANDING

Eight young, between 4 and 6 weeks old, and 12 adults were captured. The young were handheld, shaved and a copper branding iron (square, side: 1.2 cm) cooled with liquid nitrogen was applied on 2 different dorsal locations for either 20, 30, 40 or 50 seconds. The adults were anaesthetized with 40 mg of sodium pento-barbital/kg of body weight, shaved and freeze-branded on 2 different dorsal locations for either 30, 40, 50 or 60 seconds, using a brass branding iron (circle, diameter: 4 cm) cooled with liquid nitrogen. All individuals were released within 3 hours at their site of capture. Two months later, 2 adults were recaptured and freeze-branded on 3 different dorsal locations for 70, 80 and 90 seconds.

No colour change of the fur was noted after freeze-branding. As the duration of branding increased the fur grew back more slowly. In the area which was freeze-branded for 80 or 90 seconds, the hair was only half-grown after 10 weeks. When the procedure was applied for less than 50 seconds, the fur grew back to its normal state within 4 weeks.

Hadow (1972) and Newton (1978) stated that liquid nitrogen could be used as a cooling agent for freeze-branding, but a mixture of alcohol and dry ice is usually cheaper, more easily obtained and more effective than liquid nitrogen. We used the latter because it was more easily available.

Hadow (1972) using dry ice and alcohol determined that the optimal length of application ranged from 20 to 40 seconds. He observed that immediately after the iron was taken off, the skin seemed frozen and the site of application stayed bare for 3 to 5 weeks. After we freeze-branded, we also observed that the skin appeared frozen and when the application time was more than 60 seconds, it took approximately a month before dark hair grew back.

Our observations, with the exception of regrowing white hairs, were similar to those of Hadow (1972). Since the temperature of liquid nitrogen is -175°C compared to -108°C, the freezing point of carbon dioxide, our application time could only be too long. In such a case, the hairs should have grown white first, even if they would eventually turn black after several months (Hadow 1972). These results indicate the potential for freeze-branding muskrats looks poor.

RADIO IMPLANTS

Muskrats generally will not tolerate any collar or harness. Therefore, the implantation of a radio-pack is required in the use of radio-telemetry techniques for behavioral studies of this species. A first trial was carried out using a SM1 transmitter (AVM). It was connected to a RM 630-T2 battery and a 2-inch long antenna free of movement. The package was dipped in beeswax and coated with dental acrylic. It weighed approximately 12 g. 6 adult muskrats, weighing over 1 kg, were live-trapped, anaesthetized, and shaved between the shoulder blades. A 3.0-5.0 cm incision was performed, the radio-pack with the antenna was implanted between the skin and the muscles, and the wound sutured. The animals were released at the site of capture within 3 hours after the end of the operation.

3 individuals were live-trapped again. In one instance, the day of the implantation, the radio-pack was seen on the right side of the animal. Four days later, when recaptured, it had an open wound near its right anterior leg and the dorsal scar was closed. It had removed the radio-pack by cutting itself open after the pack had shifted from the back to its right anterior leg. The removal occurred between the third and fourth day after the operation. For 2 other animals, the wound healed before they shifted and removed their radios in a similar fashion. Two other individuals were never recaptured, but they were

observed transporting their radios on their backs for at least 2 weeks. We think that they subsequently lost their radios since the signals became fixed until the batteries died.

To solve the problem of radio-pack removal intra-abdominal implantation was tried. For this purpose, the radio-pack was modified, instead of leaving the antenna free, it was folded around the radio-pack. The latter was not dipped into beeswax, but only coated with dental acrylic. In one case, beeswax was left on the radio-pack which, accidentally, had not been completely covered with dental acrylic. When we later removed the pack, 2 holes each connected to an eroded space between the acrylic and the radio were present and there was tissue build up around the radio-pack. Four other adults (over 1 kg) and 2 immatures (800 and 900 g) were captured, anaesthetized and shaved between the thorax and the posterior leg. Here, a small incision was made through the skin and abdominal muscles. The radio-pack was implanted in the abdominal cavity and the skin sutured. The intra-abdominal implantation proved successful. All individuals kept their radios for at least 6 weeks and up to 4 months, until the end of our observation season.

Using the latter technique, it was possible to locate individuals within their burrows. The range of the signal varied from 15 m when the animal was in the burrow with the antenna 2 m above the ground, to 50 m or more when the animal was outside its burrow with the antenna 4.5 cm above the soil level. All observations within 48 hours after the operation were discarded to avoid any post-operative effects. No behavioral side effects of this implantation were noted.

We conclude that a study on the capacity of freeze-branding to mark different species is required and the above radio-telemetry techniques permit us to locate individuals before any behavioral observation.

CHAPTER 2

THE INFLUENCE OF RAIN ON THE FORAGING AND TERRITORIAL BEHAVIOR OF MUSKRATS*

* For submission to Ecology

Little information is available concerning the influence of rain on small mammal behavior. Since muskrats can easily be seen at a distance, a study of this species was undertaken using diurnal and nocturnal observations. Radio-telemetry and sand-tracking data from Mirabel and Lac Carré provided additional information. The results of this research are presented and discussed here.

INTRODUCTION

The activity of several nocturnal small mammals of temperate regions increases during rain (Bider 1968; Doucet and Bider 1969, 1974; Mystkowska and Sidorowicz 1961; Pearson 1960; Sidorowicz 1969; Stewart and Bider 1977; Vickery and Bider 1981). This conclusion was drawn from trapping, photographic recording or sand-tracking. Since these techniques recorded the presence of an animal at one specific location and time, they gave little information on the individual's actual behavior. Because of the effect of rain on the activity of small mammals, a study was undertaken to determine what muskrats do during periods of heightened activity. This might produce some understanding of the response of other small mammals to rain.

Ditch-dwelling muskrats were selected as experimental animals because they are large enough to observe at a distance in their linear home ranges, their daily activity is known (Stewart and Bider 1977), and their population biology is well understood (Errington 1963). Muskrats generally defend a territory within which they feed, reproduce and live throughout the year (Errington 1963). Since ditch-dwelling muskrats are more active on rainy days (Stewart and Bider 1977), we hypothesized that on rainy days the distance travelled per unit of time would increase, either through an increase of the number of movements per unit of time or through the lengthening of each displacement or both. Arbitrarily, a movement is defined as any displacement longer than 3 m from 1 point to another, a point being a den wherein the muskrats had been for more than 1 minute or a place where the muskrat reversed their direction of movement. Lengthening of each displacement is expressed as an increase in the percentage of longer (>40 m) movements. If such a lengthening of each displacement exists, more territorial boundaries should be crossed and more territorial defense should occur on rainy days. To elucidate possible changes in behavioral activity during precipitation, foraging strategies, dispersal, mating, and use of main den sites were investigated.

Because detailed observations are more easily carried out during daylight hours, more effort was put into observing the animals during daytime. Since muskrats are more active at night (Stewart and Bider 1977; Vincent 1970), we hypothesized that the behavioral differences seen during daytime would be more pronounced at night. To test this, a series of observations at the limits of territories were taken at night.

Finally, if dispersal or exploration take place during rain, then muskrats should be active at some distance from water more often at night during days with rain.

METHODS

Direct observation

The major study site (45°20'N, 74°10'W) was located in the parish of St. Joseph de Soulanges, Soulanges-Vaudreuil County, 15 km west of the Island of Montreal. Three different segments of ditches from the same drainage system were observed. The ditches were 2.5-3.5 m wide at the water surface. The water was .3 m deep on average, varying from .15 to 1.0 m depending on the water table. The surrounding agriculture land was flat sandy loam over clay.

The vegetation on the banks of the ditches was composed of grasses (Phleum pratense and Agropyron repens) plus other forbs (Equisetum pratense, Vicia cracca, Taraxacum officinale, Potentilla spp., Pastinaca sativa, Fragaria virgiana, etc.). The aquatic vegetation consisted of various associations of Typha latifolia, Scirpus spp., Sagittaria spp., Alisma spp., and Sparganium spp.

The climate of the region was classified by Trewartha as a humid continental climate with cool summers (Espenshade 1960). The time of occurrence of rainfall was noted, when possible, and the missing meteorological data were collected from the meterological station of the Service de la météorologie du Québec, located 2 km from the study site. A rainy day was defined as a day in which more than a trace of rain fell between sunrise and the end of the observation period or 0000 h, whichever came first. Rain occurring during the night preceding an observation day was ignored because the activity of muskrats is not affected by rain falling between midnight and sunrise (Stewart and Bider 1977).

Straight segments of ditches were selected as the ideal habitat in which to observe the behavior of muskrats. The linear ditches offered several advantages. In April, the territories can be delimited by tracking (Errington 1963), and, since muskrats do not usually travel far away from water, the observers can concentrate their attention on a long narrow strip of water. All movements were measured using a map (1:500) and landmarkers on the banks of the ditch.

Before the end of April, the main den, the size of the centre of activity and the territorial limits were determined by reading the tracks and signs left by the muskrats as described by Errington (1963). Our territorial boundaries were further confirmed by the subsequent mapping of observed movements. Since boundaries are not always well defined, a crossing of a territorial boundary was counted when an individual would travel at least 40 m beyond the determined point.

Between 29 May and 16 July 1979, a ground level shelter was installed in the middle of a territory where 21 periods of 4 hours of observation were taken before darkness. Night was defined as starting 1/2 hour after sunset. The observation periods covered more than 50% of the diurnal peak of the activity of muskrats (Stewart and Bider 1977; Vincent 1970). The territory under study was occupied by a male, a female and a litter of 5 young which appeared out of their burrow after 3 July.

During 1980, 2 3.5 m high towers were installed 540 m apart on the bank of a ditch. Another segment of a ditch was observed from a bridge. Each observation station was located at the interface of 2 territories.

The diurnal peak of activity of the muskrat covers a period of 6 hours before darkness (Stewart and Bider 1977; Vincent 1970). At first, we felt the quality of observations could decrease with time and we arbitrarily limited observation periods to 4 hours. Later, these periods were increased to 6 hours without any obvious loss of quality in the observation. Between 30 April and 8 August, 98 observation periods were made in the last 4 hours of the day and 24 others started 5.5 hours before sunset. Between 11 August and 7 September, 31 periods of 6 hours were recorded before night. Finally, between 16 September and 22 October, 27 observation periods of 7 hours were made. The first 4 hours were completed before darkness, followed by a 15-minute break and another 3 hours of night time observations.

Since most of the diurnal observations were taken in blocks of 4 hours, the analysis will be carried out, keeping the blocks separated. Block A started 6 hours before night time and block B ended with darkness.

The 1980 study area included 5 territories with 1 female each, 4 males were present on a regular basis and at least 8 litters were produced. Seven of these 9 adults, plus 3 others living in the adjacent territories, and 10 young were captured and freeze-branded. The freeze-branding technique was unsuccessful and the individuals could not always be identified (Chapter 1). Six individuals in the study area, plus 4 others from adjacent territories, were radio-tagged (Chapter 1). To increase the efficiency of the observers, all radios were located before the beginning of the observation periods.

All movements of the young within the week after they were first seen were discarded. At that time, too many short movements of groups of young took place to be recorded.

Muskrats fed inside or outside of their burrows. To study the effect of the rain on the feeding behavior of these animals, 3 parameters were noted, the number of times an individual carried some vegetation to its burrow, the time spent only feeding outside and the location where the plants were cut. Since the time required by an adult and a young to obtain and ingest the necessary amount of food to survive differs, the feeding behavior of the young was not included in our analysis. After 8 August, we observed adults feeding outside for short periods totalling less than 5 minutes and did not see any transportation of plants. Because the proportion of rainy to non-rainy days before and after 8 August was not the same, analysis of feeding habits of the muskrats was restricted to the period prior to that date.

During nocturnal observations, 2 red filtered automobile spotlights were installed at the interface of the territories. Their beams were pointed in opposite directions and fixed such that one could see any muskrat movements within 50 m on each side of the point of observation. The lights were on continuously through the observation period. The effect of this unnatural red light appeared minimal and was comparable to that of full moonlight.

Since only a small portion at the interface of 2 territories was under observation at night, the extent of each movement or the total distance travelled by a muskrat per unit of time, could not be seen. The number of times a muskrat crossed the territorial boundary and the number of territorial defenses were noted. A territorial defense was noted when an individual crossed the territorial boundary, encountered another individual, and returned promptly. Usually, the actual fighting was hard to see, but some water splashing could be heard.

Sand-tracking

The sand-tracking technique has been described by Bider (1968). A sand-transect is a .65 m strip of fine sand covered with a canopy of clear polyethylene. The tracks of any animal crossing the transect are read and erased every 2 hours. For a period of 8 days, the readings are done at odd hours (i.e. 2100 h) followed by another 8 days when the tracks are read at even hours (i.e. 2200 h) and so on.

At Lac Carré, 100 km northwest of Montréal, a sand-transect was constructed in 1964. It crossed a field, an ecotone and a sugar maple (*Acer saccharum*) - birch (*Betula lutea*) forest with some balsam fir (*Abies balsamea*) and white pine (*Pinus strobus*). It was located .25 km away from a stream in an unusual habitat for the muskrat. The readings were undertaken in June, July, August, and sometimes September, between 1964 and 1980.

In 1971, 4 sand-transects were installed at Mirabel, parish Sainte-Scholastique, Deux Montagnes county, in southwestern Québec. The site, vegetation and climate were described in Bider *et al*. (1976). In summary, the first sand-transect was constructed through a mature sugar maple forest. A second sand-transect passed through an abandoned sand field where corn had been grown the previous year. The 1971 vegetation was composed mostly of weeds of different heights with bare patches of soil. The last sand-transect was subdivided into 3 parts, according to the habitat it crossed. It started in a clay field, a newly abandoned pasture, ran perpendicular to an ecotone which was at the edge of a balsam fir forest mixed with white spruce and white cedar (*Thuja occidentalis*). All these transects were in various habitats not representative of muskrat habitats, in areas accessible to, but seldom visited by, muskrats. The distance between the nearest sand-transect and the ditches was more than 60 m.

Before 1 September, the tracks were read every 2 hours. The diel activity of the muskrat at Mirabel was established using the tracks read before that date. Every hour was given half a crossing for each track noted during a reading. The number of crossings was counted for each hour and an histogram drawn.

Since none of our results were normally distributed, only non-parametric statistical tests were performed (Siegel 1956).

RESULTS

Total distance travelled per 4-hour block

The increased level of activity of the muskrat during rain (Stewart and Bider 1977) should result in an increase of the total distance travelled by the muskrats in a fixed period of time. During time block A, the median distance travelled by the muskrat per block was 47 m (range: 0-450 m, mean: 104 m) on rainy days. On days without rain, the median distance travelled was 0 m (range: 0-60 m, mean: 7 m) (Mann-Whitney & test, P = .003, Table I). During block B, on rainy and non-rainy days, the medians were 150 m (range: 0-1955 m, mean: 60 m) and 0 m (range: 0-1170 m, mean: 95 m) respectively (Mann-Whitney U test, P = .003). Since some observation periods lasted 6 consecutive hours, the information gathered during the 3rd and 4th hour is used twice, increasing the chance of type II error. To avoid this error, we excluded from a second analysis the observations taken between 11 August and 16 September. After this deletion, during block A, the median distance travelled by muskrats per time block on rainy and non-rainy days were 150 m (range: 0-270 m, mean: 135 m) and 0 m (range: 0-60 m, mean: 11 m) respectively. During block B, the median on rainy days was 60 m (range 0-1955 m, mean: 194 m) and on days without rain the median distance travelled was 0 m (range: 0-1170 m, mean: 144 m). Regardless of the data used, the results did not change, and indicated that distance travelled increased with rain (Mann-Whitney U test, block A, P = .004 and block B, P = .016).

Number of movements per block

The total distance travelled by the muskrats per 4-hour block might be increased either by augmenting the number of movements per hour or by lengthening each displacement. In block A, the number of movements per hour increased from .26 on days without rain to .97 on rainy days (Chi-square test, df = 1, $\chi^2 = 55.10$, $P < .001$, Table II), but during block B, the number of movements per hour stayed about the same .94 during rainy days and 1.04 during days without rain (Chi-square test, df = 1, $\chi^2 = 1.70$, $P > .05$). These conclusions did not change when the 6 hour observation periods were excluded. During block A, the number of movements per hour increased from .34 on days without rain to 1.93 on rainy days (Chi-square test, df = 1, $\chi^2 = 62.54$, $P < .001$). During block B, the number of movements per hour on rainy days (1.06) was similar to that on days without rain (1.23) (Chi-square test, df = 1, $\chi^2 = 3.37$, $P > .05$). These results confirmed the findings of Stewart and Bider (1977). On days without rain, muskrats were almost inactive during the 5th and 6th hour before night and became active during what corresponds with block B (the last 4 hours). Since activity started earlier on rainy days, the number of movements during the 5th and 6th hour before darkness (i.e. during block A) increased during rain.

Distribution of the length of movements

Errington (1963) showed that most muskrat's movements in marshes were less than 120 m. Our observations indicated that the daily muskrat movements are even shorter, about 40 m, and that they are affected by the weather. All muskrat movements observed during daytime were combined and classified according to the weather, rainy and non-rainy days, and grouped in classes of 40 m. During days with rain, 88% of their displacements were smaller than 40 m compared to 70% during rainy days. The distribution of the length of movements shifted towards longer distances when some rain fell (Chi-square test, $\chi^2 = 52.38$, df = 6, $P < .001$, Fig. 1).

Territorial boundary crossings

The increase in the length of each displacement travelled by the muskrats on rainy days should result in an increased number of crossings of territorial limits. No territorial boundary crossings were observed in 1979. In 1980, most movements across territorial boundaries (7 out of 11) occurred on rainy days (Binomial test, P = .040). If we exclude the 2 movements across boundaries made by 2 males which were attracted by a female apparently in oestrous, then only 2 territorial boundary crossings occurred on days without rain, rendering this result even more significant (Binomial test, P = .009).

Interactions

The 9 movements across territorial boundaries, excluding the 2 movements related to reproduction resulted in 5 interactions between the intruders and the owners of the territory. All 5 defenses occurred on rainy days (Binomial test, P = .004).

The interactions between the intruders and the owners of the territory were short and ended without any physical damage to either of the opponents. In each case, the owner was seen lying in wait for the intruder at the entrance of a burrow or within a dense patch of vegetation near the edge of the territory, and the defender jumped at the intruder as the latter passed in front of it. These brief attacks were sufficient to cause the intruder to return to its own territory.

Reproduction

Four matings were observed and none occurred on rainy days. Two of these matings involved only 1 male and 1 female. During the 2 other matings, a second male was seen entering the territory and getting involved in the courtship which lasted more than 1 hour. The females seemed to entice the males into fighting by bringing any pursuing male close to the other male at the risk of being bitten herself. The attacks between males were rough and, in one case, the intruder had a forelimb cut open. In all instances, the males living within the territory of the female copulated with her.

During the courtship, it was possible for an observer to approach or be approached by a muskrat within a meter or 2. The animals were not disturbed by our presence. Hares (Lepus americanus) and chipmunks (Tamias striatus) react in a similar fashion during courtship (Bider 1968). This suggests that predation risks could be relatively high at these moments.

Diurnal feeding

Because the feeding habits of the muskrat are too complex (Errington 1941) and the exact number of plants eaten outside or transported inside their burrows could not be counted exactly, the amount of food brought to the den could not be related to the time spent outside feeding. Therefore, 2 separate analyses were carried out, one on transportation of food, the other on the time spent outside feeding. No attempt was made to separate the data into block A and B because the number of transportations and the time spent feeding outside per 4 hours was too low and the analysis of block A alone, with only 24 periods of observations, would be meaningless.

During 1979 and 1980, some plant material was carried to burrows on 113 occasions. The muskrats did not transport food more often on rainy days than rainless days (Mann-Whitney U test, $P > .05$). However, not all of these plants were consumed. On 6 occasions, an adult carried dry plants to its main burrow. We opened 3 burrows and some dry and green vegetation was found on the floor of all 3 dens.

On the average, during rainy and non-rainy days, the adults were seen feeding for 1.7 mn (median: 0 mn, range: 0-42 mn) and for 1.8 mn (median: 0 mn, range: 0-48 mn) respectively. There was no difference observed in the time spent feeding outside of dens between the 2 types of days (Mann-Whitney U test, $P > .05$).

The distance between the locations where the muskrats would feed for more than 30 seconds or where they cut some plants to be brought to burrows and their main den was tabulated against the weather (Fig. 2). The muskrats fed farther from their main den at the periphery of their territories on rainy days (Chi-square test, $\chi^2 = 14.99$, df = 2, $P < .001$). When not repelled by another muskrat, some individuals fed within their neighbor's territory.

Changes in den sites

Muskrats use several burrows of various types and functions in their territory, 1 of which is the main den where they live most of the time (Earhart 1969). A change of main den site was noted whenever a muskrat was radio-located for at least 4 consecutive days in a burrow and relocated for at least another 4 days in a different den. Furthermore, when any change in main den site was noted, the individual was relocalized at night time. This ensured that the individual had not moved to a feeding den when localized earlier in the day.

One such change in main den site was a replacement of a dead male by another male on the following rainy day. Another 2 transfers were made by 2 females, 1 of which left a litter to give birth to an additional litter in another burrow. The reason for this change is unknown, since the first litter and a male lived at the initial den for the rest of the season. No external signs of damage to the burrows was seen after any of these transfers. Finally, immature individuals changed den sites and moved towards the edges of the parental territory on 3 occasions. The replacement of dead male, and 4 out of 5 transfers within the same territory, occurred on rainy days (Binomial test, $P = .031$).

Nocturnal observations

To determine whether muskrats are more active away from den sites during diurnal or nocturnal hours, the rate at which muskrats crossed the limits of the area under nocturnal observations was calculated. Independent of the weather, the muskrat crossed those limits more often during the evening than the afternoon (Chi-square test, df = 1, rainy days, $\chi^2 = 31.28$, $P < .001$ and days without rain, $\chi^2 = 44.51$, $P < .001$, Table III).

Most nocturnal territorial boundary crossings (9 out of 11) occurred when some precipitation fell during the day or night (Binomial test, $P = .007$). Five of these movements ended by an interaction between 2 individuals and, in each case, the intruder was repelled. All 5 defenses took place on rainy days (Binomial test, $P = .011$).

Preceding the nocturnal hours of observation, a 4 hour period of observation was taken. During these corresponding diurnal periods, only 1 movement across a territorial boundary occurred and no interaction was noted. When nocturnal and diurnal data were compared, the muskrats crossed the territorial boundaries more often (Binomial test, $P < .001$) and defended their territory mostly at night (Binomial test, $P = .014$).

If we cumulate the territorial crossings, except those related to reproduction, and the interactions observed during all diurnal and nocturnal hours of observation, intruders were attacked more often during rainy days than any other time (Fisher's exact probability test, $P = .04$). In other words, territory owners had to be at the edges of their territories on rainy days ready to repel any strangers. This is why 10 out of 16 territorial crossings were followed by an attack during rainy days, but no defense activity was noted during the 4 territorial crossings occurring on days without rain. Therefore, the owners of the territories spent more time and energy to defend their territories on rainy days.

Lac Carré sand-tracking

Dispersal is a journey that a small mammal undertakes away from its natal site (Gaines and McClenaghan 1980). If, as hypothesized, the kinds of differences in activity seen during the day are more pronounced at night, then most dispersals should occur during rainy nights. To test this, data from Lac Carré sand-transects were compiled and 10 muskrat crossings were recorded over the 16 year period. Two crossings were noted during the month of June, 7 in August and 1 in September. Even if we discard this latter observation because sand-tracking data of September were not available for most years, most crossings occurred after 1 August (Binomial test, P = .0021). Since these crossings occurred far (>300 m) from any possible muskrat territory, the individuals involved were probably dispersers. They were travelling during the seasonal population peak, after the second litter had become active (Stewart and Bider 1974), and were possibly forced by population pressure to disperse. This concurs with data from Central Iowa, where the fall dispersal starts in August (Errington 1963).

With the exception of 1 individual, these dispersers travelled at night (Binomial test, P = .011). Finally, 7 of these crossings occurred during rainy days (Binomial test, P = .090). Even if these latter results are not significant at the .05 level, they strongly suggest that muskrat fall dispersal occurs on rainy nights.

Mirabel sand-transects

At Mirabel, 175 muskrat crossings occurred in a 154 day period which included 66 rainy days. Between 15 June and 17 June, a family of muskrats moved back and forth between their den in a drying spring pond and a ditch where they re-established themselves (Bider et al. 1976). The burst of 67 crossings on the adjacent sand-transect began on a day without rain, and continued at a regular pace throughout the period. These movements were considered as movements related to an emergency (i.e. drought), not as foraging or exploration movements.

The transects were located in fields where muskrats fed (Bider et al. 1976). They foraged or explored away from ditches on rainy days. 52 of 81 crossings on the first transect (Chi-square test, df = 1, $\chi^2 = 16.64$, $p < .001$) and 25 out of 28 crossings on the other sand-transects (Chi-square test, df = 1, $\chi^2 = 24.65$, $P < .001$) occurred on rainy days.

When the time of occurrence of the activity away from ditches was compiled, it was found that 93% of the activity occurred between 2100 h and 0400 h, with a peak at 2300 h (Fig. 3). This distribution of activity coincides with the daily decline in activity of the ditch-dwelling muskrats (Stewart and Bider 1977).

DISCUSSION

Selection pressure should act such that small mammals increase the benefits and minimize the costs of foraging (Krebs 1978; Krebs et al. 1981). Although small mammals need to feed on a daily basis (Bourlières 1975), they should not go too far from their den because the cost of travelling will surpass the immediate benefits of feeding (Orians and

Pearson 1979). On the other hand, if small mammals concentrate their feeding efforts around a den site, they can easily deplete their food supply. Therefore, herbivores need to occasionally forage at the periphery of their territories and look for and utilize new food patches.

Predation is one of the major forces of selection in small mammals (Errington 1946; Vaughan 1972) and the risk of being preyed upon increases when away from den sites or when travelling through unfamiliar areas (Ambrose 1972; Metzgar 1969). Small mammals should not only assess new patches of food during reduced predation pressure as suggested by Krebs et al. (1981) but they should be most active and carry out all functions away from den sites during reduced predation. If rain and darkness reduce the efficiency of predators (Bramwell 1980; Vickery and Bider 1981), then muskrats should show increased activity away from den sites during days with rain and at night. At Mirabel, muskrats fed in fields away from ditches at night, especially during rainy days. We found that there is a lengthening of movements and increased feeding away from den sites during rainy days.

Looking for new patches of food, searching for new or vacant territories, looking for new den sites, and searching for an eventual mate are all part of the muskrat's exploration process (Dewsbury 1978). We observed that muskrats changed den sites on rainy days and Stewart and Bider (1977) noted that vacant territories were visited on rainy days. Olsen (1959) suggested that muskrats look for eventual mates on rainy days, but this action cannot be completely separated from the search for a new territory because males look for territories which overlap those of females or at least are adjacent to them. Sprugel (1951) noted that spring dispersal is initiated by a warm rainy night. Our data from Lac

Carré indicate that fall dispersals occur during rainy nights. Thus, the available evidence indicates that exploration and dispersal are triggered by rainfall. Since these exploratory activities are infrequent when compared to foraging, we suggest that they occur concurrently with foraging and are extensions of foraging behavior away from den sites during rain and darkness.

The synchronous heightened level of muskrat's activity away from den sites, usually at the edges of the territories, resulted in more contacts between muskrats and led to more territorial defense during rainy days. Due to the low predation pressure during rain, the lack of awareness of predators by the muskrat during combat does not negate the benefits of defending or trying to gain part of a territory.

Rare highly beneficial activities did not necessarily seem influenced by rain. Two such events are matings and movements related to an emergency. Mating activity and copulation observed were not influenced by rain. Based on Sprugel's (1951) observations and his own data, Olsen (1959) suggested that the first matings of the season are triggered by rain and warm temperatures and within a few days of parturition, regardless of weather, females mate again. These results are consistent with our data which did not include initial matings of the year. A female produces approximately 5 litters in her life (Stewart and Bider 1974). She should not postpone copulation to the next rain at the risk of reducing her reproductive output, but she may gain some benefits by waiting for the dispersal to mate for the first time of the year (Olsen 1959). Since dispersal occurs on rainy days, so should the initial breeding.

Drought, an unpredictable event, can force muskrats to move. At Mirabel, muskrats in the process of abandoning a territory moved continuously between a den site and a ditch and these movements started under clear conditions. Obviously, they could not wait for a rainy day to undertake these movements.

Behavioral traits related to rain have probably evolved in other nocturnal small mammals. Using feeding stations, at different places in the Lac Carré forest, Vickery (1976) found that the Gapper's red-backed vole (Chlethrionomys gapperi) and the woodland jumping mouse (Napaeozapus insignis) utilize new areas and consume more of their preferred food at distant sites on rainy nights. A possible explanation would be that these rodents, like muskrats, exploit their favored resources and explore under safer conditions. Many other nocturnal rodents and soricides respond to a greater degree or more uniformly to the rain (Bider 1968; Bramwell 1980; Doucet and Bider 1969, 1974; Mystkowska and Sidorowicz 1961; Pearson 1960; Sidorowicz 1960; Vickery and Bider 1978, 1981). However, the behavioral traits which evolve under the influence of rain may differ between species.

We conclude that foraging activity far from den sites of muskrats and probably other small mammals during rainy nights is a consequence of differential predation pressure between rainy and non-rainy periods. This selection for foraging away from den sites results in increased exploration and dispersal activities under rainy conditions. Finally, as a consequence of the pressure of sharing common resources and high probability of contact during rain, muskrats have evolved aggressive and territorial behavior relatively free from predation pressure. To support this hypothesis, one should expect that the activity, or at least the efficiency of the predators, would be reduced during and possibly after rainfall. This hypothesis is discussed in Chapter 3.

CHAPTER 3

SELECTIVE PRESSURE OF AVIAN AND MAMMALIAN PREDATORS ON THE ACTIVITY OF SMALL MAMMALS DURING NON-RAINY PERIODS*

* For submission to Ecology

As suggested in the second chapter and by other investigators (Bramwell 1980; Vickery and Bider 1981), an increased level of activity during rainy days may have evolved in small mammals in response to a differential predatory pressure between rainy and non-rainy periods. To support this hypothesis, the behavior of 5 mammalian and avian predators was observed. It was determined whether they were more or less active during rainy periods. The response of small mammals to a change of predation pressure during rainfall is discussed.

INTRODUCTION

Several authors have reported that nocturnal small mammals are more active during rain (Bider 1968; Bramwell 1980; Doucet and Bider 1969, 1974; Drickamer and Capone 1977; Gentry _et al_. 1966; Gentry and Odum 1957; Getz 1968; Mystkowska and Sidorowicz 1961; Pearson 1960; Sidorowicz 1960; Stewart and Bider 1977; Vickery and Bider 1978, 1981). In a recent study (Chapter 2), we concluded that the most important effect of rain on the behavior of the muskrat was an increased utilization of the edges of territories and of unfamiliar areas. Muskrats foraged farther from den sites, crossed their territorial boundaries, defended their territories, explored and dispersed mostly on rainy days. Other small mammals such as the woodland jumping mouse (Thibault 1969), the deer mouse (_Peromyscus maniculatus_) and the Gapper's red-backed vole (Vickery 1978; Vickery and Bider 1981) moved through new areas during precipitation.

Since the risks of being preyed upon are greater in less familiar areas (Ambrose 1972; Metzgar 1969), it has been suggested that small mammals avoid moving through new areas during non-rainy periods, preferring to wait for the rainy, safer periods (Chapter 2; Bramwell 1980; Vickery and Bider 1981). If this is the case, then one would expect predators to be either less active or efficient during or just after rainfall, thus applying less predation pressure on prey species in rainy periods.

The literature on the influence of rain on the hunting activity of the avian and mammalian predators is sparse and incomplete. The black bear (<u>Ursus americanus</u>) (Garshelis and Pelton 1980), red fox (<u>Vulpes vulpes</u>) (Ables 1969), and feral cat (<u>Felis catus</u>) (Derenne 1976) are known to be less active during rainfall. Also, 3 species of harriers (<u>Circus</u> spp.) (Schipper 1979), the European Kestrels (<u>Falco tinnunculus</u>) (Cavé 1968) and the Eleonora's falcon (<u>F. eleonorae</u>) (Wink and Wink 1979) fly less during rainfall.

To test the hypothesis that small mammals have higher rates of activity, forage and explore areas away from their center of activity during rain because of reduced predation pressure, we investigated the activity of 2 avian predators: the marsh hawk (<u>Circus cyaneus</u>) and short-eared owl (<u>Asio flammeus</u>) and of 3 mammalian predators: the mink (<u>Mustela vison</u>), ermine (<u>M. erminea</u>) and feral cat.

METHODS

Raptors

The study site was in the parish of St. Joseph de Soulanges (45° 20'N, 74°14'W), Soulanges-Vaudreuil County, 15 km west of the Island of Montreal. The area consisted of agricultural lands, intermingled with newly abandoned fields and small forests. It was located within the territory of a family of marsh hawks (1 male, 1 female, plus 4 immatures) and a family of short-eared owls (1 male, 1 female and 3 immatures). Occasional marsh hawks came from surrounding territories, but most of the time they were driven out of the area. The marsh hawks roosted in a temporary marsh located 1.0 km north of the study area. The roosting sites of the short-eared owls changed from time to time.

In 1980, between 11 August and 22 October, 51 periods of 4 consecutive hours of observation were recorded. All observations ended half an hour after sunset. The observations were made from 2 towers (3.5 m high) and a bridge. Every 5 minutes, a specific area was scanned. The limits of the areas were set up such that any raptors could be seen even when it rained. Together, the 3 areas comprised 1.82 km^2. Using binoculars, the number, the activity and the location of each marsh hawk and short-eared owl within the scanning area were recorded. The activity of the individuals was categorized as: (1) hunting with intent, if it was flying and searching for food; (2) flying for relocation if it was flying and not searching for food; (3) and perching if it was perched on the ground, a post, or a tree, regardless if it was looking for food or not. Simultaneously, the weather was noted and classified according to precipitation: (1) not raining; (2) drizzling, if precipitation was less than one drop per square foot of water surface; (3) and raining if more than one drop per square foot of water surface.

Carnivora

The activity of the mammalian predators was studied at Lac Carré, Terrebonne County, Quebec, in the Laurentians, approximately 100 km northwest of Montreal. The topography, soil, climate and vegetation are described elsewhere (Bider 1968).

In 1964, a transect of fine sand, .65 m wide, 191.5 m long, covered with a polyethylene canopy was constructed. It ran through a field, an ecotone, and a sugar maple-birch forest with some balsam fir and white spruce. The tracks left by an animal on that sand-transect were identified, recorded and erased every even hour (e.g. 2000 h) for a period of 8 days followed by 8 other days when these tracks were read every odd hour (e.g. 1900 h) and so on. The sand-transect functioned from the beginning of June until 31 August, between 1964 and 1979 inclusive. After excluding the days when the sand-transect was washed out by a heavy rain, a total of 1444 days of tracking was available. In 1971, the mustelid tracks were not segregated into either mink or ermine, therefore these data were discarded.

The activity of the carnivores is measured in terms of number of "presences". A "presence" is counted whenever one or more crossings occurred within a 2 hour period, the time passed between 2 readings. Number of presences is a better index of carnivore activity than number of crossings because when actively hunting, carnivores occasionally cross the same area several times in less than 2 hours and may not come back to that specific place for a few days.

Before the tracks were read, rain was noted when more than a trace of water was found in the rain gauge. Since the time of rainfall is an important factor which influences the level of activity of several mammals (Bider 1968; Sidorowicz 1960), the days and presences were grouped into 8 categories according to the time of rainfall: days without rain, days with rain either during the morning (between 0400 and 1200), the afternoon (between 1200 and 2000), the night (between 2000 and 0400) or any combination of morning, afternoon or night periods.

To obtain the diel presence rhythm of the 3 carnivores studied, half a presence is given to each of the 2 hours preceding the reading, the total number of presences by hour is added and an histogram drawn. Since the units of measurement are frequencies, the Chi-square one sample test is applied in the analysis of the mammalian predator results (Siegel 1956).

RESULTS

Raptors

Marsh hawks

Marsh hawks were seen avoiding localized rainfall by moving or going to their roosting sites during widespread rainfall for the duration of the precipitation. To test if they avoided rainfall or stayed inactive during precipitation, the number of times an individual was seen perched or hunting and the number of scanning periods were grouped into 3 categories according to the precipitation and compared.

The marsh hawks were not seen hunting during rainfall (Chi-square test, $\chi^2 = 18.78$, df = 2, $P < .001$, Fig. 4). The number of times that hunting occurred during drizzle was lower than expected, however not significantly different when compared with non-rainy periods (Chi-square test, $\chi^2 = 1.60$, df = 1, $P > .05$). No perching occurred while rain fell (Chi-square test, $\chi^2 = 23.70$, df = 2, $P < .001$). The number of times the marsh hawks were perched did not differ between the drizzling and non-rainy periods (Chi-square test, $\chi^2 = .22$, df = 1, $P > .05$). Therefore, marsh hawks could not be hunting from a post during rainfall, but possibly during drizzle.

Since the marsh hawks hid while it rained, it should be expected that marsh hawks perch and hunt less on rainy than on rainless days. During the 4 hour blocks, the marsh hawks perched in groups and for periods lasting more than 5 minutes. The median number of perched individuals during rainy and non-rainy 4 hour blocks was 0, in both cases, and the range were respectively 0-45 (mean: 5.1) and 0-46 (mean: 5.8). There was no difference in those medians (Median test, χ^2 est. = .26, $P > .05$). The median number of times a marsh hawk was observed hunting during a time block was 3.0 (range: 0-23 and mean: 5.1) on days without rain and 4.0 (range: 0-8 and mean: 4.0) on rainy days. There was no difference between those medians (Median test, χ^2 est. = 0.34, $P > .05$).

Since rainfall did not usually last too long without interruption and the marsh hawks were inactive most of the day, they waited for non-rainy periods to hunt. Marsh hawks began to hunt a few minutes after the end of rain and increased their hunting activity above normal during the hour following rainfall (Chi-square test, $\chi^2 = 9.23$, df = 2, $P < .01$). Therefore, the daily intensity of hunting did not differ between days with or without rain. Marsh hawks were also noted to perch more during the hour preceding the rainfall (Chi-square test, $\chi^2 = 39.60$, df = 2, $P < .001$).

Between 31 May and 1 August, the marsh hawks were observed flying to the nest 43 times with prey. Three of these prey were unidentified, 6 were classified as frogs and 34 identified as small mammals (2 unidentified, 2 young muskrats and 30 meadow voles [Microtus pennsylvanicus]). 22 of 34 small mammals were captured on rainy days (Chi-square test, $\chi^2 = 5.28$, df = 1, $P < .05$), but not during periods of rainfall.

Short-eared owls

By 15 October, the short-eared owls under observation had presumably migrated. In the 45 4-hour blocks which were used for this analysis, owls appeared before sunset 3 times. On 4 occasions, just as the rain started, a short-eared owl was seen flying off a tree down to a bush 15 m below, where it spent most of the day. Rain fell during the 3 daylight periods. However, the owls were never seen hunting during rain (Chi-square test, $\chi^2 = 17.77$, df = 1, $P < .001$, Fig. 5). The number of times they hunted during drizzle and non-rainy scans was not different (Binomial test, $P = .94$). During the half hour after sunset, the owls were seen hunting 39 times. They did not hunt during the 3 half hours when it rained (Binomial test, $P = .055$). The .05 level of significance is almost but not quite attained in this case, likely because of a lack of rainy periods during the half hour following sunset.

Before sunset, the short-eared owls were observed perching on 46 occasions, but never during rain (Chi-square test, $\chi^2 = 38.92$, df = 1, $P < .001$). There was no difference between the number of times an individual was seen perched during drizzle and non-rainy scans (Binomial test, $P = .34$). Since the owls are mostly crepuscular (Craighead and Craighead 1969), they were seen perched only 10 times after sunset. This value is too low to draw any conclusion, even though no perching was noted while it rained.

Carnivora

The diel presence rhythm of the ermine, mink and feral cat are similar. These mammalian predators are mostly nocturnal with respectively

65.6%, 69.3% and 81.8% of their daily visits occurring during night time, beginning at 2000 h and finishing around 0400 h (Fig. 6).

To determine if the number of presences per day of these carnivores is influenced by rainfall, the distribution of the number of days of sand-tracking classified according to the time of rainfall was compared to the number of presences in each of these types of days. No difference was located for either the feral cat ($\chi^2 = 6.14$, df = 7, $P > .05$, Fig. 7), the ermine ($\chi^2 = 12.50$, df = 7, $P > .05$) or the mink ($\chi^2 = 10.93$, df = 7, $P > .05$). In other words, the presence of these carnivores on a daily basis is not influenced by the occurrence of rain.

Since these carnivores are nocturnal, a nocturnal rain is more likely to influence them. The distributions of the number of presences and types of days when grouped into days without rain, days with nocturnal rain, and days with only diurnal rain are not different from each other, for either the mink ($\chi^2 = 4.08$, df = 2, $P > .05$), the ermine ($\chi^2 = .80$, df = 2, $P > .05$) or the feral cat ($\chi^2 = .72$, df = 2, $P > .05$).

DISCUSSION

Other recent studies have shown that raptors do not hunt during rain. In the Netherlands, 3 species of harriers, including marsh hawks, do not hunt during substantial rain (Schipper 1979). The European Kestrel (Cavé 1968) and the Eleonora's falcon (Wink and Wink 1979) fly less in the rain. Harriers (Schipper 1979), Harpy eagles (<u>Harpia harpyia</u>) (Rettig 1978), and gyrfalcons (<u>F. rusticolus</u>) (Jenkins 1978) must protect their nestlings from rainfall, otherwise they may die. Such behavior explains why Craighead and Craighead (1969) did not see any marsh hawks on their surveys during rainfall.

During daylight observation, the feral cat of Kerguelen is seen less often under rainy conditions (Derenne 1976). Wild minks change their behavior upon the occurrence of a heavy rainfall (Burgess 1978; Gerell 1969), but the effect of light or normal rain on the behavior of this species is not known. The activity of the red fox in summer and spring at nighttime is negatively influenced by the amount of precipitation, but not during daytime or in fall (Ables 1969). The black bear is less active during rainfall, and its activity increases above normal within 30 minutes after the end of the precipitation (Garshelis and Pelton 1980). Using Lac Carré tracking data, we were unable to note a change in the level of daily presences of the ermine, mink or feral cat in relation to the time of rainfall. Since the decrease of activity during precipitation seems to be a general characteristic of carnivores, it is thought to be temporary and synchronized with rainfall. The daily level of activity of carnivores is not reduced during rainy days because the periods of rainfall rarely last too long, and the carnivores wait for periods of non-rain to become active, as in the black bear (Garshelis and Pelton 1980).

Predation and small mammal activity

If increased nocturnal small mammal activity during rainfall evolved because of reduced predation pressure, then two assumptions have to be met: the predators must be as nocturnal as their prey and the increase and subsequent decrease of activity of the small mammals should be synchronized with the beginning and ending of the rain when the predators decrease and subsequently increase their hunting activity.

Most small mammals influenced by rain are nocturnal but their activity is not restricted to nighttime (Bider 1968; Doucet and Bider 1974; Mystkowska and Sidorowicz 1961; Pearson 1969; Sidorowicz 1960; Stewart and Bider 1977). To meet the first assumption, a large proportion of the predation pressure should occur at night. There are no specific data on nocturnal raptor activity because most raptors are studied from blinds during daylight hours. It appears that cessation of hunting during rainfall is a general characteristic of diurnal raptors and it is thought to be equally valid for nocturnal raptors. Short-eared owls can hunt either during the day or night (pers. obs.) even though they are mostly crepuscular (Craighead and Craighead 1969). This species did not hunt during rainfall.

With few exceptions, cat, mink, and ermine are nocturnal. In 2 cases, the least weasel (M. nivalis) (King 1975) and ermine (Bracher 1981) were found to be diurnal. The diurnal habits of the individuals observed by King (1975) were probably an adaptation to the woodlands of England. In that area, more diurnal prey were available and competition with the tawny owl (Strix aluco) was intense at night (King 1980). Bracher (1981) found that ermine activity became predominantly diurnal when passerine activity increased on the forest floor following a forest insect control program. Carnivores change their diel activity rhythm depending on different factors, including food pattern (Ables 1969; Eguchi and Nakazona 1980; Gerell 1980). Presumably, they select the best hunting time of the day and the most beneficial prey (Krebs 1978).

Therefore, a constant predation pressure exists on the nocturnal small mammals.

With the available literature, we can verify the second assumption. The time of occurrence of rain is important to determine if an individual will react to it (Bider 1968; Mystowska and Sidorowicz 1961). When the behavior of the meadow vole and woodland jumping mouse is influenced by the rain, their activity increases rapidly as the rainfall starts and decreases afterwards (Bider 1968). When the activity of the masked shrew (Sorex cinereus), muskrat and other rodents and insectivores is influenced by rain, the heightened level of activity occurs during the same part of the day as ~~the~~ precipitation does (Mystkowska and Sidorowicz 1961; Sidorowicz 1960; Stewart and Bider 1977; Vickery and Bider 1981).

Even if predation pressure is constant on days without rain, there are some activities which small mammals have to carry out daily, such as feeding (Bourlières 1975), others such as any exploratory activities can be postponed. Since the risk of being preyed upon is greater when small mammals travel through unfamiliar areas (Ambrose 1972; Metzgar 1967), they should move into these areas when predation pressure is reduced consequently during rainfall. The foraging rate of muskrats does not change in response to rain but they forage farther on rainy days (Chapter 2), and most of their exploratory activities occur on rainy days (Chapter 2). The woodland jumping mouse moves away from stream beds as precipitation starts (Thibault 1969). The deer mouse and the Gapper's red-backed vole utilize new areas during rain (Vickery 1976).

We found that more meadow voles are brought to the nest by marsh hawks on rainy days. Bider (1968) showed that activity of the meadow vole declines gradually after the end of precipitation. We presume that meadow voles act as other nocturnal small mammals and travel farther during rain. Some probably get stranded far from their center of activity and secure routes when the rain ends and become more vulnerable. Since marsh hawks start to hunt actively as precipitation ends, they need not even increase their hunting pressure to capture more prey since the latter are more available.

We conclude that the lack of predation pressure during precipitation caused the evolution of heightened activity and exploration away from den sites in several small mammals of the north temperate regions during rain.

SUMMARY AND CONCLUSIONS

In summary, two techniques were tried on muskrats. Freeze-branding was unsuccessful. Radio-telemetry can be used on muskrats, but the range of the signal is limited.

The study of muskrat behavior revealed that they travel, forage farther from their burrows, disperse and explore more during the night-time hours of rainy days. Consequently, more territorial boundary crossings and territorial defenses were noted during those days. However, not all aspects of muskrat behavior are influenced by rainfall. Matings and movements related to a drought are two examples of such behaviors.

As hypothesized, the activity of mammalian and avian predators decreased during periods of rainfall and a similar decrease in the activity of mammalian predators during rainy days is documented. This reduction in predation pressure coincided with an increase in small mammal activity. Therefore, small mammals have evolved an increased level of activity under a differential predation pressure between rainy and non-rainy periods. To lend further support to this theory, additional studies are required, especially those dealing with the influence of rain on other avian and mammalian predators, and on the different foraging, exploring and dispersing strategies of other species of nocturnal small mammals.

CLAIM TO ORIGINALITY

1 The utilization of freeze-branding and radio-pack implantation in muskrats had never before been described.

2 The systematic visual observation of the behavior of the ditch-dwelling muskrat under natural conditions is original.

3 The visual observation under natural conditions of the behavior of a small mammal in relation to rainfall was studied for the first time.

4 It is clearly demonstrated for the first time that muskrats feed farther from their main den, disperse and explore more on rainy days.

5 It was established for the first time that some aspects of the behavior of nocturnal small mammals, including matings and movements related to an emergency (i.e. drought), are not influenced by rainfall.

6 The study of the influence of rain on mammalian and avian predators, as a group, is original.

7 It is shown for the first time that increased nocturnal small mammal activity can be related to decreased predatory pressure.

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Figure 1. Distribution of the lengths of the displacement made by muskrat during rainy and non-rainy days. The figures in brackets represent the number of movements that occurred in each length class.

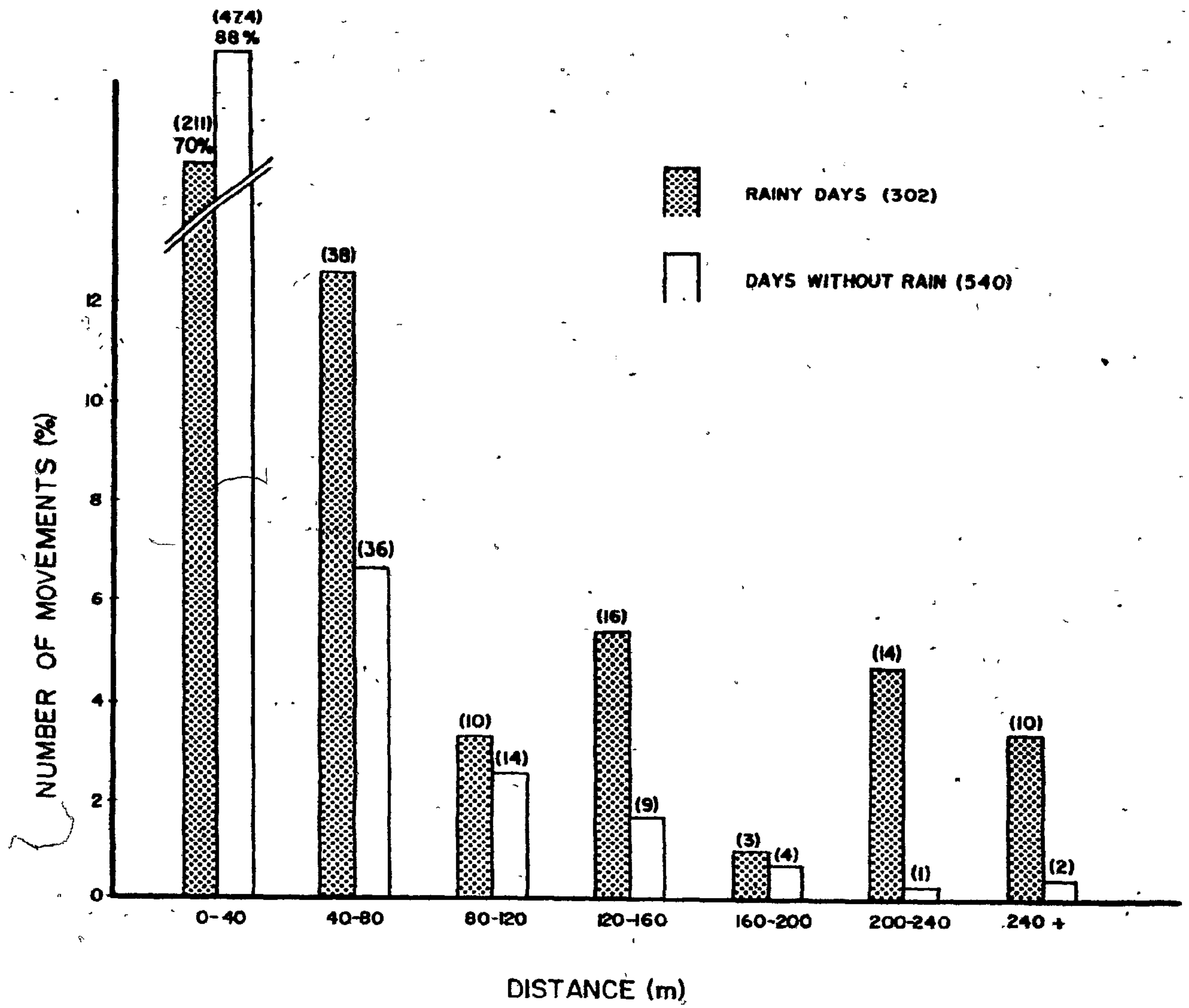

RAINY DAYS (302)
DAYS WITHOUT RAIN (540)
NUMBER OF MOVEMENTS (%)
0
2
4
6
8
10
12
(211)
70%
(474)
88%
(38)
(36)
(10)
(14)
(16)
(9)
(3)
(4)
(14)
(1)
(10)
(2)
0-40
40-80
80-120
120-160
160-200
200-240
240 +
DISTANCE (m)

Figure 2. Distribution of the number of times muskrats were seen eating for more than 30 seconds or cutting vegetation at different distances from den sites on days with and without rain. The figures in brackets represent the number of days in each category. The 80-120 and 120+ classes were grouped together in the statistical analysis since the expected values were smaller than 5.0.

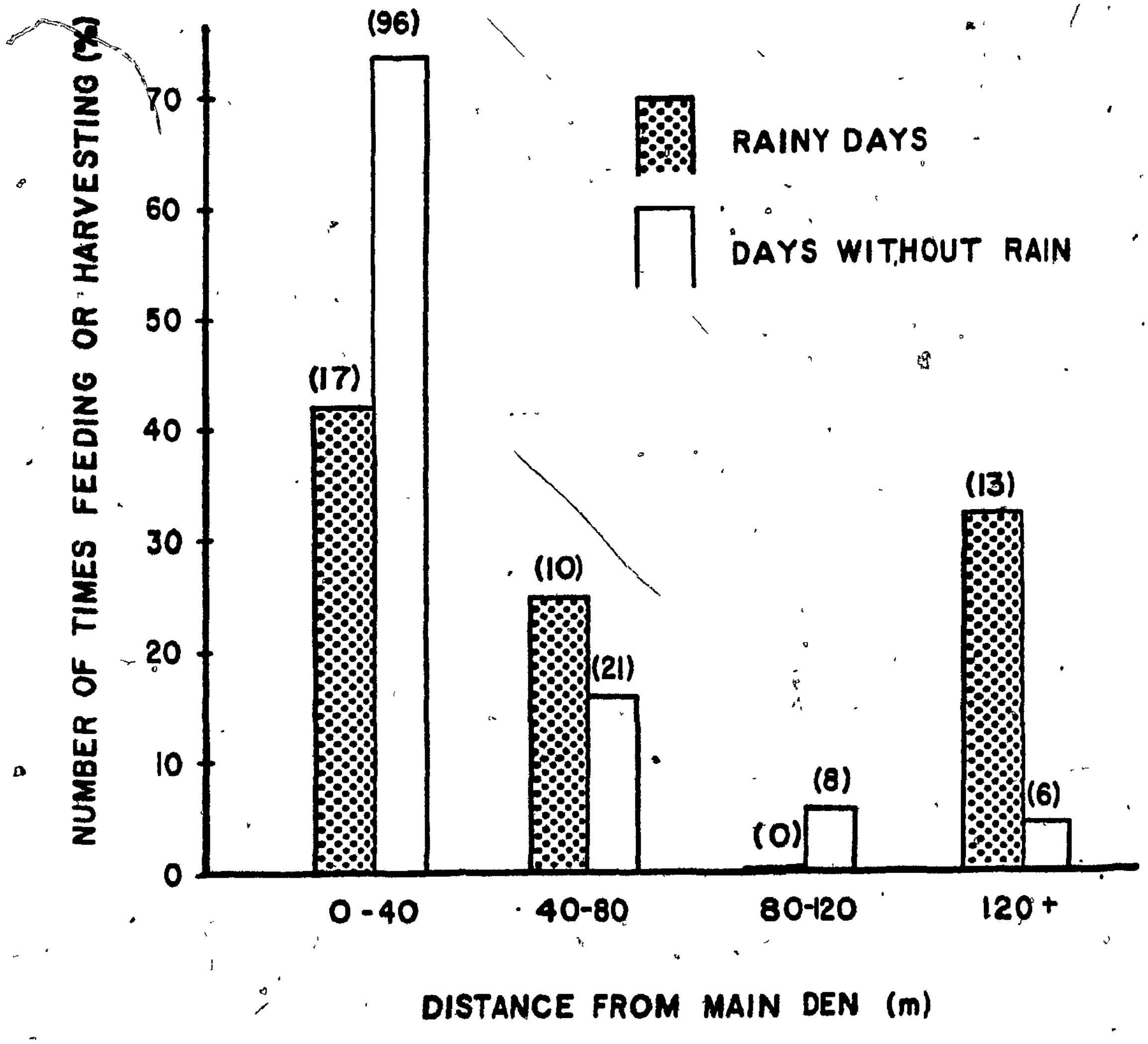

NUMBER OF TIMES FEEDING OR HARVESTING (%)
0
10
20
30
40
50
60
70
(96)
(17)
(10)
(21)
(0)
(8)
(13)
(6)
RAINY DAYS
DAYS WITHOUT RAIN
0-40
40-80
80-120
120+
DISTANCE FROM MAIN DEN (m)

Figure 3. Time of exploration activity based on Mirabel tracking data taken at least 60 meters away from ditches.

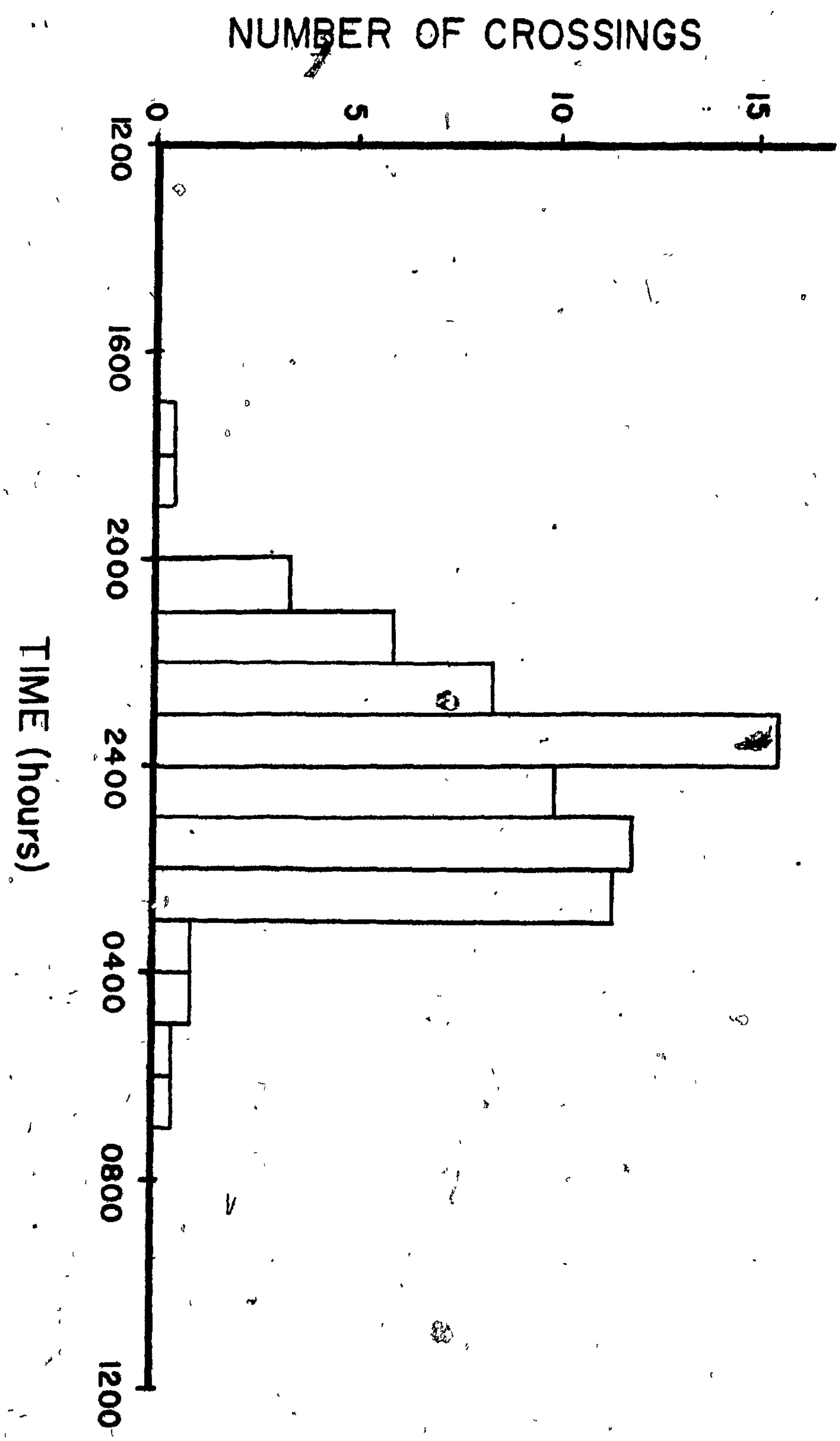
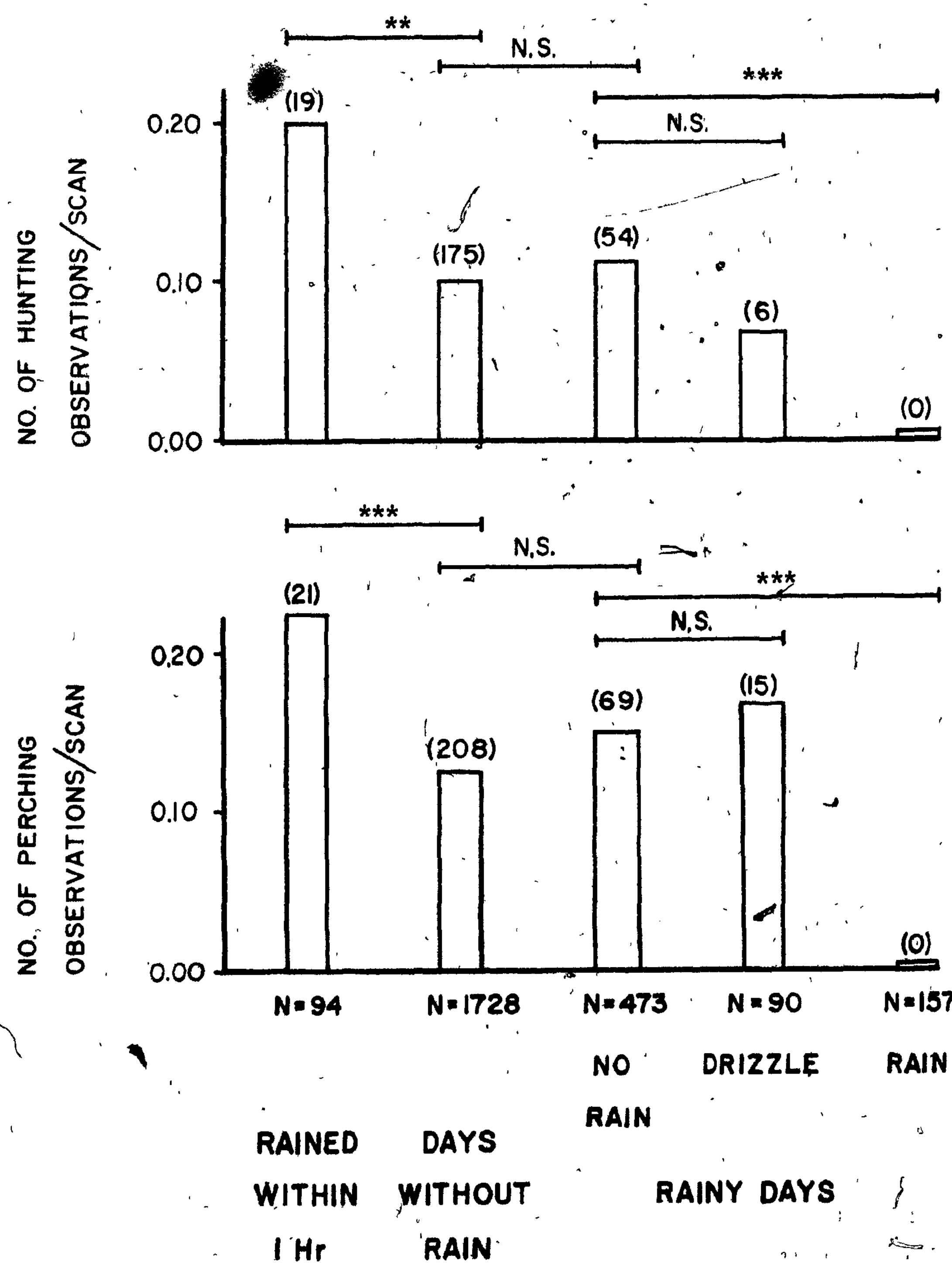

NUMBER OF CROSSINGS
0
5
10
15
1200
1600
2000
2400
0400
0800
1200
TIME (hours)

Figure 4. Distribution of the number of marsh hawk hunting and perching observations during days without rain, the non-rainy, drizzling and rainy scans of the rainy days, and the hour preceding rainfall. The numbers in parentheses are the number of hunting or perching observations. N represents the number of scans for each category.

All tests performed are Chi-square one-sample tests.

P > .05 = N.S., P < .01 = **, P < .001 = ***.

MARSH HAWK



**
N.S.
***
N.S.
(19)
(175)
(54)
(6)
(0)
0.20
0.10
0.00
NO. OF HUNTING OBSERVATIONS/SCAN
***
N.S.
***
N.S.
(21)
(208)
(69)
(15)
(0)
0.20
0.10
0.00
NO. OF PERCHING OBSERVATIONS/SCAN
N=94
N=1728
N=473
N=90
N=157
NO RAIN
DRIZZLE
RAIN
RAINED WITHIN 1 Hr
DAYS WITHOUT RAIN
RAINY DAYS

Figure 5. Distribution of the number of short-eared owl hunting and perching observations during non-rainy, drizzling and normal rain scans of the 3 4-hour blocks when the owls were seen during daytime. The numbers in parentheses are the number of hunting and perching observations. N represents the number of scans for each type scan.

$P > .05$ = N.S., $P < .001$ = ***

N.B. For the Chi-square test, the non-rainy and drizzling scans were grouped together, since the expected value of the drizzle class would have been smaller than 5.0 (Siegel 1956).

SHORT-EARED OWL

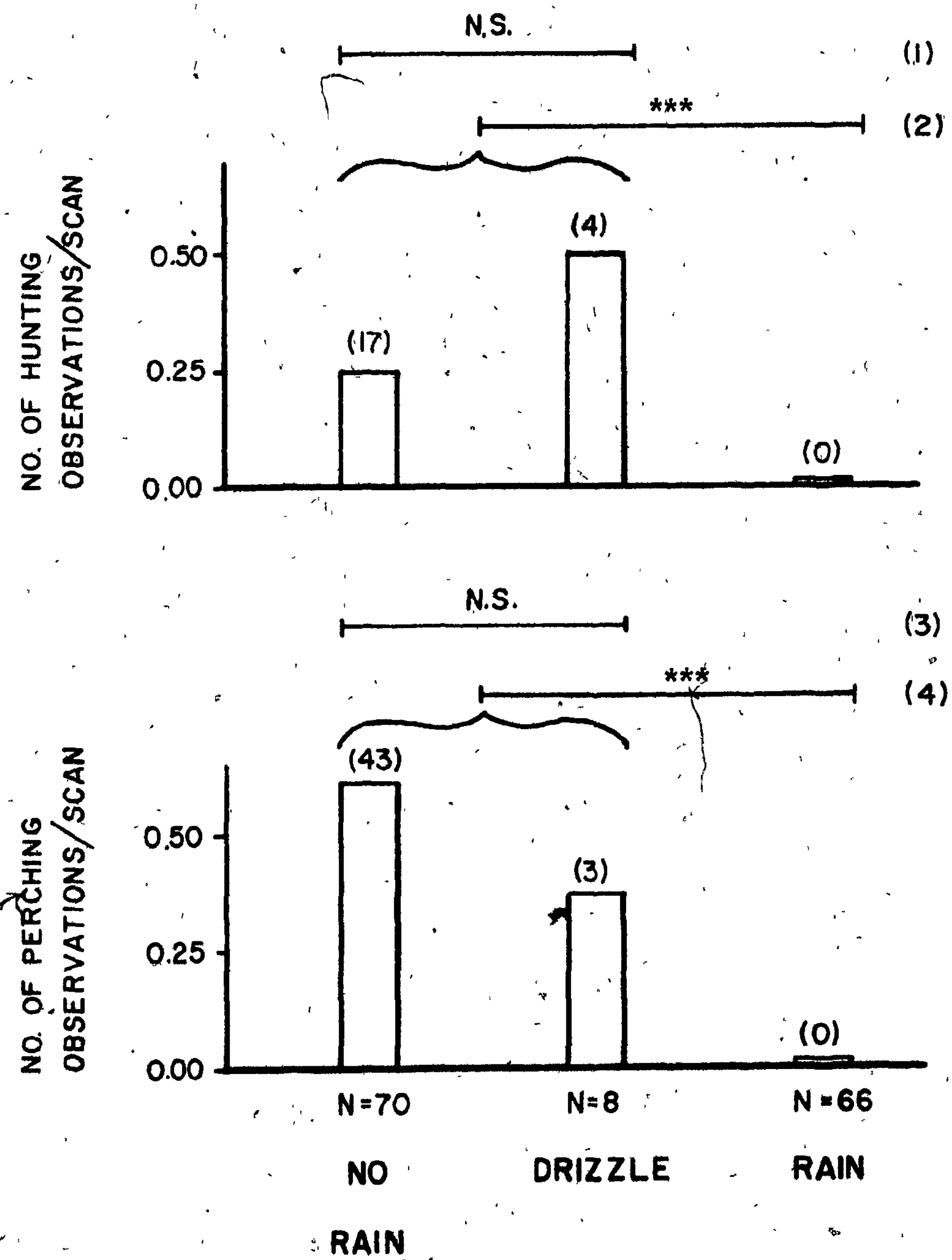


Figure 6. The diel activity of the feral cat, ermine and mink.

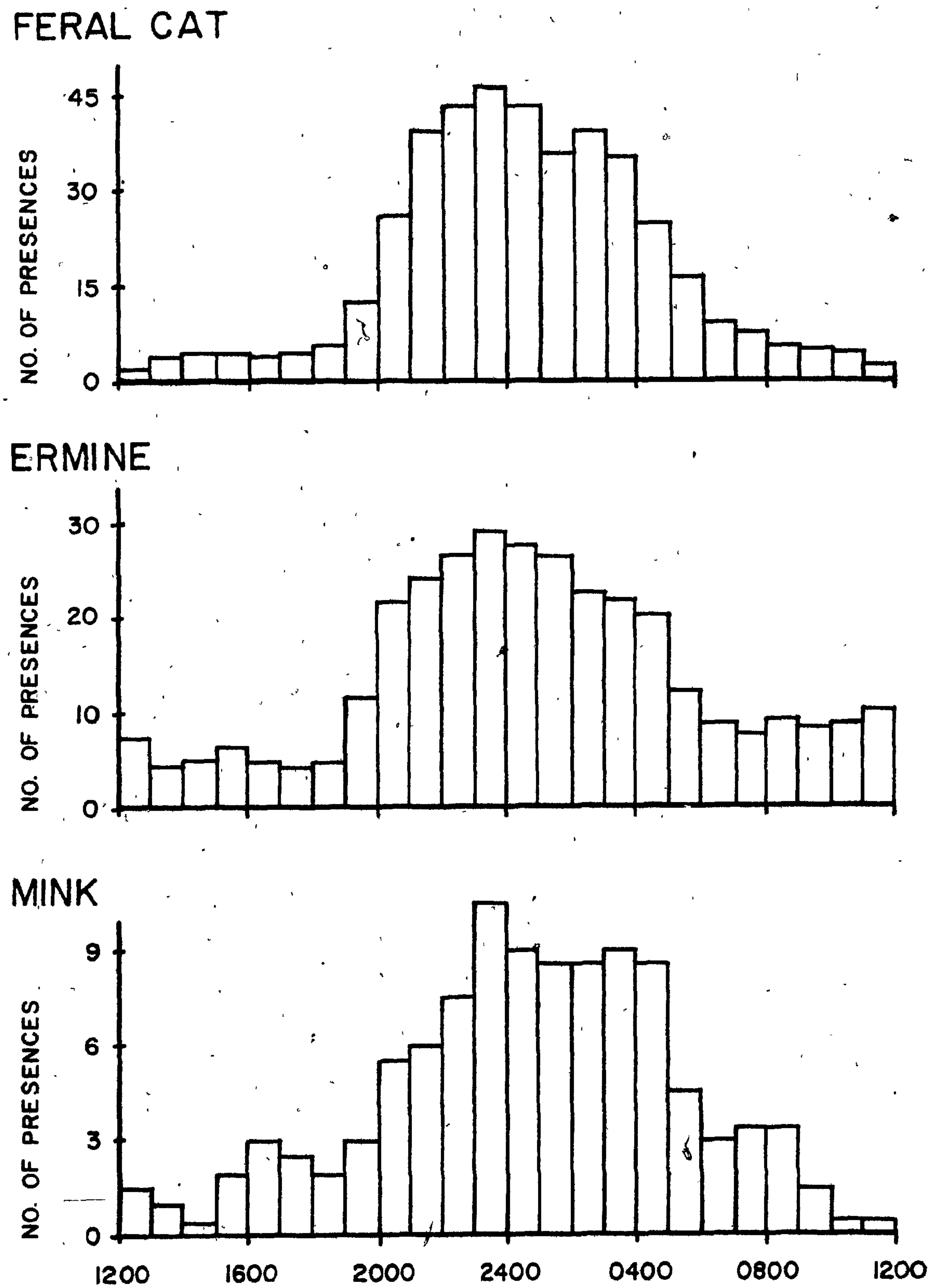

FERAL CAT
NO. OF PRESENCES
45
30
15
0
ERMINE
NO. OF PRESENCES
30
20
10
0
MINK
NO. OF PRESENCES
9
6
3
0
1200
1600
2000
2400
0400
0800
1200

Figure 7. Distributions of the number of presences of the feral cat, ermine and mink according to the time of occurrence of rainfall.

$P > .05 = N.S.$

All tests performed are Chi-square one-sample test.

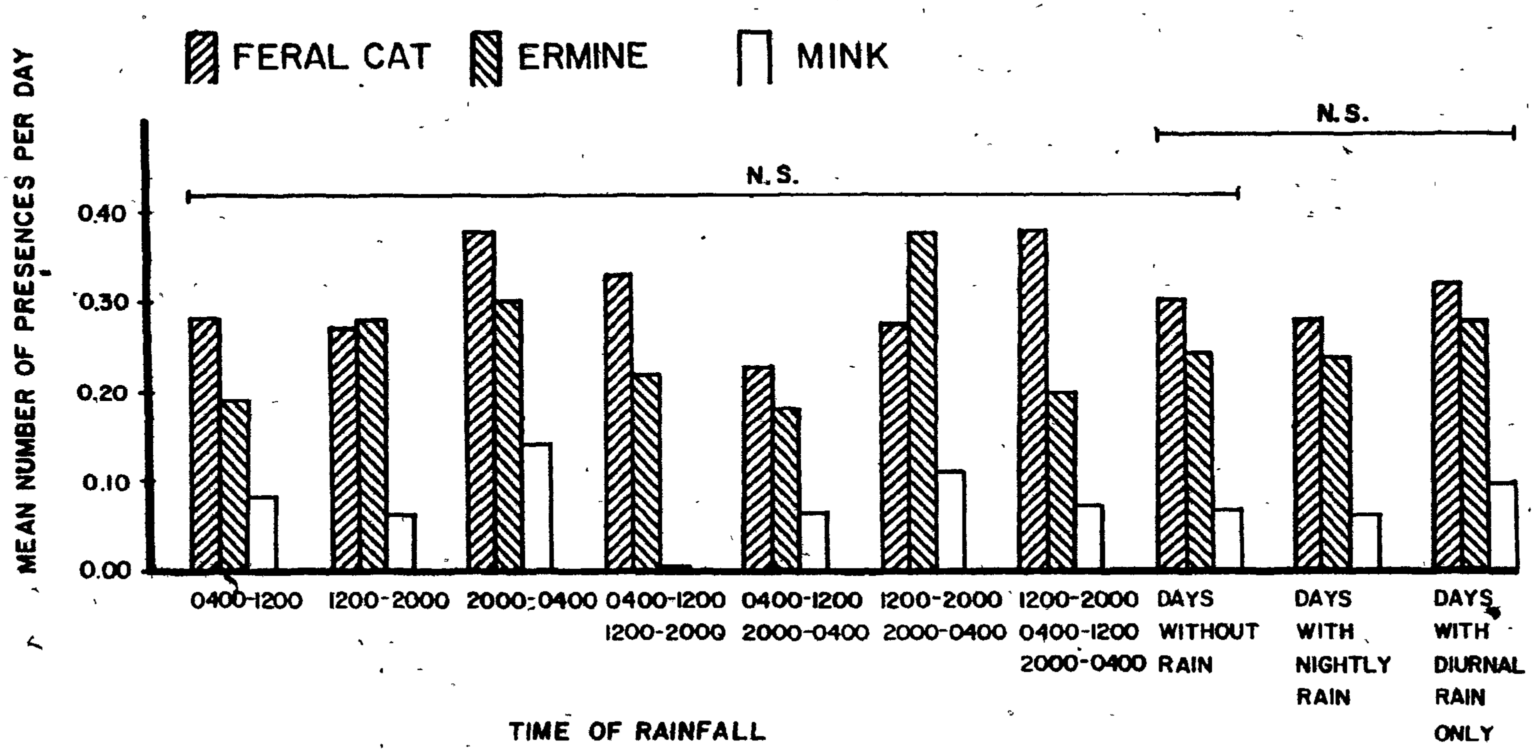

FERAL CAT
ERMINE
MINK
N.S.
N.S.
MEAN NUMBER OF PRESENCES PER DAY
0.40
0.30
0.20
0.10
0.00
0400-1200
1200-2000
2000-0400
0400-1200 1200-2000
0400-1200 2000-0400
1200-2000 2000-0400
1200-2000 0400-1200 2000-0400
DAYS WITHOUT RAIN
DAYS WITH NIGHTLY RAIN
DAYS WITH DIURNAL RAIN ONLY
TIME OF RAINFALL

Table I. Distance travelled in meters by muskrats per 4 hour block on rainy and non-rainy days.

		BLOCK A		BLOCK B	
		(inc. 6 hour observation periods)	(exc. 6 hour observation periods)	(inc. 6 hour observation periods)	(exc. 6 hour observation periods)
Rainy days	Median	47.5	150	60	60
	Mean	(104)	(135)	(177)	(194)
	Range	(0-450)	(0-270)	(0-1955)	(0-1955)
Days without rain	Median	0	0	0	0
	Mean	(7.17)	(11.18)	(95.34)	(114.72)
	Range	(0-60)	(0-60)	(0-1170)	(0-1170)
Probability		P = .003	P = .004	P = .003	P = .016

BLOCK A starts 5.5 hours before sunset and BLOCK B ends at night.

Mann-Whitney U tests were used to determine probability.

Table II. Number of movements travelled by muskrats per 4 hour block.

		BLOCK A		BLOCK B	
		(inc. 6 hour observation periods)	(exc. 6 hour observation periods)	(inc. 6 hour observation periods)	(exc. 6 hour observation periods)
Rainy days	No. of movements	66	54	244	238
	No. of hours	(64)	(28)	(260)	(224)
Days without rain	No. of movements	41	23	511	496
	No. of hours	(156)	(68)	(492)	(404)
Chi-square		$\chi^2 = 55.097$	$\chi^2 = 62.540$	$\chi^2 = 1.700$	$\chi^2 = 3.366$
test, df = 1		($P < .001$)	($P < .001$)	($P > .05$)	($P > .05$)

Table III. Difference between the number of diurnal and nocturnal sightings on rainy and non-rainy days.

	No. of sightings on the nocturnal observation area		Chi-square test
	Diurnal	Nocturnal	(df = 1)
Rainy days	9	41	$\chi^2 = 31.28$ $P < .001$
Days without rain	8	50	$\chi^2 = 44.51$ $P < .001$