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THE IMPACT OF HUMAN DISTURBANCE ON NEST PREDATION PATTERNS IN FRESHWATER MARSHES

by

Benoît Jobin

A thesis submitted to the Faculty of Graduate Studies and Research
in partial fulfillment of the requirements for the degree of
Master of Science.

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ABSTRACT

Although predation is the major factor responsible for nest losses in birds, predation patterns in marshes and adjacent uplands are poorly known. This study examined the factors affecting nest predation on marsh-nesting birds found in areas affected by different intensities of human disturbance (urban, agricultural, natural). Artificial nests simulating waterfowl and passerine nests were used for that purpose. The nests, located along transects running from the center of the marshes to the adjacent upland habitats, were set up in the months of May, June and July 1989 and 1990. Eggshell remains were used to identify the predators.

Predation was higher on passerine than on waterfowl nests and on nests located in upland habitats. Deep water prevented mammalian predators from foraging deep in the marsh. Predation rates in urban and natural areas were high while nests located in agricultural areas suffered lower predation. Nest camouflage was generally unimportant in reducing chances of predation. Mammals were responsible for most of the predation events. Differences in density and/or diversity of predators in urban, agricultural and natural areas were the main causes of different predation patterns observed in the three areas.

RÉSUMÉ

Bien que la prédation soit la principale cause d'échec chez les nids d'oiseaux, les facteurs causant la prédation des nids situés dans les marais ainsi que dans les terres hautes adjacentes sont peu connus. La présente étude identifie les facteurs pouvant causer la prédation des nids d'oiseaux nichant dans des marais situés dans des régions où l'activité humaine a altéré les habitats originaux (urbain, agricole, naturel). Des nids artificiels simulant ceux de passereaux et de sauvagine ont été utilisés à cette fin. Les nids, disposés le long de transects allant du centre des marais vers les terres hautes adjacentes, ont été soumis à la prédation pendant les mois de mai à juillet 1989 et 1990. Les prédateurs ont été identifiés grâce aux traces laissées près des nids.

La prédation était plus importante sur les nids de passereaux que sur ceux de sauvagine. Aussi, les nids situés dans les terres hautes étaient plus sujets à la prédation que ceux situés dans les marais. Les zones d'eau profonde entravaient les déplacements des mammifères assurant ainsi une meilleure protection contre la prédation. Les nids situés dans les régions urbaines et naturelles ont subi des taux de prédation similaires alors que ceux dans les régions agricoles étaient détruits à moindre degré. Le camouflage des nids ne procurait que peu d'avantages contre la prédation. Les mammifères étaient responsables de la majorité des cas de prédation. La densité et/ou la diversité des prédateurs habitant les régions urbaines, agricoles et naturelles influencent la prédation observée dans les trois régions .

INTRODUCTION

Many people view marshes as useless, but marsh habitats have great ecological importance. The primary productivity of marshes is one of the highest of all habitats. They are also natural filters where plants can take up nutrients and toxic substances from the water, leaving clean and unpolluted water behind. Water level regulation can be controlled by the action of marshes. Bank erosion is reduced by the vegetation in place. Several rare plant species can only be found in marshes and wildlife benefits greatly from them (Ontario Ministry of Natural Resources and Environment Canada, 1984; Mitsch and Gosselink, 1986; Moore et al., 1989).

Because the productivity of marshes is high, they play an important role in the ecology of surrounding ecosystems. Various animals rely on marshes for their survival and reproduction as shown by the high density and diversity of insects, amphibians, fish, birds, and mammals observed in these habitats (Weller, 1987). Several passerine and waterfowl bird species that nest in or near marshes can reach high breeding densities (Orians, 1980; Giroux, 1981). The birds rely on marshes for nesting, rearing and/or feeding sites crucial for their successful reproduction. However, environmental factors such as food (Fretwell and Lucas, 1969) and predation (Lack, 1968; Ricklefs, 1969) play a role in determining population density and distribution of individuals in space. Predation is, however, likely to play the most important role in the survival of adults and their progeny. Being highly mobile animals, birds can overcome a local food shortage by foraging in nearby areas. Some young may perish due to starvation but this partial reproductive loss is relatively less important than one resulting from predation where the whole brood or the breeding adult(s) is killed.

Predation is a major cause of nesting mortality in birds (Lack, 1954; Nice, 1957; Ricklefs, 1969; Talent et al., 1983; Sargeant et al., 1984; Picman et al., 1988). Avian biologists are always confronted with the problem of nest predation in their studies on the reproductive ecology of birds. The proportion of nests destroyed by predators is always of concern (Nice, 1957; Ricklefs, 1969) and predation may be a strong selective force shaping the reproductive behavior of birds (Wittenberger, 1976; Møller, 1987; Picman et al., 1988). The observer's presence causes a potential bias in any study of breeding birds. Some studies have shown that repeated nest visits increased the probability of failure to predation because of more frequent parental departures (Hammond and Forward, 1956; Salathé, 1987; Major, 1990), although other studies failed to demonstrate such effect (Gottfried and Thompson, 1978; Livezey, 1980; Galbraith, 1987). Such potential observer-induced biases can be controlled for by the use of artificial nests which can provide useful information on factors affecting nest destruction while eliminating the inevitable influence of the observer's presence at real nests.

Artificial nests have been widely used to study predation on both waterfowl and passerine nests. Nests were either built from dry grass (Andersson and Wiklund, 1978; Picman et al., 1988), from the actual vegetation found at the nest location (Rearden, 1951; Yahner and Wright, 1985), from metal wires (Yahner and Cypher, 1987), or old deserted nests were re-used (Martin, 1987; Møller, 1987; Major, 1990). The experimental eggs may come from quail (Martin, 1987; Small and Hunter, 1988) or chicken farms (Schranck, 1972; Picman, 1988; Sullivan and Dinsmore, 1990), pheasant nests (Jones and Hungerford, 1972) or may even be made from plasticine (Møller, 1987). Although this technique provides valuable information, many authors have suggested that artificial nests should be used with caution (Salathé, 1987; Willebrand and Marcström, 1988) because predation rates on artificial and natural nests may differ (Storaas, 1988; O'Reilly and Hannon, 1989). However, in contrast to these studies, several other studies showed predation rates on natural and experimental nests to be similar (Gottfried and Thompson, 1978; Major, 1990). In any case, special care should be taken when using artificial nests for predation studies.

To mimic natural predation as closely as possible, artificial nests need to be set up in the most natural way possible and repeated visits should be minimized. Vegetation surrounding the nests should remain undisturbed (Hammond and Forward, 1956; Dwernychuk and Boag, 1972). Nest distribution poses another problem. Many studies demonstrated a positive relationship between artificial nest density and predation rates (Tinbergen et al., 1967; Göransson et al., 1975; Andersson and Wiklund, 1978; Sugden and Beyersbergen, 1986). On the other hand, O'Reilly and Hannon (1989) and Gottfried (1978) concluded that there was no density-dependent effect in the nest predation patterns occurring on their experimental plots. Taking into consideration the previous results, it is likely that random or uniform distribution of artificial nests would provide more unbiased results on predation patterns than clumped nest distribution where a predator could destroy a large number of nests in a small area.

Numerous factors can contribute to nest predation, such as nest camouflage, breeding bird density and the predator community in a given habitat. Site selection is therefore important for a nest to be successful. The vast majority of predation studies attempted to identify different variables responsible for nest losses. Those variables are either site-specific or area-specific. Site-specific factors usually refer to the nest location *per se* (e.g. nest cover, vegetation density, nest height) and published information on that matter is extensive. Most studies on waterfowl nest predation were conducted in the Prairie Pothole area in Canada and Northern United States, while most studies on passerine nests were conducted in the United States and Europe. The authors usually concluded that one or a few physical factors were important in reducing chances of nest predation. Because the experiments were conducted at different times, in different areas, employed different methods, and differed with respect to their main objectives, contradictory results were frequently obtained on the role of specific factors in predation events. Variables most often found to be important included: vegetation density (Schranck, 1972; O'Reilly and Hannon, 1989), nest concealment (Bowman and Harris, 1980; Storaas, 1988), nest height (Wilcove, 1985; Yahner and Scott, 1988), and vegetation height (Caccamise, 1977; Sugden and Beyersbergen, 1987; Sullivan and Dinsmore, 1990).

Another important factor that should be taken into consideration in any predation study is the location of the nests (area-specific factors).

Attempts to compare predation pressures between adjacent habitats sometimes yielded opposite results, and especially so in the case of marsh-nesting birds and their upland-nesting counterparts. Past studies showed that predation was lower in the marsh area than in dry adjacent uplands both for passerine and waterfowl nests. This suggested that some mammalian predators did not invade the flooded area (Robertson, 1972; Giroux, 1981; Picman, 1988). However, Shipley (1979) found similar predation rates on nests located in marsh and upland habitats and Ricklefs (1969) even concluded that marsh habitats were the ones where passerine nest predation was the highest.

The time in the nesting season when the predation study is conducted can also influence the outcome of the predation experiment. Martin (1987) and Sullivan and Dinsmore (1990), working with artificial passerine and waterfowl nests, respectively, concluded that the predation pressure in their study area remained constant during the nesting season. Conversely, other studies showed that nest survival increased (Gottfried and Thompson, 1978; Crabtree et al., 1989) or decreased (Angelstam, 1986) as the nesting season progressed.

Predation on nests of passerines and waterfowl nesting in marshes has been the subject of many studies. It is, however, difficult to generalize on the factors responsible for the observed predation patterns. One main reason why so many contradictory results have been obtained in spite of similar objectives of these studies could be that different habitats were sampled. Every habitat supports a particular fauna. Density and diversity of avian and mammalian predators will be characteristic of the local environment. Since these two groups of predators hunt for their food in different ways (Storaas, 1988), the predation pressure on a given nest type will be exerted in different ways with respect to the study area. The predator community in a marsh will be greatly influenced by the adjacent upland. Consequently, we should expect that nests located in different marshes with different surrounding upland habitats should suffer different predation pressures.

Since the arrival of early settlers in North America, habitat modification through human activities has been intense and wetland losses for urban, industrial and agricultural purposes have been severe (Lynch-Stewart, 1983). Even where freshwater marshes remain relatively intact, their adjacent upland habitats have often suffered drastic changes followed by changes in their endemic fauna, including predators. Because different habitats support different predator communities (Gottfried, 1978; Møller, 1987; Picman, 1988), we can expect differences in predation pressures between marshes situated in relatively undisturbed areas and those located in areas with urban, industrial or agricultural developments.

It is known that human activities have adverse effects on bird populations (Nuorteva, 1971; Beissinger and Osborne, 1982). However, some individuals can take advantage of human presence (Beissinger and Osborne, 1982; Figley and Van Druff, 1982). In addition, new types of predators such as dogs (Henry, 1969; Urban, 1970), rats (Heusmann and Burrell, 1974; Hill, 1984) and domestic cats (Howard, 1974; Warner, 1985) may occur in more disturbed areas. Agricultural practices have had negative effects on waterfowl nesting success through destruction of nests during the mowing season (Duebbert and Kantrud, 1974; Masse et Raymond, 1988), increase in predator density (Andrén et al., 1985), or destruction of the nesting cover around the marsh, rendering the foraging behavior of predators easier (Krasowski and Nudds, 1986). Because human activities are spread over most regions of North America, any management policies designed to protect and increase wildlife populations in marshes must take into account information on the effects of human-related disturbance on density and diversity of predators operating in the marsh. Predation patterns are therefore likely to change as a function of the amount of habitat perturbation observed in a given area.

With respect to the previously mentioned physical, ecological and micro-geographical variables affecting predation, it is evident that broad generalizations of factors responsible for nest predation are probably impossible to achieve. It would be more useful to concentrate our efforts on studies of local predation patterns.

Several predation studies have been conducted in North America in recent years. However, only a few studies which examined predation on nests of marsh-nesting birds have been done in southern Québec and southeastern Ontario (Laperle, 1974; Weatherhead and Robertson, 1977; Masse et Raymond, 1988; Picman, 1988) although the region's potential for wildlife production has been the subject of an earlier study (Fink et al., 1985). In addition, nobody, so far, has attempted to evaluate the effect of human activities on predation pressures and their related causes on nests of birds breeding in marshes and in adjacent uplands.

The present study was designed to answer the following questions arising from the effects of human-related disturbance on nest predation patterns in selected marshes:

1. What are the nest predation patterns in a sample of marshes?

2. Do predation patterns vary among marshes?

3. Are the nest predation patterns similar for waterfowl and passerine nests?

4. Within a marsh, which factors influence chances of predation on a given nest?

5. What are the effects of human-related disturbance on nest predation patterns?

6. Which predators operate in marshes and what is their relative importance?

7. How predictable is predation between marshes in the same year and in consecutive years?

MATERIAL AND METHODS

Sampled marshes

As different habitats support different predator communities, the modification of the natural habitats by human activities must have changed their predator fauna. Consequently, nests located in marshes adjacent to various upland habitats may experience different predation rates. To determine the effect of human disturbance on predation on marsh-nesting birds' nests, I studied marshes in areas with different levels of human impact. I selected three marshes with relatively little disturbance (henceforth natural marshes: NAT); three marshes surrounded by intensive farming areas (henceforth agricultural marshes: AGR); and two marshes located in urban areas (henceforth urban marshes: URB). All eight marshes were situated in the Ottawa-Hull area, Canada.

Artificial nests

I used artificial nests throughout this study. I constructed waterfowl nests from dead vegetation found nearby by pressing it together to form a shallow cup (ext. diam. ≈30 cm, int. diam. ≈12 cm, depth ≈8 cm). The nests were either placed directly on the ground or on a few occasions in the deep-water areas of the marsh on floating platforms. They were constructed with submerged vegetation and dead cattail leaves. Torn up cattail (Typha sp.) seed packs simulated duck down and were placed underneath the eggs. A single large, fresh, brown chicken egg was placed in each nest. I constructed passerine nests from dry grass and white glue. They were approximately of the size and shape of the red-winged blackbird

(Agelaius phoeniceus) nest (ext. diam. ≈10 cm, int. diam. ≈7 cm, depth ≈4 cm). Each nest was placed in vegetation in such a way to simulate as much as possible the location of natural nests. Their height varied from 0 cm to a maximum of 200 cm, depending on the available vegetation and suitable nest locations. Each nest contained one fresh Chinese painted quail (Coturnix chinensis) egg (from the UBC Quail Farm; Vancouver, B.C.) treated with acetic acid to reduce eggshell thickness (Picman et al., 1988), thereby making it breakable to small predators such as the marsh wren (Cistothorus palustris). The eggs turned from brown to creamy white color after this treatment. Special care was taken not to disturb the vegetation surrounding the nest location. Actual manipulations of the nest occurred only when setting it up. On some occasions, the vegetation above the nest was bent to provide some concealment from above, both for waterfowl and passerine nests. No nest markers were used; natural landmarks were used to find the nests.

Nest distribution

I placed the nests along transects running perpendicular to the edge of the marsh for a distance of 100 m in either direction. Nests were placed along these transects at 10 m intervals, with waterfowl and passerine nests alternating, so that there were 20 m between two nests of the same type. I introduced a minimum of four transects in each marsh with a minimum of 40 m between each.

Physical parameters

I measured several physical parameters at each nest. Nest height (NH) and nest concealment when viewed from above (overhead concealment: OC) were recorded when the nest was set up; water depth (WD), height of dead (VEGD) and live (VEGL) vegetation as well as vegetation density (VD) were measured when the nest had been destroyed or when the experiment was over. Nest height, water depth and height of dead and live vegetation were measured to the nearest 5 cm. Whenever the vegetation was higher than 3 m, I gave it a score of 500 cm. Vegetation density and overhead concealment were given a relative index. Nesting cover and vegetation structure (species composition, density, height) which define vegetation density, were categorized as light, medium or heavy in the near vicinity of the nest (radius = 5 m) (see Schranck, 1972; Bowman and Harris, 1980). Overhead concealment is defined as the percentage of the nest that is visible when the observer is 1 m above the nest. This variable was rated on a scale of 0 to 4; 0= completely visible from above; 1= 1-10% of the nest is concealed; 2= 11-50% of the nest is concealed; 3= 51-90% is concealed; 4= 90-100% is concealed (see Dwernychuk and Boag, 1972). The actual distances (DIST) of nests from the edge of the marsh were not used in the analysis. I instead placed nests into 4 categories: 1) marsh nests located farther than 50 m from the marsh edge, 2) marsh nests that were set up within 50 m of the marsh edge, 3) upland nests located within 50 m of the edge and 4) upland nests farther than 50 m from the marsh edge.

Occurrence of predation

In 1989, after the nests were set up, I inspected them the following day and four subsequent times at 3-day intervals. In 1990, I visited the nests only twice after seven and 13 days of exposure because results from the first year showed that the change in predation rates occurring over three days was negligible and that repeated visits increased damage to the vegetation. A destroyed egg was not replaced after a predation event was registered, i.e. when the egg was found damaged, moved or destroyed. I removed the "successful" nests after the last visit. The duration of the experiments (13 days) was chosen because (a) the standard incubation period for passerine birds is about 13 days; (b) the experiments were conducted in consecutive months and (c) to give a resting period of at least a week between subsequent experiments.

In 1989, I set up artificial passerine and waterfowl nests in the following periods: May 9th to 24th (M89), June 19th to July 6th (J89) and July 17th to August 3rd (JY89). In 1990, the same experiments were conducted from May 21st to June 6th (M90), June 12th to 27th (J90) and July 10th to 26th (JY90). In addition, I set up artificial waterfowl nests from April 25th to May 11th 1990 (A90). By repeating the experiments, I attempted to record the changes in the predation pressure during the nesting season.

Predators and breeding birds identification

We know that different predators search for their food in various ways. In general, mammals are more scent-oriented predators, whereas birds rely more on sight to find their prey (Storaas, 1988). I employed several methods to identify which predator came to a nest. The most important one was the observation of the cues left by the predator at a depredated nest. Eggshell remains and the appearance of the nest allowed me to categorize predators into several classes (avian, large or small mammal) and possibly directly identify the predator using Sowls' (1948), Rearden's (1951) and Shipley's (1979) techniques. The presence of different predators in a given marsh was also estimated from tracks and scats (Murie, 1989), hairs, visual observation of the animals and through discussions with local people. In addition, automatic cameras which took pictures of predation events (Picman, 1987) were used in some marshes in 1989. These camera setups were placed between the transects with artificial waterfowl and passerine nests to reduce interference with the predation experiments.

I recorded nesting activities of birds during every visit to a marsh to list the breeding birds found in the upland and marsh habitats of every marsh. Observations included nest searching, singing activity by adults, fledgling sightings and behavior of foraging adults.

Statistical analysis

As the data gathered during this project dealt mostly with survival of nests after a certain period of time, I performed contingency table analyses using Chi-square tests calculated with the Yates continuity correction. Fisher's exact test was used when appropriate (Zar, 1984). I used contingency tables to determine the variations in predation rates during the seasons, to compare the predation rates between nests set up in the upland and marsh habitats, and to examine the nest losses between passerine and waterfowl nests. I also used contingency tables to compare the predation rates among the three areas. One of the most important objectives of this project was to compare the predation pressure and factors affecting predation on marsh-nesting birds found in three areas (Urb., Agric., Nat.) rather than comparing individual marshes. For all previously mentioned analyses, I pooled the data gathered in different marshes according to their respective area. All statistical analyses in which predation rates were involved were performed with the results of total number of nests destroyed after they were exposed for 13 days. Waterfowl and passerine nests were always treated separately since different nest types represent different stimuli (Martin, 1987).

To determine which physical parameters were important for the success of a nest, I used the BMDPLR program for stepwise logistic regression (Dixon, 1985) with variable entry and removal levels set at $p=0.10$ and $p=0.15$ respectively. The method used to select the next term to enter or remove in the stepwise process was based on the maximum likelihood ratio (MLR). Categorical variables included DIST, OC, and VD. The physical parameters were compared between passerine and waterfowl nests using unpaired two-sample t-test. I performed logistic regression and t-test analyses on data sets collected at the time when approximately 50% of the nests were predated. Fluctuations in water depth were examined using one-way ANOVA. I also computed Pearson correlation coefficients (r) between WD and DIST for all trials. All statistical analyses were performed on SAS version 5 and BMDP (1983 version) statistical packages as well as with Statview 512+ and FISH6 1.001 (categorical statistics) for Macintosh computers. Statistical significance was set at $p<0.01$ except for tests concerning means when it was set at $p<0.05$.

STUDY AREA

All eight marshes selected in this study were located in the immediate Ottawa-Hull region, Canada (Fig. 1). I defined urban, agricultural and natural marshes as follows:

Urban marsh: A marsh where man-made structures (homes, buildings, highways) cover more than 50% of the immediate 1 km radius surrounding dry land area and where the population of the community is over 5000.

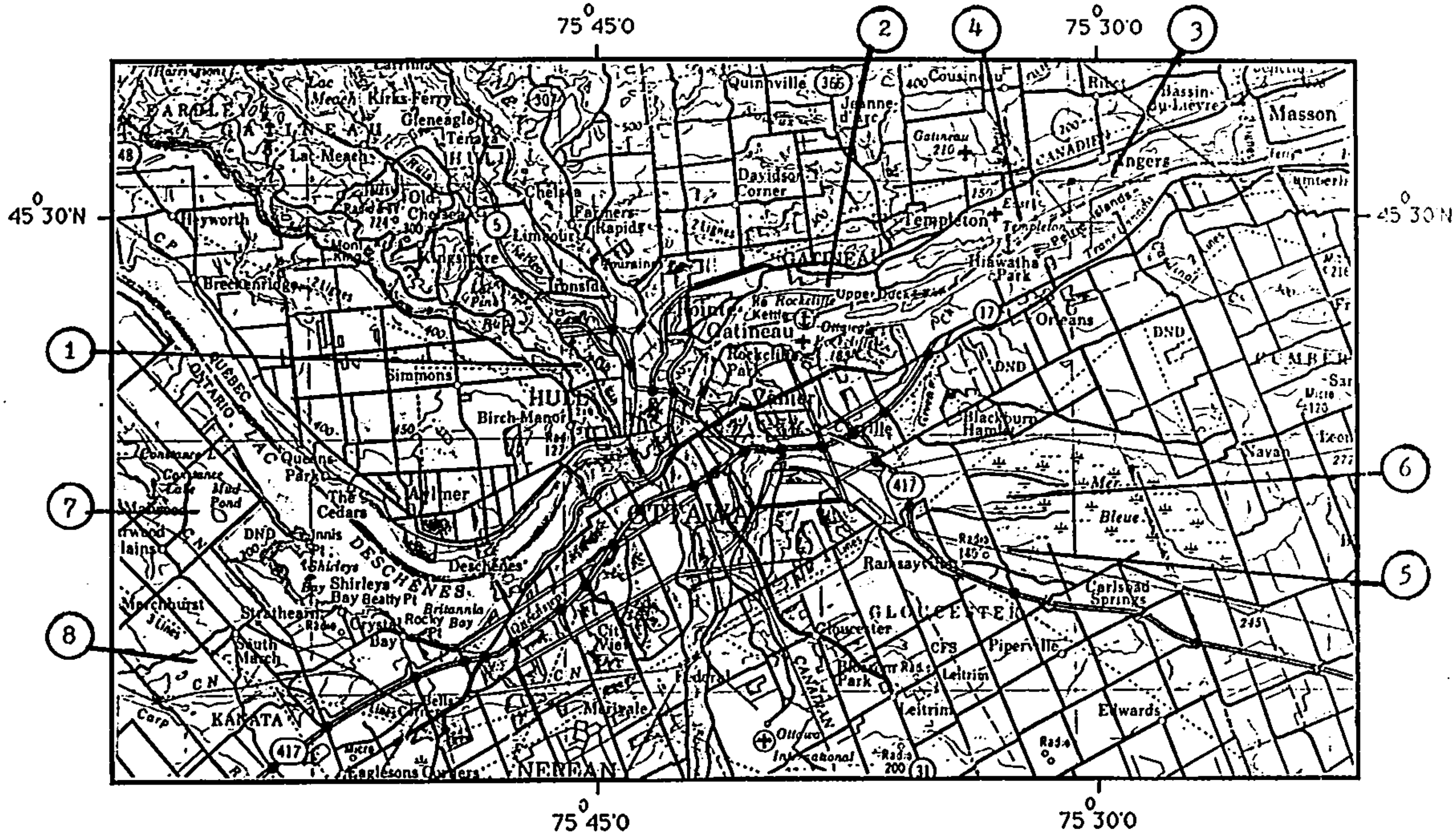
Agric. marsh: A marsh where cultivated fields form more than 50% of the immediate 1 km radius adjacent upland and where there is no major city (population over 5000) closer than 5 km.

Natural marsh: A marsh located in an area where mature forests represent more than 50% of the immediate 1 km radius dry land area surrounding the marsh and where building density is less than 5 per km^2.

The surface area (%) covered by different microhabitats (forested and urban areas, free water, marsh, abandoned and cultivated fields) surrounding the studied marshes in a circle of 1 km radius was determined using topographic maps (scale 1:50000) and aerial photographs. Table 1 presents these results for the total area (1 km radius around the marsh) as well as for the dry land area only.

The vegetation of each marsh was characterized at uniformly distributed sampling points. Every 20 meters along the experimental transects, the plant species were identified within an area of 5 m radius

Figure 1: Location of the studied marshes in the Ottawa-Hull region, Québec and Ontario.



Marshes:
1) Hull
2) Gatineau
3) Angers
4) Laîches
5) Ramseyville
6) Mer Bleue
7) Constance
8) Kanata

Scale: 1:250 000

↔ 5 km

Table 1: Surface area (%) covered by different microhabitats around the studied marshes in a circle of r = 1 km. (Numbers in brackets represent the area covered on dry land only).

	URBAN		AGRIC.			NATURAL		
HABITAT	HULL	GAT	ANG	LAI	RAM	M. BL.	CON	KAN
Forested area	16.8 (17.0)	3.8 (8.1)	4.8 (9.5)	4.6 (7.2)	7.9 (10.9)	31.2 (51.7)	69.1 (84.9)	67.3 (77.3)
Free water	0.7 (0.0)	27.2 (0.0)	30.9 (0.0)	17.3 (0.0)	0.0 (0.0)	2.1 (0.0)	2.6 (0.0)	8.1 (0.0)
Marsh	0.6 (0.0)	25.3 (0.0)	18.6 (0.0)	19.3 (0.0)	27.7 (0.0)	37.7 (0.0)	16.1 (0.0)	5.0 (0.0)
Urban area	66.7 (67.5)	43.3 (91.9)	11.0 (21.7)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)
Abandonned field	15.3 (15.5)	0.0 (0.0)	9.6 (19.0)	25.0 (39.4)	13.1 (18.1)	12.8 (21.2)	10.5 (12.9)	13.6 (15.6)
Cultivated field	0.0 (0.0)	0.0 (0.0)	25.2 (49.8)	33.9 (53.4)	51.3 (71.0)	16.4 (27.2)	1.8 (2.2)	6.2 (7.1)

and each species was given a score of percentage cover area: Abundant: >50% ; Common: 20%-50%; Localised: 5%-20%. A score of 3, 2 and 1, respectively, was ascribed to these categories. These scores were then added up for every sampling point and for every species and the result was divided by the number of sampling points. The three categories were therefore rearranged as follows: Abundant: ≥ 1.0; Common: $0.5 \leq X < 1.0$; Localised: $0.2 \leq X < 0.5$. Marsh and upland habitats were analysed separately.

Description of the marshes

A description of the marshes is appropriate to stress the differences between the three areas involved in this project. They are all cattail marshes and the dominant plant species are listed in Table 2.

HULL: Urban. This 2 ha marsh is located at the edge of the city of Hull and the Parc de la Gatineau, Québec. It is the only remaining cattail marsh within the city limits. The adjacent upland consists of abandoned fields with scattered trees and shrubs. Human activities around the marsh are important.

GATINEAU: Urban. Located at the heart of the city of Gatineau, Québec, this 4.8 ha marsh sits between heavy urban and industrial developments and the Ottawa river. Second-growth forest and abandoned fields form the upland area.

ANGERS: Agricultural. This 44 ha marsh lies on the banks of the Ottawa river. Located south of the Angers community, Québec, this marsh is surrounded by intensively farmed land and moderate urban development.

LAICHES: Agricultural. This large marsh (80 ha) can be found 5 km east of the city of Gatineau, Québec, on the banks of the Ottawa river. Ducks Unlimited and the Ministère du Loisir de la Chasse et de la Pêche, Québec, are managing this marsh for waterfowl production. Hay fields form the adjacent upland.

RAMSEYVILLE: Agricultural. Located in the Mer Bleue Bog Conservation Area, southeast of the city of Ottawa, Canada, this 36 ha marsh is at the heart of intensive farming activity. The upland area consists of abandoned fields and scattered trees.

MER BLEUE: Natural. Also located in the Mer Bleue Bog Conservation Area, this active beaver pond supports an important 14 ha cattail marsh surrounded by second-growth deciduous forest.

CONSTANCE: Natural. A 3.2 ha beaver pond found 35 km west of Ottawa, Canada. Mixed forest characterizes the upland area of this marsh. Human activity is practically absent in this area.

KANATA: Natural. This 10 ha active beaver pond is located 30 km west of Ottawa, Canada. The upland area supports a mature deciduous forest community. Urban development is slowly invading this wilderness area.

Table 2: Abundant and common plant species in ulpand and marsh habitats of the studied marshes.

URBAN

	SPECIES ABUNDANCE	
	ABUNDANT	COMMON
HULL		
UPLAND	Rhamnus catharticus Solidago canadensis Unidentified grasses	Asclepias syriaca Cornus stolonifera Fragaria virginiana Pinus divaricata
MARSH	Typha angustifolia	Lemna minor
GATINEAU		
UPLAND	Acer saccharinum Phalaris arundinacea	Fraxinus americana Osmunda cinnamomea Solidago canadensis
MARSH	Hydrocharis morsus-ranae Lemna minor Typha angustifolia	Salix petiolaris Sium suave Sparganium eurycarpum

Table 2: (Continued)

AGRICULTURAL

	SPECIES ABUNDANCE	
	ABUNDANT	COMMON
ANGERS		
UPLAND	Phalaris arundinacea	Vicia Cracca
MARSH	Typha angustifolia	Galium obtusum Lemna minor
LAICHES		
UPLAND	Lotus corniculatus Phleum pratense Unidentified grasses	Carex sp. Fragaria virginiana Salix petiolaris Spiraea alba Taraxacum officinale Vicia Cracca
MARSH	Carex sp. Hydrocharis morsus-ranae Lythrum salicaria Sparganium eurycarpum Typha angustifolia	Butomus umbellatus Galium obtusum Lemna minor Sium suave
RAMSEYVILLE		
UPLAND	Phalaris arundinacea Spiraea alba	Solidago canadensis Vicia Cracca Unidentified grasses
MARSH	Typha angustifolia Lemna minor Hydrocharis morsus-ranae	

Table 2: (Continued)

NATURAL

	SPECIES ABUNDANCE	
	ABUNDANT	COMMON
MER BLEUE		
UPLAND	Acer rubrum Alnus rugosa Osmunda cinnamomea	Cornus alternifolia Corylus cornuta Impatiens capensis Onoclea sensibilis Populus tremuloides Rubus idaeus Unidentified grasses
MARSH	Hydrocharis morsus-ranae Lemna minor Typha angustifolia	
CONSTANCE		
UPLAND	Fraxinus nigra Picea glauca Thuja occidentalis	Corylus cornuta Laportea canadensis Rhus radicans Waldsteinia fragarioides
MARSH	Hydrocharis morsus-ranae Typha latifolia	Carex sp. Lemna minor Lythrum salicaria Scirpus validus Sium suave Unidentified grasses
KANATA		
UPLAND	Acer rubrum Acer saccharum Ostrya virginiana	Abies balsamea Fraxinus americana Picea glauca Pinus strobus Pteridium aquilinum Thuja occidentalis
MARSH	Typha latifolia Utricularia vulgaris	Carex sp. Potamogeton sp.

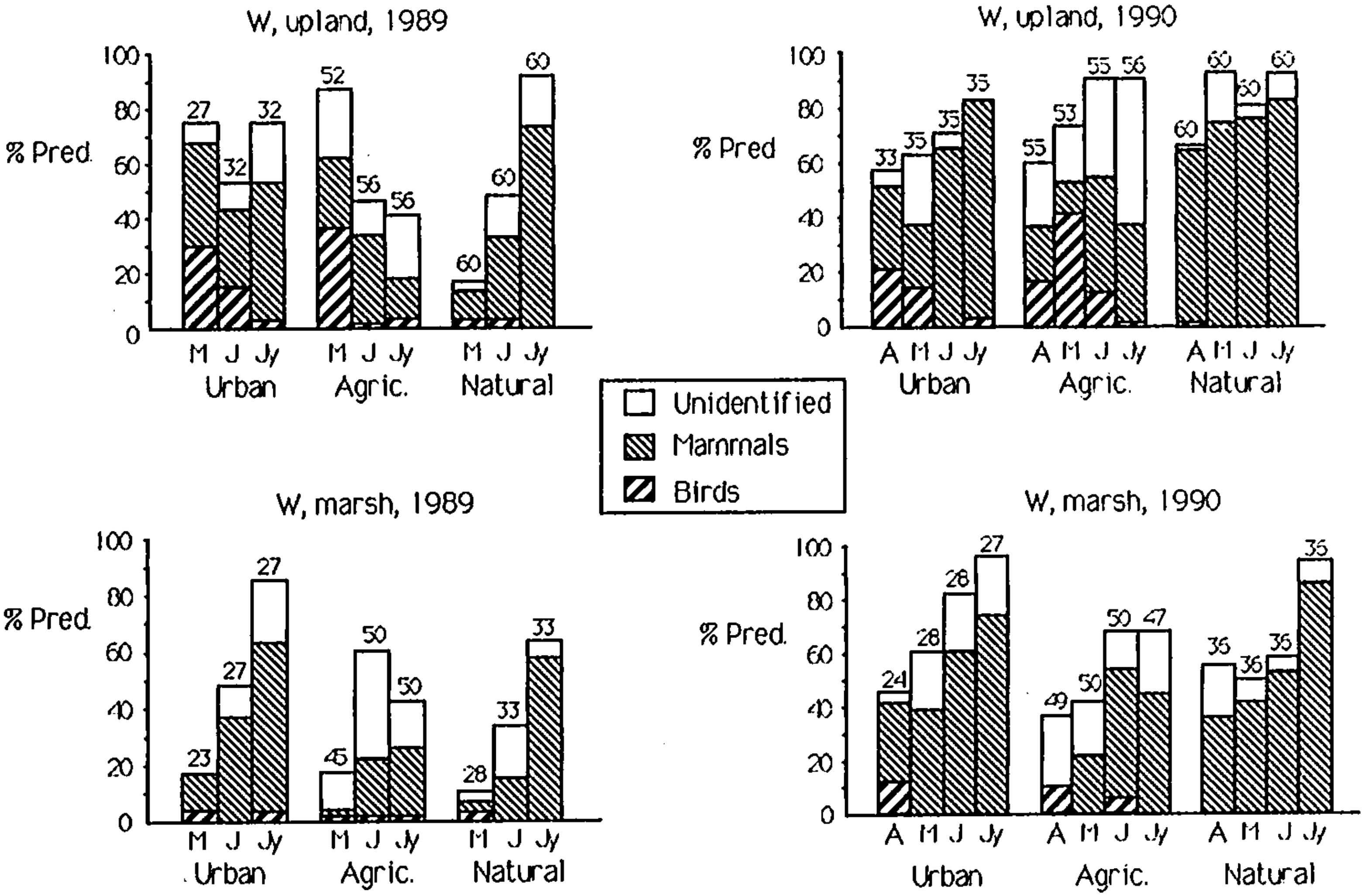
RESULTS

A total of 3326 nests were set up in the course of this 2-year study: 765 in urban areas, 1344 in agricultural areas and 1217 in natural areas of which 578 (76%), 879 (65%) and 874 (72%) were depredated in each area, respectively. The potential predators and breeding birds found in each marsh are listed in Appendix 1.

Predators

Eggshell remains left at the depredated nests were the most common cues used to assign the predators to the following categories: birds, mammals and unidentified. Because the eggs in passerine nests were smaller than those in waterfowl nests, eggshell remains were harder to find in passerine nests and, therefore, more cases of unidentified predators appeared in this category. The predation events included in the last category involved cases when the nest was not damaged and no eggshell could be found. Small mammals, small birds and snakes may have been responsible for those events (Best and Stauffer, 1980). The predators responsible for waterfowl nest losses are shown in Figure 2. American crows (Corvus brachyrhynchos) were important predators in upland habitats of urban and agricultural areas, especially early in the season. Avian predators were generally absent from the upland habitat of natural areas. In the marsh habitat, mammals were the dominant predators in every area. Raccoons (Procyon lotor) and skunks (Mephitis mephitis) were responsible for most of the predation events ascribed to mammalian

Figure 2: Distribution of avian, mammaliar and unidentified predators of waterfowl (W) nests in upland and marsh habitats of urban, agricultural and natural areas for all 1989 and 1990 trials performed in April (A), May (M), June (J) and July (Jy). Bars represent the predation rates at day 13, sample size is shown above each bar



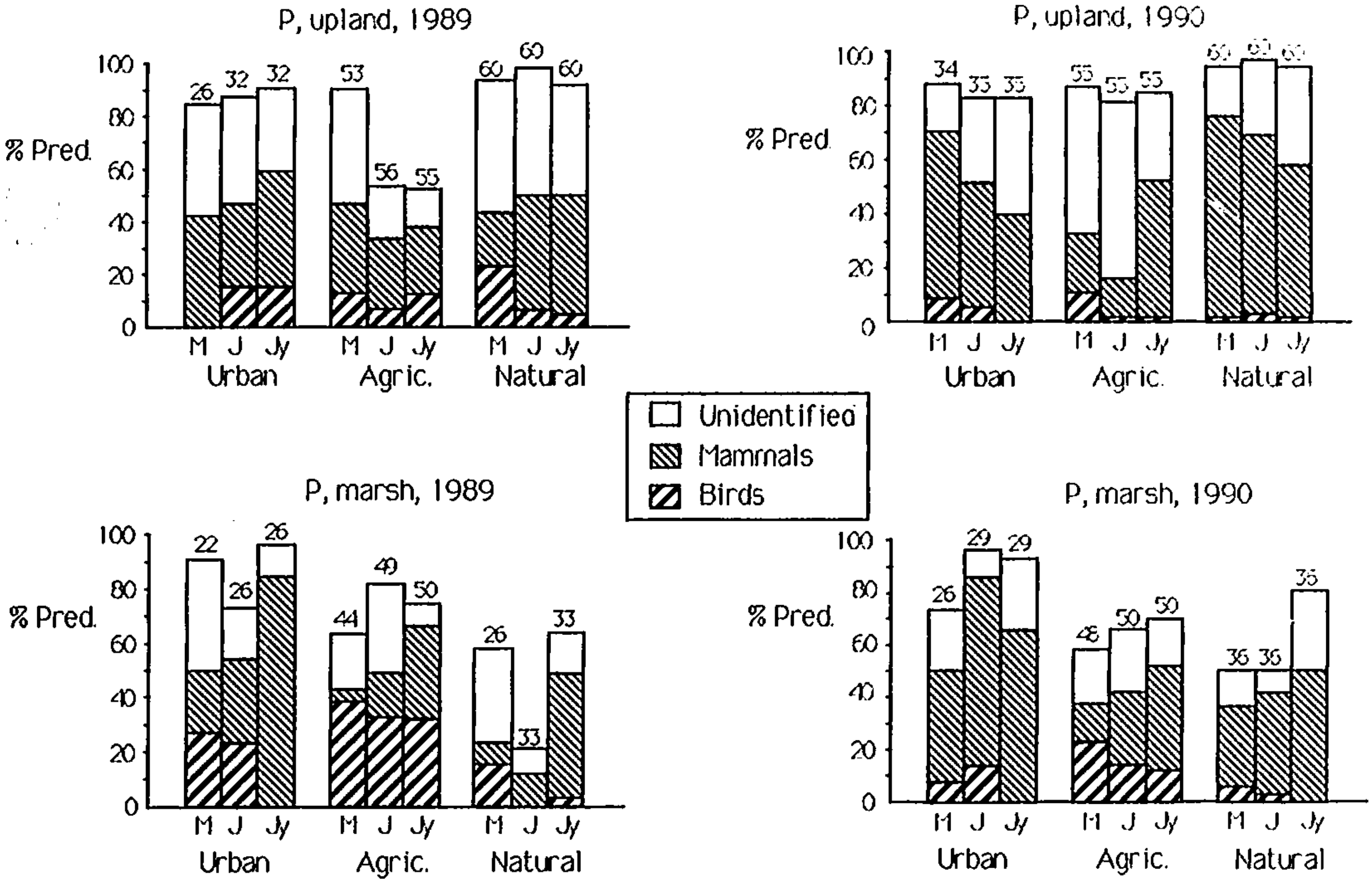
predators in all areas. Mink (Mustela vison) were also present in urban and agricultural areas (Appendix 1).

Predators on passerine nests are shown in Figure 3. In the upland habitat, mammals (mostly skunks and raccoons) were the most important predators in every marsh. As for avian predators, blue jays (Cyanocitta cristata) were present in urban and natural areas. In the marsh habitat, marsh wrens were breeding in one urban marsh (Gatineau) and in all three agricultural marshes (Appendix 1). They were responsible for several predation events. No marsh wrens were breeding in the natural marshes. Marsh-nesting common grackles (Quiscalus quiscula) are potential nest predators (Shipley, 1979; Small and Hunter, 1988) and were also abundant in the two urban marshes.

Small rodents (presumably Clethrionomys sp., Microtus sp., Peromyscus sp.) were also reported in every marsh (Appendix 1). Red squirrels (Tamiasciurus hudsonicus) and chipmunks (Tamias striatus) were also abundant in urban and natural areas. Garter snakes (Thamnophis sirtalis) were seen in all areas and northern water snakes (Nerodia sipedon) were observed in two natural marshes (Appendix 1).

Because unidentified predators were responsible for a number of predation events (Figs. 2,3), statistical analyses comparing the importance of avian and mammalian predators could be severely biased and were not performed. The trends in the importance of the identified predator types were however well-defined. In general, mammalian predation was more important than avian predation in every area (Figs.

Figure 3 : Distribution of avian, mammalian and unidentified predators of passerine (P) nests in upland and marsh habitats of urban, agricultural and natural areas for all 1989 and 1990 trials performed in April (A), May (M), June (J) and July (Jy). Bars represent the predation rates at day 13, sample size is shown above each bar

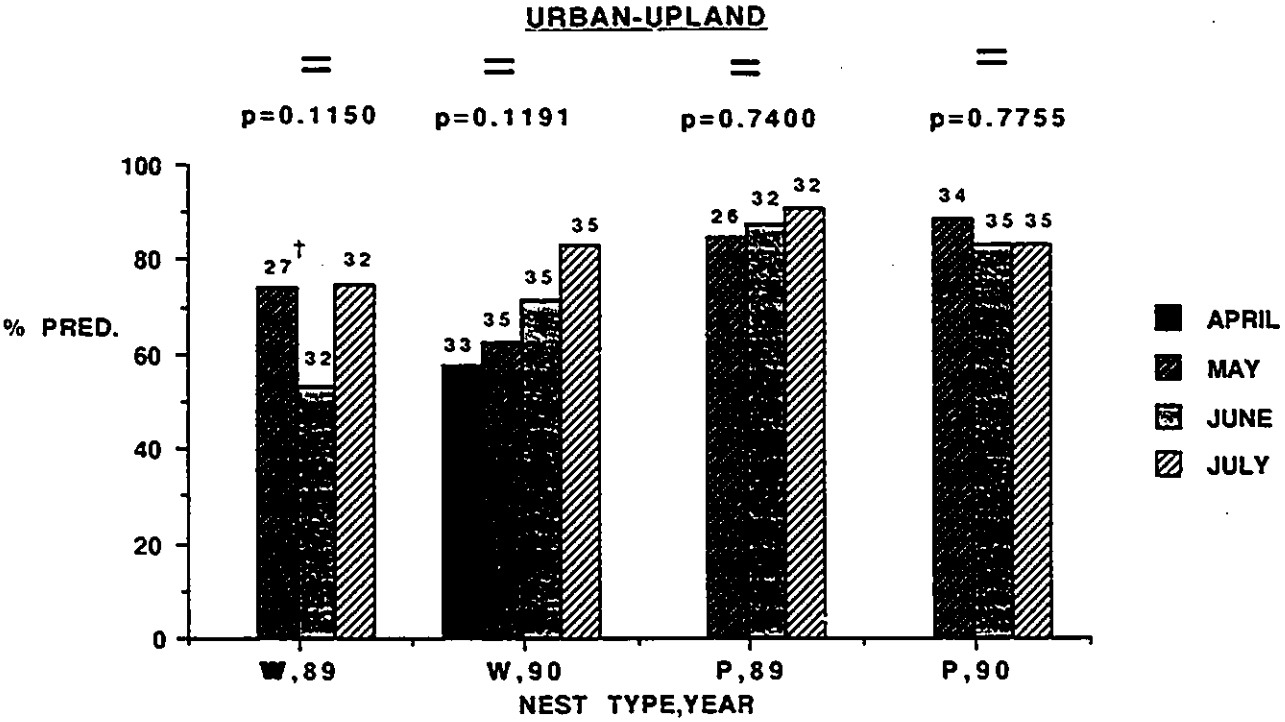


2,3) except for passerine nests located in the marsh habitat of agricultural areas for all three months of 1989. Generally, in upland habitats, the importance of avian predators was constant or decreased with time in all areas, whereas the frequency of mammalian predation tended to remain constant throughout the season or to increase as the season progressed. In marsh habitats, the temporal pattern of the importance of the predator types was similar in all areas: avian predation tended to remain constant while predation by mammals tended to increase.

Seasonal predation patterns

Nests may be depredated at different rates with respect to time in the season because of changes in vegetation structure, predator types and behavior, or in water level. Predation rates on waterfowl and passerine nests were high and tended to remain constant throughout the season in the upland habitat of urban areas (Fig. 4) whereas in the marsh habitat, waterfowl nests suffered from increasing predation rates as the season progressed. Passerine nests were heavily attacked throughout the season (Fig. 5). Nests located in the upland habitat of agricultural areas showed different predation patterns for the two years of the study (Fig. 6). In 1989, predation rates on waterfowl and passerine nests decreased with time whereas in 1990, the opposite was found for waterfowl nests. Predation was constantly heavy on passerine nests in the summer of 1990 (Fig. 6). Predation rates on waterfowl nests in the marsh habitat of agricultural areas were low early in the season and increased in the following months (Fig. 7). Predation on passerine nests was, however,

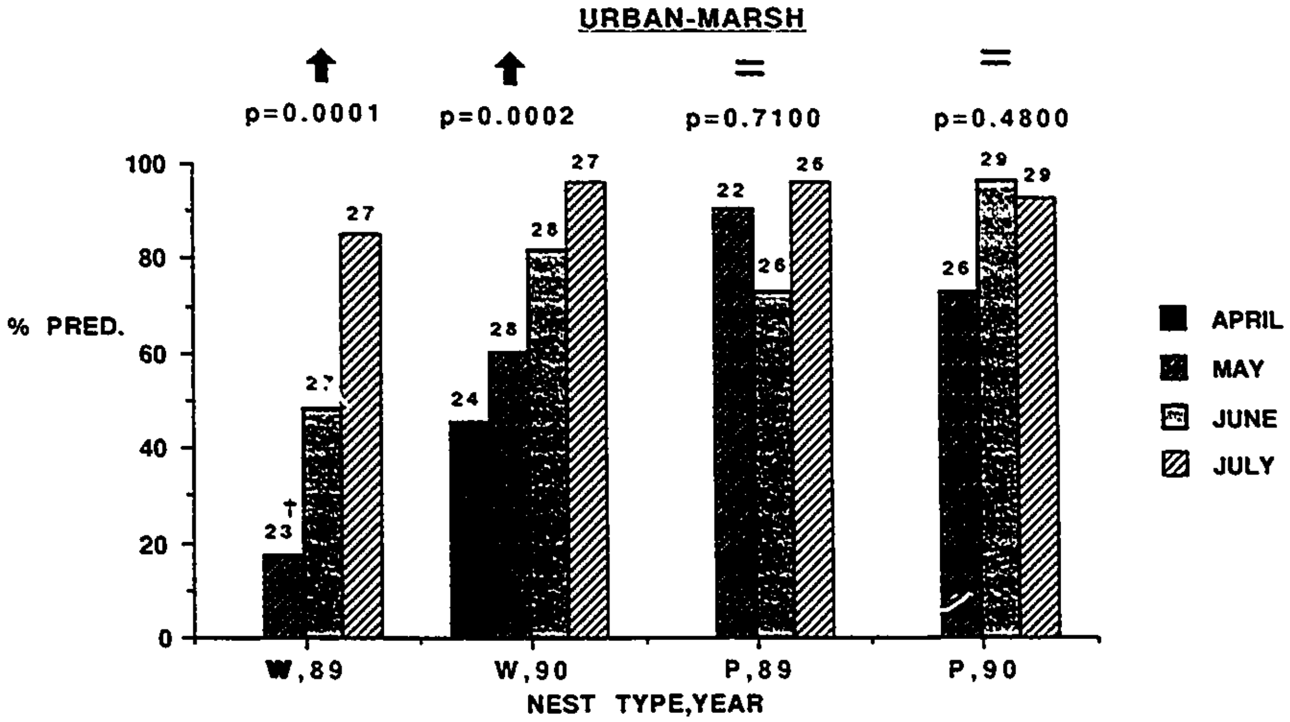
Figure 4: Predation rates on waterfowl (W) and passerine (P) nests in upland habitats of urban areas. Variation in predation rates throughout the season is shown above the bar graphs (= stands for constant predation).



Note: Statistical significance calculated by Chi-square analysis except for P,89 when Fisher's exact probability (2-tailed) was calculated (May and June data combined)

† Number above each bar is the sample size

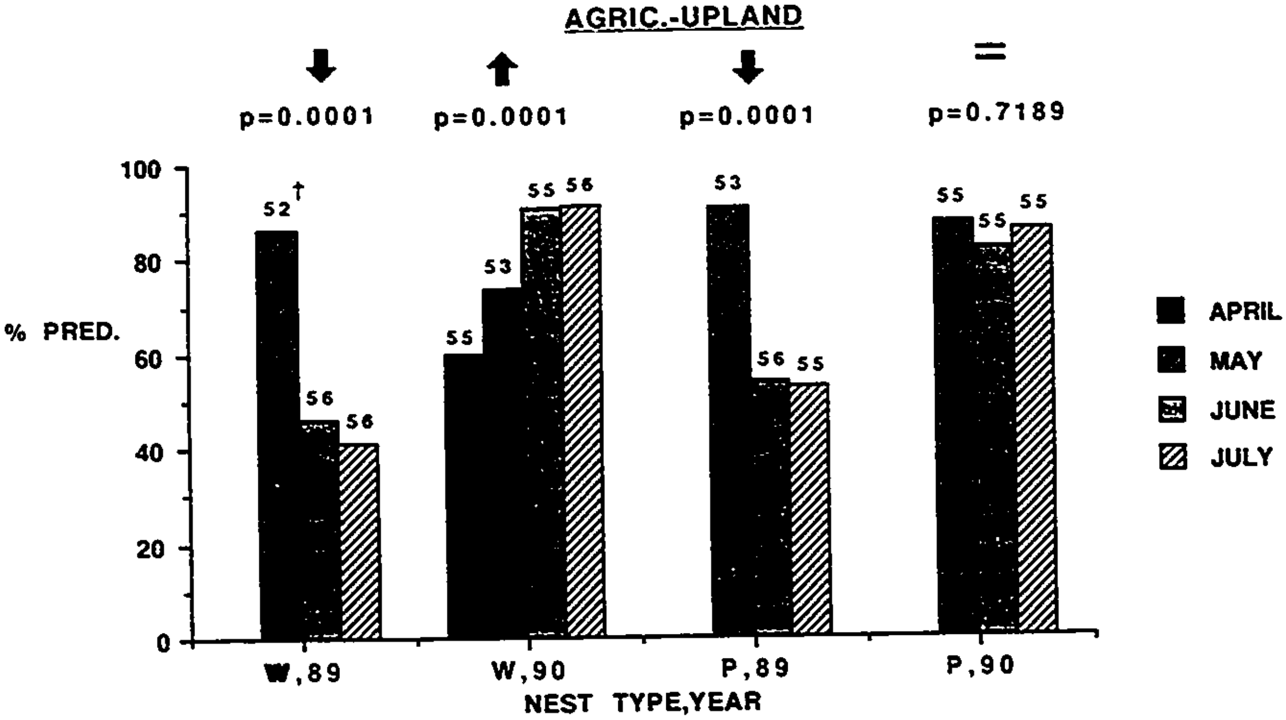
Figure 5: Predation rates on waterfowl (W) and passerine (P) nests in marsh habitats of urban areas. Variation in predation rates throughout the season is shown above the bar graphs (= stands for constant predation, ↑ stands for increasing predation).



Note: Statistical significance calculated by Chi-square analysis except for P,89 and P,90 when Fisher's exact probability (2-tailed) was calculated (June and July data combined for P,89; May and June data combined for P,90)

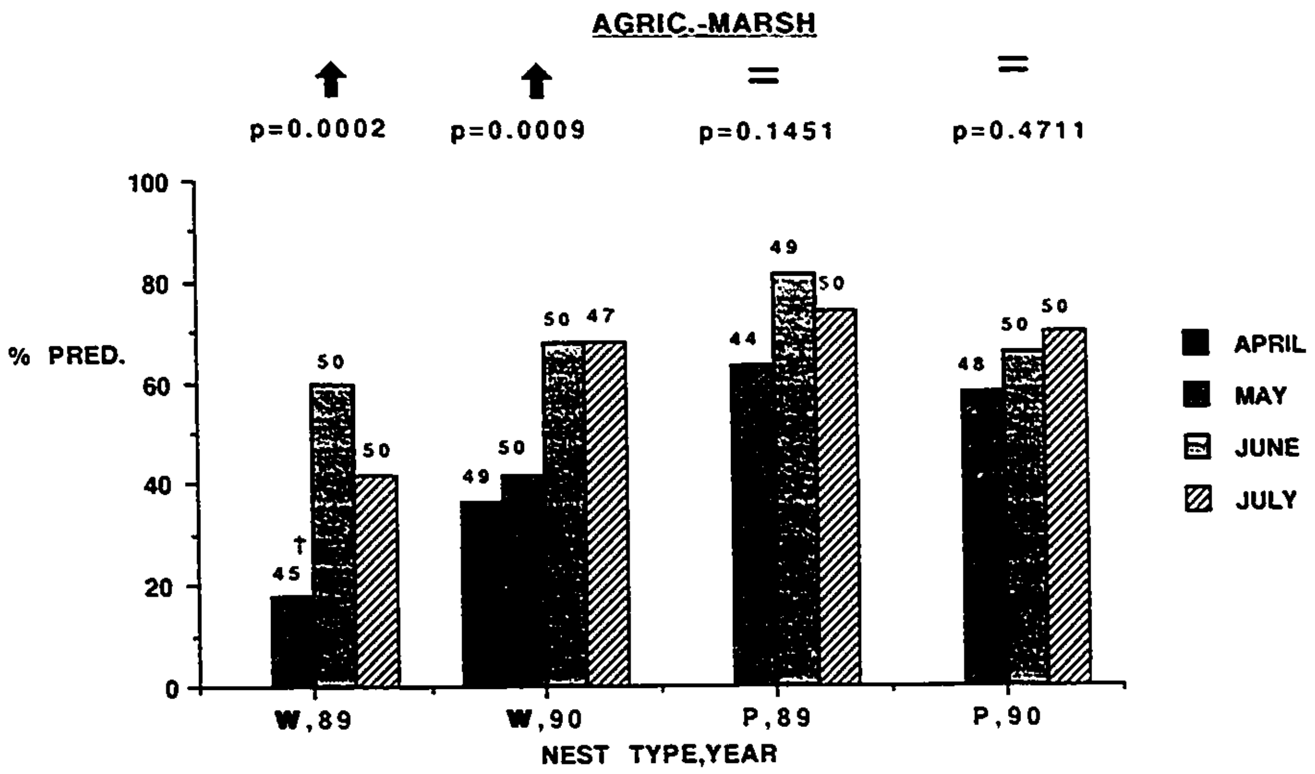
† Number above each bar is the sample size

Figure 6: Predation rates on waterfowl (W) and passerine (P) nests in upland habitats of agricultural areas. Variation in predation rates throughout the season is shown above the bar graphs. (= stands for constant predation, ⬆ stands for increasing predation ,⬇ stands for decreasing predation).



Note: Statistical significance calculated by Chi-square analysis
† Number above each bar is the sample size

Figure 7: Predation rates on waterfowl (W) and passerine (P) nests in marsh habitats of agricultural areas. Variation in predation rates throughout the season is shown above the bar graphs. (= stands for constant predation, ⬆ stands for increasing predation).



Note: Statistical significance calculated by Chi-square analysis

† Number above each bar is the sample size

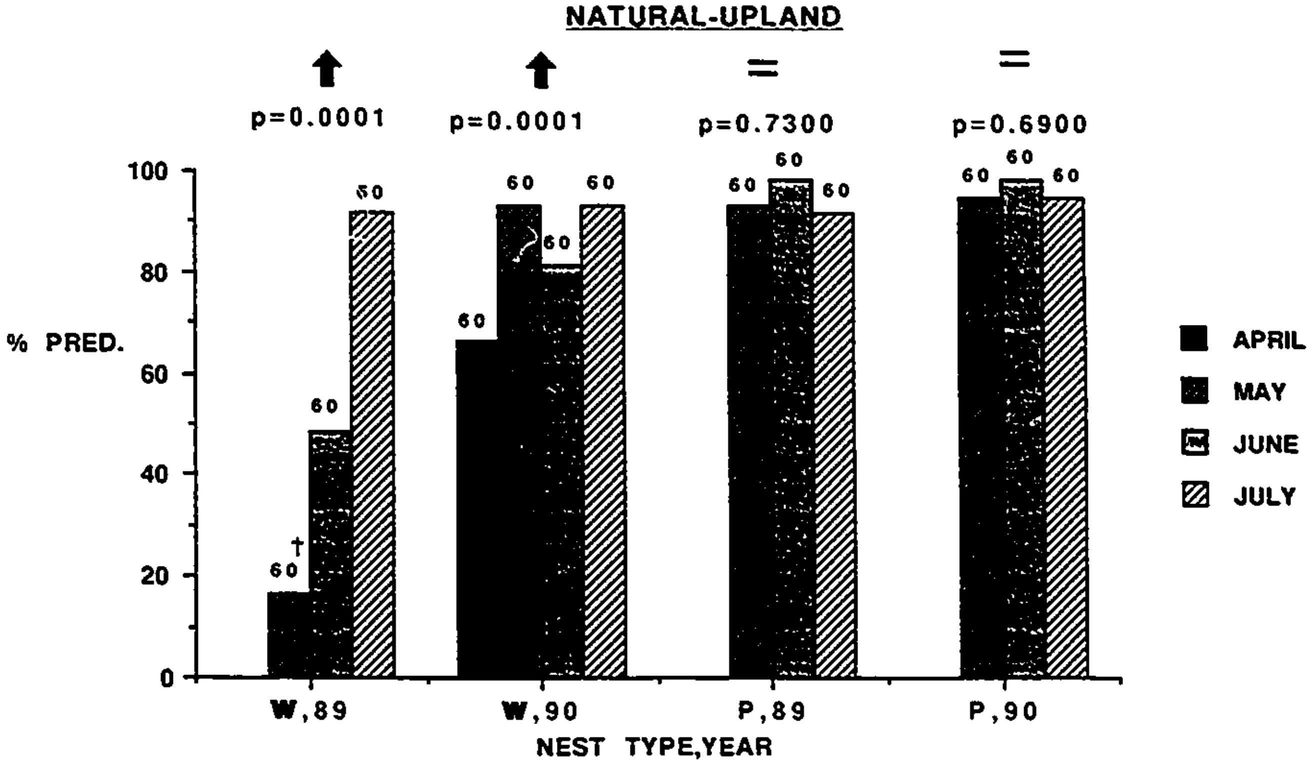
relatively constant in time throughout the two seasons (Fig. 7). In undisturbed areas, predation on waterfowl nests increased with time in the upland habitat; passerine nests suffered heavy predation throughout the season (Fig. 8). Finally, predation rates on nests located in the marsh habitat of natural areas increased with time except for passerine nests in 1989 when a decline in predation was rapidly reversed (Fig. 9).

To summarize, in upland habitats, predation rates on passerine nests usually remained constant in all areas while results for waterfowl nests differed among the three areas (Table 3). Similarly, in marsh habitats, predation on passerine nests was similar throughout the seasons in urban and agricultural areas but tended to increase with time in natural areas. Waterfowl nests in marsh habitats generally suffered higher predation later in the season in all areas (Table 3). The predation patterns were similar in both years in the majority of cases, the main difference occurring in the upland habitat of agricultural areas. Finally, the predation rates on passerine nests were similar in the two years (with the exception of upland habitat of agric. areas). In contrast, waterfowl nests suffered higher predation in 1990 (with the exception of upland habitat of urban areas) (Table 3).

Comparison between waterfowl and passerine nests

Table 4 presents the results of the comparisons of the predation rates between waterfowl and passerine nests for all trials in urban areas. Predation rates on passerine nests in the upland habitat were either higher or similar to those on waterfowl nests, whereas in the marsh habitat, the

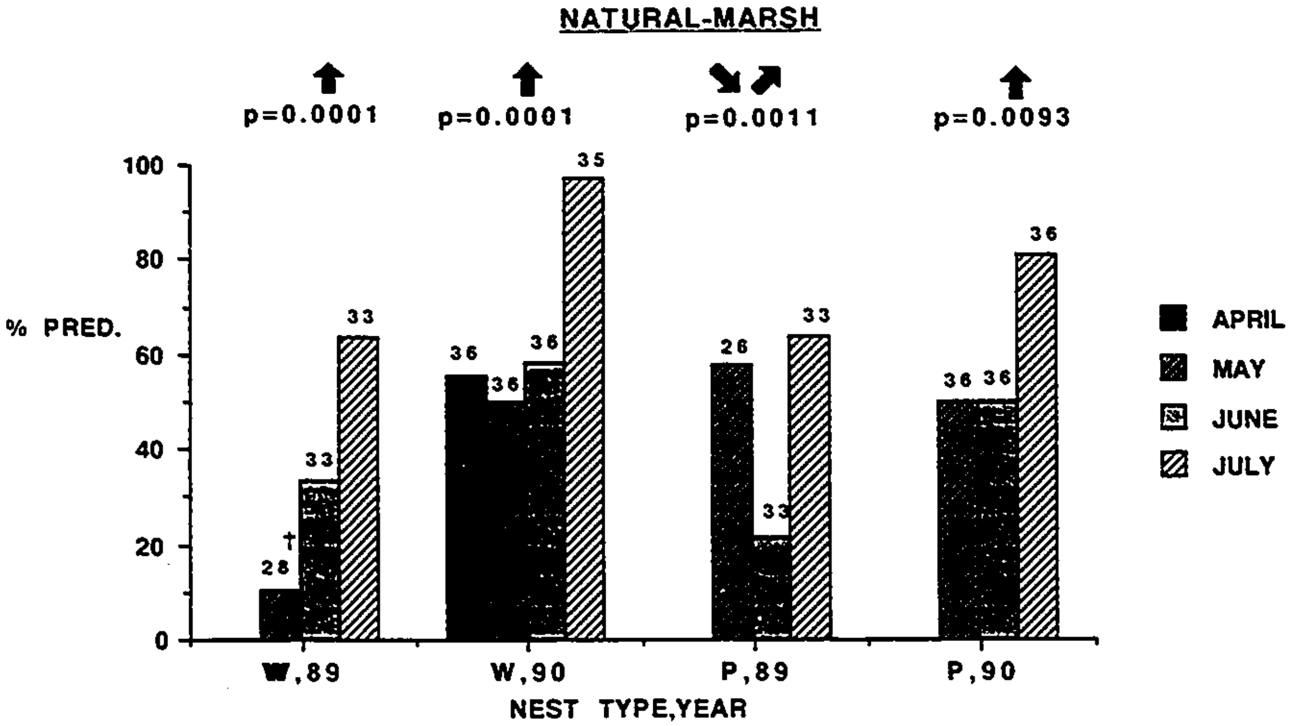
Figure 8: Predation rates on waterfowl (W) and passerine (P) nests in upland habitats of natural areas. Variation in predation rates throughout the season is shown above the bar graphs. (= stands for constant predation, ⬆ stands for increasing predation).



Note: Statistical significance calculated by Chi-square analysis except for P,89 and P,90 when Fisher's exact probability (2-tailed) was calculated (June and July data combined for P,89 and P,90)

† Number above each bar is the sample size

Figure 9: Predation rates on waterfowl (W) and passerine (P) nests in marsh habitats of natural areas. Variation in predation rates throughout the season is shown above the bar graphs. (⬆ stands for increasing predation, ↘↗ stands for variable predation).



Note: Statistical significance calculated by Chi-square analysis

† Number above each bar is the sample size

Table 3: Summary of the predation patterns on passerine (P) and waterfowl (W) nests located in the marsh and adjacent upland habitats of urban, agricultural and natural areas. Chi-square analyses compare the predation rates obtained in 1989 and 1990 (Months combined).

	URBAN		AGRICULTURAL		NATURAL	
	1989	1990	1989	1990	1989	1990
UPLAND						
	P =	**P =**	**P ↓**	**P =**	**P =**	**P =**
	\ / X^2= 0.18 p=0.6696 N=194 n.s.*		\ / X^2= 15.86 p=0.0001 N=329 1990>1989		\ / X^2= 0.25 p=0.6192 N=360 n.s.	
	W =	**W =**	**W ↓**	**W ↑**	**W ↑**	**W ↑**
	\ / X^2= 0.43 p=0.5106 N=196 n.s.		\ / X^2= 30.20 p=0.0001 N=328 1990>1989		\ / X^2= 58.57 p=0.0001 N=360 1990>1989	
MARSH						
	P =	**P =**	**P =**	**P =**	**P ↘↗**	**P ↑**
	\ / X^2= 0.004 p=0.9492 N=158 n.s.		\ / X^2= 2.11 p=0.1463 N=291 n.s.		\ / X^2= 3.10 p=0.0785 N=200 n.s.	
	W ↑	**W ↑**	**W ↑**	**W ↑**	**W ↑**	**W ↑**
	\ / X^2= 12.37 p=0.0004 N=160 1990>1989		\ / X^2= 9.26 p=0.0023 N=292 1990>1989		\ / X^2= 18.10 p=0.0001 N=201 1990>1989	

Note: Waterfowl nests set up in April 1990 were removed from the analysis.
* n.s.=not significant

Table 4: Comparison of the predation rates on passerine (P) and waterfowl (W) nests located in upland and marsh habitats of urban areas.

Area: Urban		% depredated (N)		Statistical test		Conclusion
Habitat	Month	Waterfowl	Passerines	$X^2_{adj.}$	P value	
Upland	May 89	74.1 (27)	84.6 (26)	0.37	0.5437	W=P
	May 90	62.9 (35)	88.2 (34)	4.69	0.0303	W=P
	June 89	53.1 (32)	87.5 (32)	7.49	0.0062	W<P
	June 90	71.4 (35)	82.9 (35)	0.73	0.3932	W=P
	July 89	75.0 (32)	90.6 (32)	1.76	0.1851	W=P
	July 90	82.9 (35)	82.9 (35)	0.10	0.7511	W=P
Marsh	May 89	17.4 (23)	90.9 (22)	21.55	0.0001	W<P
	May 90	60.7 (28)	73.1 (26)	0.45	0.5003	W=P
	June 89	48.1 (27)	73.1 (26)	2.48	0.1155	W=P
	June 90	82.1 (28)	96.6 (29)	(Fisher)*	0.1000	W=P
	July 89	85.2 (27)	96.1 (26)	(Fisher)*	0.3500	W=P
	July 90	96.3 (27)	93.1 (29)	(Fisher)*	1.0000	W=P

* Fisher's exact test, 2-tailed

predation rates on the two nest types tended to be similar. Predation rates on passerine and waterfowl nests were similar in the upland habitat of agricultural areas (Table 5). However, in the marsh habitat, in 1989, passerine nests suffered higher losses than waterfowl nests in two trials (May and July), whereas in 1990, there was no difference between the two nest types (Table 5). Finally, in natural areas, passerine nests were destroyed at a higher rate than waterfowl nests early in the season (May and June) in the upland habitat (Table 6). In all but one case, predation on waterfowl and passerine nests was similar in the marsh habitat of natural areas (Table 6).

A total of 36 comparisons (12/area) were performed between waterfowl and passerine nests (Tables 4-6). Eight of these resulted in predation rates being higher on passerine than on waterfowl nests and 28 resulted in predation rates being similar on the two nest types. Predation rates were never higher on waterfowl than on passerine nests.

To provide a more comprehensive analysis of predation on the two nest types in the nesting season as a whole, I combined data for all months. Because no passerine nests were set up in April 1990, waterfowl nests distributed during this periods are excluded from the analysis. The incidence of predation on the two nest types varied among the three areas (Table 7). In the upland habitat, passerine nests suffered similar or higher losses than waterfowl nests both in urban and natural areas, while all nests were destroyed at similar rates in agricultural areas. On the other hand, predation rates on waterfowl and passerine nests located in the marsh habitats were similar in all areas with the exception of urban and

Table 5: Comparison of the predation rates on passerine (P) and waterfowl (W) nests located in upland and marsh habitats of agricultural areas.

Area: Agricultural		% depredated (N)		Statistical test		Conclusion
Habitat	Month	Waterfowl	Passerines	$X^2_{adj.}$	P value	
Upland	May 89	86.5 (52)	90.6 (53)	0.12	0.7325	W=P
	May 90	73.6 (53)	87.3 (55)	2.41	0.1203	W=P
	June 89	46.4 (56)	53.6 (56)	0.32	0.5708	W=P
	June 90	90.9 (55)	81.8 (55)	1.24	0.2664	W=P
	July 89	41.1 (56)	52.7 (55)	1.08	0.2982	W=P
	July 90	91.1 (56)	85.5 (55)	0.39	0.5320	W=P
Marsh	May 89	17.8 (45)	63.6 (44)	17.57	0.0001	W<P
	May 90	42.0 (50)	58.3 (48)	2.00	0.1572	W=P
	June 89	60.0 (50)	81.6 (49)	4.60	0.0321	W=P
	June 90	68.0 (50)	66.0 (50)	0.00	1.0000	W=P
	July 89	42.0 (50)	74.0 (50)	9.24	0.0024	W<P
	July 90	68.1 (47)	70.0 (50)	0.00	0.9873	W=P

Table 6: Comparison of the predation rates on passerine (P) and waterfowl (W) nests located in upland and marsh habitats of natural areas.

Area: Natural		% depredated (N)		Statistical test		Conclusion
Habitat	Month	Waterfowl	Passerines	$X^2_{adj.}$	P value	
Upland	May 89	16.7 (60)	93.3 (60)	68.18	0.0001	W<P
	May 90	93.3 (60)	95.0 (60)	(Fisher)*	1.0000	W=P
	June 89	48.3 (60)	98.3 (60)	35.84	0.0001	W<P
	June 90	81.7 (60)	98.3 (60)	7.50	0.0062	W<P
	July 89	91.7 (60)	91.7 (60)	0.11	0.7412	W=P
	July 90	93.3 (60)	95.0 (60)	(Fisher)*	1.0000	W=P
Marsh	May 89	10.7 (28)	57.7 (26)	11.36	0.0008	W<P
	May 90	50.0 (36)	50.0 (36)	0.06	0.8137	W=P
	June 89	33.3 (33)	21.2 (33)	0.69	0.4070	W=P
	June 90	58.3 (36)	50.0 (36)	0.22	0.6362	W=P
	July 89	63.6 (33)	63.6 (33)	0.07	0.7980	W=P
	July 90	97.1 (35)	80.6 (36)	(Fisher)*	0.0600	W=P

* Fisher's exact test, 2-tailed

Table 7 Comparison of predation rates on Waterfowl (W) and Passerine (P) nests in urban, agricultural and natural areas for the entire nesting season (Months combined, April waterfowl nests excluded).

		% depredated (N)		Statistical test		Conclusion
Area	Habitat	Waterfowl	Passerines	$X^2_{adj.}$	P value	
Urban	Upland 89	67.0 (91)	87.8 (90)	9.96	0.0016	P>W
	Upland 90	72.4 (105)	84.6 (104)	3.93	0.0473	P=W
	Marsh 89	51.9 (77)	86.5 (74)	19.42	0.0001	P>W
	Marsh 90	79.5 (83)	88.1 (84)	1.68	0.1953	P=W
Agric.	Upland 89	57.3 (164)	65.2 (164)	1.85	0.1738	P=W
	Upland 90	85.4 (164)	84.8 (165)	0.00	0.9816	P=W
	Marsh 89	40.7 (145)	73.4 (143)	30.15	0.0001	P>W
	Marsh 90	59.2 (147)	64.9 (148)	0.78	0.3760	P=W
Natural	Upland 89	52.2 (180)	94.4 (180)	79.90	0.0001	P>W
	Upland 90	89.4 (180)	96.1 (180)	5.02	0.0251	P=W
	Marsh 89	37.2 (94)	46.7 (92)	1.36	0.2441	P=W
	Marsh 90	68.2 (107)	60.2 (108)	1.18	0.2770	P=W

agricultural areas in 1989 when passerine nest losses were more important.

I compared the various physical parameters measured at each nest between waterfowl and passerine nests. Water depth under the nest, which is likely to influence chances of nest predation, differed significantly between the nests in only one out of 18 trials (Table 8). Nest camouflage, which may also be an important factor in preventing a nest from predation, was assessed by measuring four parameters: overhead concealment (OC), vegetation density (VD), height of dead (VEGD) and live (VEGL) vegetation. Table 9 indicates that, in urban areas, passerine nests were as camouflaged as,or better camouflaged than, waterfowl nests. The same conclusion can be drawn for nests located in agricultural areas (Table 10) except for May 1989 when waterfowl nests had higher values for OC and VD, as well as lower water depth (Table 8). In that trial, passerine nests suffered higher predation than waterfowl nests when the nests in the upland and marsh habitats were combined (X^2= 11.20, p=0.0008, N=194). Better camouflage for waterfowl nests might therefore explain this difference. Finally, nest camouflage indices for the two nest types were generally similar in natural areas (Table 11).

Comparison between upland and marsh habitats

Although the studied marshes were all dominated by cattail, the vegetation structure of their adjacent uplands varied (Table 2). The breeding bird communities found in the upland and marsh habitats were also distinct (Appendix 1). I compared the predation rates on nests located

Table 8: Comparison of water depths [X±SD (N)] at waterfowl and passerines nests located in marsh habitats of urban, agricultural and natural areas.

TRIAL	Waterfowl	Passerines	t*	P value	CONCl.**
URBM89	29.8±13.0 (23)	36.6±13.6 (22)	1.72	0.0930	n.s.
AGRM89	25.2±13.6 (45)	33.5±14.9 (44)	2.75	0.0072	P>W
NATM89	33.9±18.3 (28)	38.5±20.6 (26)	0.86	0.3952	n.s.
URBJ89	24.3±15.0 (27)	24.0±13.6 (26)	0.06	0.9555	n.s.
AGRJ89	13.3±11.7 (50)	18.4±16.7 (49)	1.75	0.0835	n.s.
NATJ89	35.6±25.4 (33)	36.2±23.3 (33)	0.10	0.9199	n.s.
URBJY89	10.4±15.9 (27)	9.6±13.6 (26)	0.19	0.8536	n.s.
AGRJY89	4.1±7.6 (50)	5.3±9.9 (50)	0.68	0.4988	n.s.
NATJY89	23.9±26.5 (33)	22.3±21.4 (33)	0.28	0.7799	n.s.
URBM90	27.0±19.3 (28)	26.3±18.5 (26)	0.12	0.9048	n.s.
AGRM90	17.1±11.6 (50)	18.8±15.1 (48)	0.61	0.5442	n.s.
NATM90	39.2±22.7 (36)	37.8±22.5 (36)	0.26	0.7948	n.s.
URBJ90	22.9±16.5 (28)	24.0±18.5 (29)	0.24	0.8122	n.s.
AGRJ90	13.8±13.6 (50)	14.5±13.5 (50)	0.26	0.7967	n.s.
NATJ90	27.8±21.9 (36)	25.0±20.5 (36)	0.56	0.5801	n.s.
URBJY90	14.4±15.5 (27)	17.8±17.7 (29)	0.74	0.4603	n.s.
AGRJY90	13.8±14.5 (47)	12.6±13.4 (50)	0.43	0.6652	n.s.
NATJY90	21.3±22.4 (35)	20.1±20.2 (36)	0.23	0.8215	n.s.

* 2-tailed unpaired t-test

** n.s.= not significant

Table 9: Comparison of nest camouflage indices [X±SD (N)] at waterfowl and passerines nests in urban areas.

TRIAL	Variable*	Waterfowl	Passerines	t**	P value	CONCL.***
URBM89	OC	1.4±0.8 (50)	1.2±0.7 (48)	1.14	0.2557	n.s.
	VD	1.5±0.5 (50)	1.5±0.5 (48)	0.21	0.8320	n.s.
	VEGD	34.3±27.1 (50)	53.9±83.6 (48)	1.57	0.1196	n.s.
	VEGL	90.7±158.9 (50)	137.0±195.5 (48)	1.29	0.2007	n.s.
URBM90	OC	1.9±1.0 (63)	2.5±0.8 (60)	3.39	0.0009	P>W
	VD	1.8±0.5 (63)	1.8±0.5 (60)	0.39	0.6954	n.s.
	VEGD	40.5±44.6 (63)	49.4±75.1 (60)	0.81	0.4210	n.s.
	VEGL	177.5±186.5 (63)	193.1±193.8 (60)	0.45	0.6511	n.s.
URBJ89	OC	2.2±0.9 (59)	2.1±0.9 (58)	0.57	0.5689	n.s.
	VD	2.1±0.5 (59)	2.1±0.5 (58)	0.37	0.7151	n.s.
	VEGD	30.5±33.6 (59)	63.8±112.7 (58)	2.17	0.0318	P>W
	VEGL	116.5±66.1 (59)	247.9±163.4 (58)	5.72	0.0001	P>W
URBJ90	OC	2.3±0.8 (64)	2.7±0.6 (63)	3.83	0.0002	P>W
	VD	2.0±0.5 (64)	2.0±0.5 (63)	0.18	0.8599	n.s.
	VEGD	31.6±38.5 (64)	30.2±40.8 (63)	0.20	0.8424	n.s.
	VEGL	199.5±154.5 (64)	206.9±166.1 (63)	0.26	0.7939	n.s.
URBJY89	OC	2.6±0.9 (59)	2.3±0.9 (58)	1.51	0.1337	n.s.
	VD	2.1±0.5 (59)	2.0±0.5 (58)	0.89	0.3759	n.s.
	VEGD	23.2±31.8 (59)	43.7±75.5 (58)	1.90	0.0576	n.s.
	VEGL	119.6±47.0 (59)	268.3±161.6 (58)	6.80	0.0001	P>W
URBJY90	OC	2.9±0.9 (62)	2.8±0.8 (65)	0.37	0.7104	n.s.
	VD	2.2±0.5 (62)	2.2±0.6 (65)	0.39	0.6961	n.s.
	VEGD	31.7±41.5 (62)	53.1±107.6 (65)	1.46	0.1458	n.s.
	VEGL	231.9±141.1 (62)	234.3±150.3 (65)	0.09	0.9272	n.s.

* OC: Overhead concealment. VD: Vegetation density. VEGD: Height of dead vegetation
VEGL: Height of live vegetation

** 2-tailed unpaired t-test

*** n.s.= not significant

Table 10: Comparison of nest camouflage indices [X±SD (N)] at waterfowl and passerines nests in agricultural areas.

TRIAL	Variable*	Waterfowl	Passerines	t**	P value	CONCL.***
AGRM89	OC	1.5±0.8 (97)	1.2±0.8 (97)	2.03	0.0437	W>P
	VD	1.6±0.9 (97)	1.4±0.5(97)	2.10	0.0364	W>P
	VEGD	43.7±30.3 (97)	55.2±62.8 (97)	1.63	0.1046	n.s.
	VEGL	44.6±96.5 (97)	82.7±149.9 (97)	2.10	0.0369	P>W
AGRM90	OC	1.5±1.0 (103)	2.1±1.1 (103)	4.26	0.0001	P>W
	VD	1.6±0.6 (103)	1.7±0.5 (103)	0.38	0.7042	n.s.
	VEGD	49.6±36.3 (103)	56.2±43.9 (103)	1.18	0.2408	n.s.
	VEGL	70.6±96.3 (103)	76.1±119.9 (103)	0.36	0.7178	n.s.
AGRJ89	OC	2.1±0.7 (106)	2.1±0.9 (105)	0.44	0.6590	n.s.
	VD	2.3±0.5 (106)	2.2±0.5 (105)	1.70	0.0914	n.s.
	VEGD	20.8±20.7 (106)	31.2±38.9 (105)	2.44	0.0157	P>W
	VEGL	128.7±36.1 (106)	147.9±88.3 (105)	2.07	0.0398	P>W
AGRJ90	OC	2.3±0.8 (105)	2.6±0.9 (105)	2.70	0.0072	P>W
	VD	2.0±0.6 (105)	2.1±0.6 (105)	0.36	0.7180	n.s.
	VEGD	39.7±37.5 (105)	41.9±42.2 (105)	0.41	0.6850	n.s.
	VEGL	111.8±54.3 (105)	115.7±74.7 (105)	0.43	0.6653	n.s.
AGRJY89	OC	2.5±0.8 (106)	2.5±0.9 (105)	0.29	0.7706	n.s.
	VD	2.5±0.7 (106)	2.3±0.7 (105)	2.27	0.0243	W>P
	VEGD	24.0±22.7 (106)	28.4±29.2 (105)	1.24	0.2157	n.s.
	VEGL	146.3±58.7 (106)	176.1±99.8 (105)	2.64	0.0088	P>W
AGRJY90	OC	2.6±0.8 (103)	2.9±0.8 (105)	1.99	0.0479	P>W
	VD	2.4±0.7 (103)	2.4±0.7 (105)	0.02	0.9851	n.s.
	VEGD	35.9±36.2 (103)	40.5±41.3 (105)	0.85	0.3993	n.s.
	VEGL	152.6±64.1 (103)	178.8±107.2 (105)	2.14	0.0337	P>W

* OC: Overhead concealment, VD: Vegetation density, VEGD: Height of dead vegetation VEGL: Height of live vegetation

** 2-tailed unpaired t-test

*** n.s.= not significant

Table 11: Comparison of nest camouflage indices [X±SD (N)] at waterfowl and passerines nests in natural areas.

TRIAL	Variable*	Waterfowl	Passerines	t**	P value	CONCL.***
NATM89	OC	1.3±0.9 (88)	1.3±1.0 (86)	0.27	0.7884	n.s.
	VD	1.5±0.6 (88)	1.6±0.6 (86)	0.67	0.5046	n.s.
	VEGD	47.0±104.9 (88)	62.5±116.3 (86)	0.92	0.3566	n.s.
	VEGL	194.7±225.7 (88)	158.7±212.3 (86)	1.08	0.2809	n.s.
NATM90	OC	1.7±0.8 (96)	1.7±0.9 (96)	0.17	0.8674	n.s.
	VD	1.5±0.5 (96)	1.5±0.5 (96)	0.00	1.0000	n.s.
	VEGD	40.7±64.0 (96)	39.2±62.0 (96)	0.17	0.8638	n.s.
	VEGL	133.3±167.6 (96)	170.8±193.5 (96)	1.44	0.1529	n.s.
NATJ89	OC	2.1±1.0 (93)	1.7±0.9 (93)	2.41	0.0168	W>P
	VD	1.7±0.6 (93)	1.8±0.5 (93)	0.55	0.5800	n.s.
	VEGD	27.0±30.9 (93)	45.1±91.0 (93)	1.81	0.0723	n.s.
	VEGL	106.9±108.4 (93)	246.5±196.0 (93)	6.01	0.0001	P>W
NATJ90	OC	2.2±0.7 (96)	2.2±0.9 (96)	0.00	1.0000	n.s.
	VD	1.7±0.6 (96)	1.7±0.6 (96)	0.35	0.7240	n.s.
	VEGD	32.8±34.4 (96)	38.9±62.3 (96)	0.84	0.4026	n.s.
	VEGL	157.2±152.3 (96)	172.0±165.1 (96)	0.65	0.5196	n.s.
NATJY89	OC	2.2±0.8 (93)	1.9±0.7 (93)	3.21	0.0016	W>P
	VD	1.9±0.6 (93)	1.8±0.6 (93)	0.84	0.4001	n.s.
	VEGD	27.8±34.5 (93)	44.5±81.7 (93)	1.81	0.0714	n.s.
	VEGL	123.1±118.2 (93)	262.0±177.0 (93)	6.30	0.0001	P>W
NATJY9O	OC	2.3±0.7 (95)	2.5±0.7 (96)	1.15	0.2537	n.s.
	VD	1.8±0.6 (95)	1.8±0.6 (96)	0.32	0.7475	n.s.
	VEGD	40.7±61.6 (95)	46.2±65.2 (96)	0.60	0.5487	n.s.
	VEGL	179.3±160.4 (95)	214.3±181.2 (96)	1.41	0.1599	n.s.

* OC: Overhead concealment, VD: Vegetation density, VEGD: Height of dead vegetation VEGL: Height of live vegetation

** 2-tailed unpaired t-test

*** n.s.= not significant

in the upland and marsh habitats. In urban areas, nest losses in upland and marsh habitats were generally similar for waterfowl and for passerine nests (Table 12). However, in agricultural areas, predation on waterfowl nests was generally greater in the upland than in the marsh (Table 13). Passerine nests suffered lower predation in the marsh early in the season (May). However, as the nesting period progressed, predation rates in the marsh reached or even surpassed (in June 1989) the levels observed in the upland (Table 13). In natural areas, waterfowl nest losses were either equal for the two areas or higher in the upland regardless of the time in the season (Table 14). Passerine nests, however, did consistently better if located in the marsh habitat.

A total of 39 comparisons (13/area) involving upland and marsh habitats (Tables 12-14) resulted in 14 cases where nest predation in the upland habitat was greater than in the adjacent marsh habitat and 24 cases where predation rates were similar in the two habitats. Only one case (passerine nests in agric. areas, June 1989) occured where predation in the marsh was higher than in the adjacent upland habitat.

Finally, I compared the nest predation rates in upland and marsh habitats for the entire nesting season (Table 15). In urban areas, the nest location (upland or marsh habitat) was not important for nest survival, whereas in natural areas, upland nests were depredated at a higher rate. In agricultural areas, marsh nests were generally better protected except for passerine nests in 1989. These conclusions are generally similar for the two years.

Table 12: Comparison of predation rates in upland and marsh habitats of urban areas for passerine (P) and waterfowl (W) nests.

Area: Urban		% depredated (N)		Statistical test		Conclusion
Nest type	Month	Upland	Marsh	$X^2_{adj.}$	P value	
Ⓦ	April 90	57.6 (33)	45.8 (24)	0.37	0.5432	Upl.=marsh
	May 89	74.1 (27)	17.4 (23)	13.80	0.0002	Upl.>marsh
	May 90	62.9 (35)	60.7 (28)	0.01	0.9307	Upl.=marsh
	June 89	53.1 (32)	48.1 (27)	0.01	0.9048	Upl.=marsh
	June 90	71.4 (35)	82.1 (28)	0.48	0.4874	Upl.=marsh
	July 89	75.0 (32)	85.2 (27)	0.41	0.5198	Upl.=marsh
	July 90	82.9 (35)	93.1 (27)	(Fisher)*	0.1300	Upl.=marsh
Ⓟ	May 89	84.6 (26)	90.9 (22)	(Fisher)*	0.6700	Upl.=marsh
	May 90	88.2 (34)	73.1 (26)	(Fisher)*	0.1800	Upl.=marsh
	June 89	87.5 (32)	73.1 (26)	(Fisher)*	0.1900	Upl.=marsh
	June 90	82.9 (35)	96.6 (29)	(Fisher)*	0.1200	Upl.=marsh
	July 89	90.6 (32)	96.1 (26)	(Fisher)*	0.6200	Upl.=marsh
	July 90	82.9 (35)	93.1 (29)	(Fisher)*	0.2800	Upl.=marsh

* Fisher's exact test, 2-tailed

Table 13: Comparison of predation rates in upland and marsh habitats of agricultural areas for passerine (P) and waterfowl (W) nests.

Area: Agricultural		% depredated (N)		Statistical test		Conclusion
Nest type	Month	Upland	Marsh	$X^2_{adj.}$	P value	
Ⓦ	April 90	60.0 (55)	36.7 (49)	4.72	0.0298	Upl.=marsh
	May 89	86.5 (52)	17.8 (45)	43.29	0.0001	Upl.>marsh
	May 90	73.6 (53)	42.0 (50)	9.30	0.0023	Upl.>marsh
	June 89	46.4 (56)	60.0 (50)	1.45	0.2292	Upl.=marsh
	June 90	90.9 (55)	68.0 (50)	7.22	0.0072	Upl.>marsh
	July 89	41.1 (56)	42.0 (50)	0.01	0.9199	Upl.=marsh
	July 90	91.1 (56)	68.1 (47)	7.22	0.0072	Upl.>marsh
Ⓟ	May 89	90.6 (53)	63.6 (44)	8.75	0.0031	Upl.>marsh
	May 90	87.3 (55)	58.3 (48)	9.65	0.0019	Upl.>marsh
	June 89	53.6 (56)	81.6 (49)	8.04	0.0046	Upl.<marsh
	June 90	81.8 (55)	66.0 (50)	2.65	0.1034	Upl.=marsh
	July 89	52.7 (55)	74.0 (50)	4.21	0.0403	Upl.=marsh
	July 90	85.5 (55)	70.0 (50)	2.81	0.0937	Upl.=marsh

Table 14: Comparison of predation rates in upland and marsh habitats of natural areas for passerine (P) and waterfowl (W) nests.

Area: Natural		% depredated (N)		Statistical test		Conclusion
Nest type	Month	Upland	Marsh	$X^2_{adj.}$	P value	
W	April 90	66.7 (60)	55.6 (36)	0.76	0.3838	Upl.=marsh
	May 89	16.7 (60)	10.7 (28)	0.17	0.6815	Upl.=marsh
	May 90	93.3 (60)	50.0 (36)	21.53	0.0001	Upl.>marsh
	June 89	48.3 (60)	33.3 (33)	1.39	0.2384	Upl.=marsh
	June 90	81.7 (60)	58.3 (36)	5.08	0.0242	Upl.=marsh
	July 89	91.7 (60)	63.6 (33)	9.40	0.0022	Upl.>marsh
	July 90	93.3 (60)	97.1 (35)	(Fisher)*	0.6500	Upl.=marsh
P	May 89	93.3 (60)	57.7 (26)	13.62	0.0002	Upl.>marsh
	May 90	95.0 (60)	50.0 (36)	24.09	0.0001	Upl.>marsh
	June 89	98.3 (60)	21.2 (33)	57.77	0.0001	Upl.>marsh
	June 90	98.3 (60)	50.0 (36)	30.14	0.0001	Upl.>marsh
	July 89	91.7 (60)	63.6 (33)	9.40	0.0022	Upl.>marsh
	July 90	95.0 (60)	80.6 (36)	(Fisher)*	0.0400	Upl.=marsh

* Fisher's exact test, 2-tailed

Table 15: Comparison of predation rates in upland (U) and marsh (M) habitats of urban, agricultural and natural areas for waterfowl (W) and passerine (P) nests for the entire nesting season (Months combined).

		% depredated (N)		Statistical test		Conclusion
Area	Nests	Upland	Marsh	$X^2_{adj.}$	P value	
Urban	W, 1989	67.0 (91)	51.9 (77)	3.35	0.0670	U=M
	W, 1990	68.8 (138)	72.0 (107)	0.15	0.6972	U=M
	P, 1989	87.8 (90)	86.5 (74)	0.00	0.9909	U=M
	P, 1990	84.6 (104)	88.1 (84)	0.23	0.6350	U=M
Agric.	W, 1989	57.3 (164)	40.7 (145)	7.86	0.0051	U>M
	W, 1990	79.0 (219)	53.6 (196)	29.09	0.0001	U>M
	P, 1989	65.2 (164)	73.4 (143)	2.03	0.1546	U=M
	P, 1990	84.8 (165)	64.9 (148)	15.74	0.0001	U>M
Natural	W, 1989	52.2 (180)	37.2 (94)	4.98	0.0256	U=M
	W, 1990	83.8 (240)	65.0 (143)	16.56	0.0001	U>M
	P, 1989	94.4 (180)	46.7 (92)	78.79	0.0001	U>M
	P, 1990	96.1 (180)	60.2 (108)	58.25	0.0001	U>M

Physical parameters at the nests

Because predation pressure varied between the upland and marsh habitats in certain marshes, nest location seems to be an important factor in survival of a nest. Camouflage should also influence survival of a nest. The following physical parameters measured at each nest were included in a stepwise logistic regression analysis for every trial to identify which of these factors played a role in nest survival: Distance from marsh edge (DIST), water depth under the nest (WD), vegetation density (VD), overhead concealment (OC), nest height (NH) and height of dead (VEGD) and live (VEGL) vegetation. I pooled all data collected in the upland and marsh habitats into a single data set.

The significant variables are listed in Tables 16 and 17 for waterfowl and passerine nests, respectively. The result of each analysis is indicated in small boxes (cells) according to area and time of year. A total of 21 and 18 analyses were performed on waterfowl and passerine nests, respectively. The variable order in the cells is the same as the order of entry in each analysis. The results from the previous analyses comparing upland and marsh areas (Tables 12-14) is indicated in every cell of the two tables. Starting with waterfowl nests (Table 16), nest location played an important role in nest survival; WD and/or DIST was included in 12 of the 21 analyses. In addition, VD was included in all three cases in 1989 in urban areas, whereas in agricultural areas, OC was entered in four of the seven cases. The growth of live vegetation with time seemed to affect predation rates in agricultural and natural areas. WD and/or DIST were included in five of the seven cases when predation in the

Table 16: Explanatory variables provided by stepwise logistic regression for waterfowl nests' trials. Variable order in the cells is the same as in the order of entry in the models. (The result of the comparison of predation rates in upland (U) and marsh (M) habitats for each trial is indicated in each cell).

NESTS	AREA	APRIL	MAY	JUNE	JULY
Ⓦ	URBAN, 89	X	U>M WD, OC, VD	U=M WD, DIST, VD	U=M WD, DIST, OC, VD, VEGD
	URBAN, 90	U=M VEGD, DIST, WD	U=M ---------	U=M DIST	U=M VEGD, VEGL
	AGRIC., 89	X	U>M DIST, VEGD, OC	U=M VD	U=M OC
	AGRIC., 90	U=M OC, WD	U>M VD, VEGL	U>M VEGL, VEGD	U>M DIST, OC
	NATURAL, 89	X	U=M OC	U=M VD, WD	U>M WD, VEGD, VEGL, DIST
	NATURAL, 90	U=M WD, VD, OC	U>M DIST	U=M VEGD	U=M VEGL

Table 17: Explanatory variables provided by stepwise logistic regression for passerine nests' trials. Variable order in the cells is the same as in the order of entry in the models. (The result of the comparison of predation rates in upland (U) and marsh (M) habitats for each trial is indicated in each cell).

NESTS	AREA	APRIL	MAY	JUNE	JULY
Ⓟ	URBAN, 89	X	U=M NH	U=M WD	U=M WD, DIST
	URBAN, 90	X	U=M ----------	U=M ----------	U=M VEGL
	AGRIC., 89	X	U>M DIST	U<M DIST	U=M DIST, OC, VEGD
	AGRIC., 90	X	U>M VD, WD, OC	U=M VD, VEGD	U=M VEGD
	NATURAL, 89	X	U>M DIST, VEGD, VD	U>M DIST	U>M WD, DIST
	NATURAL, 90	X	U>M DIST	U>M DIST, VD	U=M NH, WD, VD

upland and marsh habitats differed and in seven of the 14 cases when predation was similar in the two habitats.

For passerine nests (Table 17), no one variable had a consistent effect in urban areas, whereas DIST and WD were important in the other two areas. In addition, VEGD and VD played a role in agricultural and natural areas, respectively. NH, VEGL and nest camouflage (OC,VD) were relatively unimportant in reducing chances of nest predation. WD or DIST appear in two thirds of the cells. They are also present in all eight cells when predation in the upland and marsh habitats differed and in four of the 10 cases when predation was similar in the two habitats. These two variables are generally the first ones to be entered in the models both for waterfowl and passerine nests.

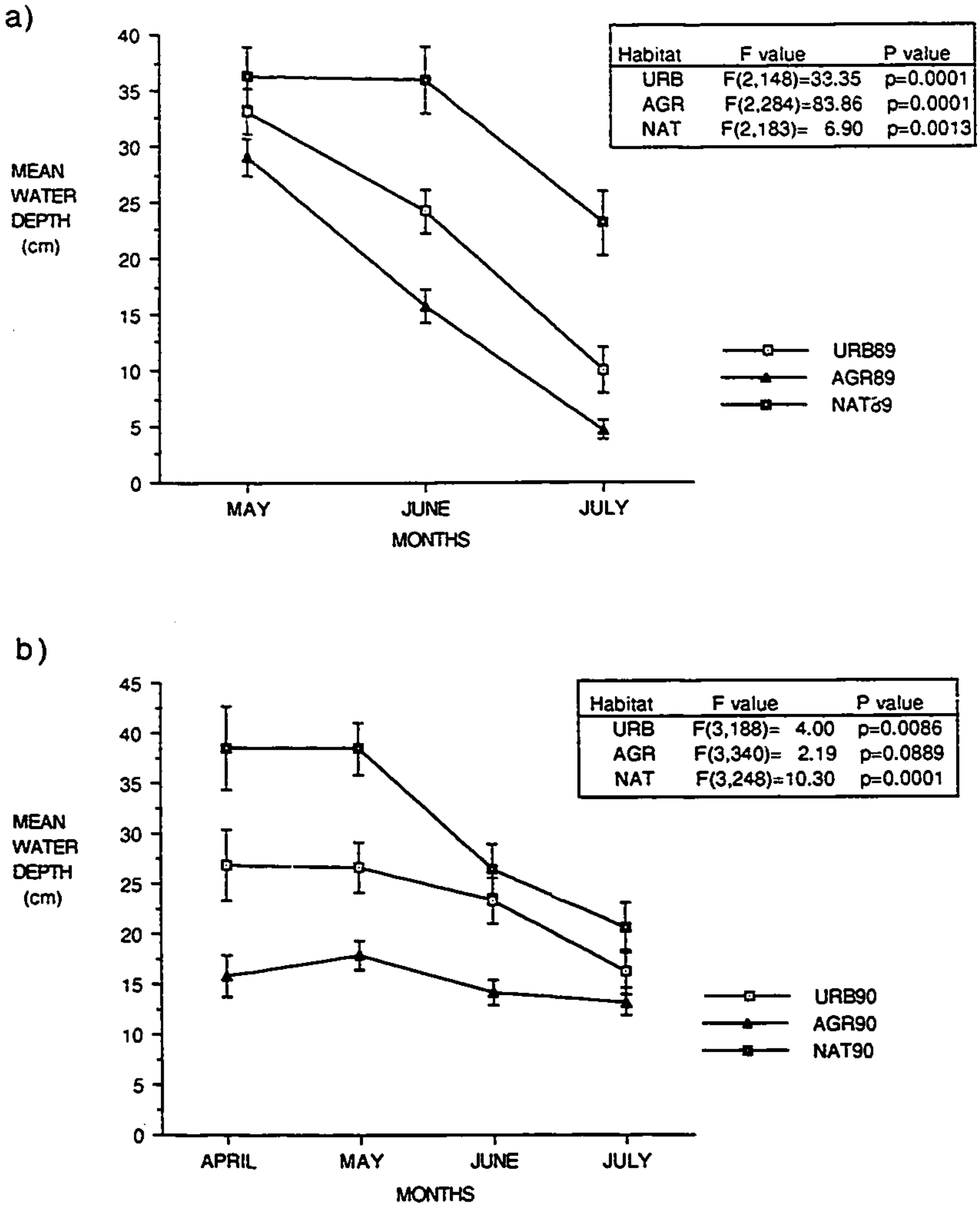
WD and DIST are treated together because the two variables are highly correlated (Table 18). This is because water depth increases with distance from the marsh edge. However, the correlation coefficients become smaller with time in the season (Spearman rank correlation analyses, Rho values corrected for ties. Urban area: Rho=0.70, $p<0.01$, N=13; Agric. area: Rho=0.59, $p<0.025$, N=13; Natural area: Rho=0.73, $p<0.01$, N=13). This is due to a decrease in water levels as the marshes were drying out during the summer (Fig. 10). Natural marshes were deeper than urban marshes, which in turn, were deeper than agricultural marshes. Late in the season, water level was greatly reduced in every marsh and only a floating mat of mud and submerged vegetation remained. The "water barrier" no longer prevailed presumably allowing mammalian predators to invade the marsh habitats. Water depth in agricultural marshes did not

Table 18: Pearson correlation coefficients (r) between WD and DIST.

TRIALS	N	r
URBA90W	57	-0.71
URBM89W	50	-0.82
URBM90W	63	-0.70
URBM89P	48	-0.81
URBM90P	60	-0.78
URBJ89W	59	-0.75
URBJ90W	63	-0.72
URBJ89P	58	-0.77
URBJ90P	64	-0.71
URBJY89W	59	-0.48
URBJY90W	62	-0.63
URBJY89P	58	-0.48
URBJY90P	64	-0.62
AGRA90W	104	-0.56
AGRM89W	97	-0.77
AGRM90W	103	-0.73
AGRM89P	97	-0.81
AGRM90P	103	-0.62
AGRJ89W	106	-0.64
AGRJ90W	105	-0.55
AGRJ89P	105	-0.62
AGRJ90P	105	-0.61
AGRJY89W	106	-0.44
AGRJY90W	103	-0.57
AGRJY89P	105	-0.39
AGRJY90P	105	-0.59
NATA90W	96	-0.65
NATM89W	88	-0.76
NATM90W	96	-0.70
NATM89P	86	-0.68
NATM90P	96	-0.73
NATJ89W	93	-0.69
NATJ90W	96	-0.65
NATJ89P	93	-0.69
NATJ90P	96	-0.66
NATJY89W	93	-0.50
NATJY90W	95	-0.56
NATJY89P	93	-0.58
NATJY90P	96	-0.61

Note: All correlation coefficients are significant at the $p<0.0001$ level.

Figure 10: Mean water depth (± 1 SE) for all nests located in the marsh habitat of urban, agricultural and natural areas in a) 1989 and b) 1990. Results of one-factor ANOVA are in the boxes.



a)

Habitat	F value	P value
URB	F(2,148)=33.35	p=0.0001
AGR	F(2,284)=83.86	p=0.0001
NAT	F(2,183)= 6.90	p=0.0013

b)

Habitat	F value	P value
URB	F(3,188)= 4.00	p=0.0086
AGR	F(3,340)= 2.19	p=0.0889
NAT	F(3,248)=10.30	p=0.0001

decrease in 1990 because water was already relatively shallow early in the season.

Comparison between areas

Results of the previous analyses suggest that nests located in the three areas are under different predation pressures. To determine in which area nests are subject to the lowest chance of predation, I did a total of 26 comparisons between these areas with respect to nest type, location, and time in the season (Table 19). For each comparison, I assigned each area to one of the following categories: Highest if the focal area experienced higher predation rate than the other areas; equal if there was no significant difference in predation rates among the three areas; lowest if nests in that area suffered lower predation than in the other areas; and middle if nests in that particular area experienced intermediate predation rates than in the other two areas. For example, in the trial where waterfowl nests were located in the upland area in May 1989, urban and agricultural areas were assigned to the highest category, whereas natural area was assigned to the lowest category. This procedure was performed for all 26 trials described in Table 19.

The compilation of all the assignments is shown in Table 20. No significant effect of habitat type on nest predation was found in more than half (16/26) of the trials. Urban and natural areas were assigned only twice and three times to the lowest category, respectively, whereas agricultural area was assigned only twice to the highest category. In general, nests in urban areas seemed to be exposed to similar predation

Table 19: Comparison of nest predation rates in urban (URB), agricultural (AGR) and natural (NAT) areas for waterfowl (W) and passerine (P) nests located in the upland and the marsh habitats.

NESTS	X^2 (df=2)	Prob. (p)	N	CONCLUSION
W,upland,April,1990	0.92	0.6306	148	URB=AGR=NAT
W,upland,May,1989	60.20	0.0001	139	URB=AGR>NAT
W,upland,May,1990	13.89	0.0010	148	NAT>URB=AGR
W,upland,June,1989	0.37	0.8313	148	URB=AGR=NAT
W,upland,June,1990	5.73	0.0569	150	URB=AGR=NAT
W,upland,July,1989	35.32	0.0001	148	NAT>URB>AGR
W,upland,July,1990	2.81	0.2451	151	URB=AGR=NAT
P,upland,May,1989	1.63	0.4433	139	URB=AGR=NAT
P,upland,May,1990	2.30	0.3162	149	URB=AGR=NAT
P,upland,June,1989	36.81	0.0001	148	NAT>URB>AGR
P,upland,June,1990	9.32	0.0095	150	NAT>URB=AGR
P,upland,July,1989	28.82	0.0001	147	URB=NAT>AGR
P,upland,July,1990	4.14	0.1265	150	URB=AGR=NAT
W,marsh,April,1990	2.98	0.2253	109	URB=AGR=NAT
W,marsh,May,1989	0.73	0.6960	96	URB=AGR=NAT
W,marsh,May,1990	2.53	0.2820	114	URB=AGR=NAT
W,marsh,June,1989	5.67	0.0587	110	URB=AGR=NAT
W,marsh,June,1990	4.14	0.1262	114	URB=AGR=NAT
W,marsh,July,1989	13.93	0.0009	110	URB=NAT>AGR
W,marsh,July,1990	16.72	0.0002	109	URB=NAT>AGR
P,marsh,May,1989	7.01	0.0301	92	URB=AGR=NAT
P,marsh,May,1990	3.35	0.1877	110	URB=AGR=NAT
P,marsh,June,1989	32.36	0.0001	108	URB=AGR>NAT
P,marsh,June,1990	16.48	0.0003	115	URB>AGR=NAT
P,marsh,July,1989	8.70	0.0129	109	URB=AGR=NAT
P,marsh,July,1990	6.00	0.0500	115	URB=AGR=NAT

Note: See tables 12-14 for predation rate values.

Table 20: Compilation of the indices given to each area from the results of the comparisons of the predation rates between urban, agricultural and natural areas for all 26 trials. (See text for explanations)

	HIGHEST (ex.:URB>AGR=NAT)	= (ex.:URB=AGR=NAT)	LOWEST (ex.:URB=AGR>NAT)	MIDDLE (ex. URB>AGR>NAT)
URBAN	6	16	2	2
AGRIC.	2	16	8	0
NATURAL	7	16	3	0

pressures as those in natural areas. Nests in agricultural areas, however, seemed to suffer lower predation rates than those in the other two areas (Table 20).

To further examine nest predation patterns, I combined all waterfowl and all passerine nests set up in the two years and compared the predation rates among the three areas (Table 21). Predation on waterfowl nests in the upland was similar in the three areas but passerine nests were more frequently depredated in the upland habitat of natural areas. In the marsh habitat, urban areas were worst in terms of nest predation, and natural areas the safest.

Table 21: Predation rates (n= total sample size) on Waterfowl (W) and Passerine (P) nests in Urban, Agricultural and Natural areas. Data from all months of 1989 and 1990 were combined.

	URBAN	AGRICULTURAL	NATURAL			
NESTS	% pred. (n)	% pred. (n)	% pred. (n)	X^2	P value	Conclusion
W, Upland	68.1 (229)	69.7 (383)	70.2 (420)	0.32	0.8526	URB=AGR=NAT
W, Marsh	63.6 (184)	48.1 (341)	54.0 (237)	11.55	0.0031	URB>AGR=NAT
P, Upland	86.1 (194)	75.1 (329)	95.3 (360)	57.37	0.0001	NAT>URB>AGR
P, Marsh	87.3 (158)	69.1 (291)	54.0 (200)	45.78	0.0001	URB>AGR>NAT

Note: Statistical comparisons between the three areas with 2 df.

DISCUSSION

Several factors may contribute to the observed differences in predation rates among different areas and habitats, as well as to the changes in predation rates that occurred as the season progressed. Site-specific factors such as nest location within a marsh, nest camouflage and vegetation growth, as well as area-specific factors such as water level fluctuations and the predator community dwelling in a given habitat all affected predation rates.

Vegetation growth with time was considerable in all areas (Tables 9-11); although the effect was smaller in the understory of natural areas. As the nests became better camouflaged later in the season, we might expect predation rates to decrease. However, an increase in predator density or efficiency could mask this pattern. In fact, predation rates generally remained constant or increased with time in all habitats. In addition, the stepwise logistic regression analyses performed on waterfowl and passerine nests revealed that nest camouflage played a minor role in preventing nest predation. The amount of water at the nest and the predator density, diversity and seasonal activity in a given marsh thus seem to be the main factors determining the predation patterns observed in the three areas.

Birds are visual predators, whereas mammals mostly rely on scent to find their prey (Storaas, 1988). O'Reilly and Hannon (1989) speculated that birds were not the major predator type on their simulated ptarmigan (*Lagopus lagopus*) nests because good nesting cover did not protect nests from predation. My results also showed that mammals were the most important predators on artificial nests. In addition, a wide variety of small predators can easily destroy the small quail eggs while the hard-shelled chicken eggs offer more resistance to breakage. Such predators were present in all marshes (Appendix 1) and included small birds such as marsh wrens, house wrens (Troglodytes aedon), common grackles and possibly blue jays; small mammals such as chipmunks, possibly red squirrels, and other small rodents; snakes such as garter snakes and possibly northern water snakes. Fretwell (1972) noted that blue jay predation was important on open passerine nests. Marsh wrens destroy eggs of other small birds but cannot destroy the large chicken eggs (Picman, 1977; Picman et al., 1988). In my study, on several occasions in urban and natural areas, chicken eggs in waterfowl nests were displaced and covered with tooth marks. Presumably small mammalian predators were thus unable to break shells of chicken eggs. Such small predators are thought to be responsible for most of the predation events where the predator could not be categorized as avian or mammalian. Predation by large mammals was important in every area. Hence, changes in predation rates with time presumably reflected changes in the density, efficiency and/or diversity of mammalian predators.

Seasonal predation patterns

Predation rates on nests located in the upland habitat of urban areas remained similar throughout the nesting seasons. Avian predation was less important than mammalian predation and tended to decrease with time on waterfowl nests. The constant rate of nest losses with time would presumably reflect a stable community of mammalian predators. The decrease in avian predation on waterfowl nests may have reflected changes in crow activity patterns. Nest predation by crows was also found to be less severe later in the season in other areas (Sugden and Beyersbergen, 1986; Johnson et al., 1989), probably because the growth of vegetation improved nest concealment. I observed a similar pattern of crow activity in the upland habitat of agricultural areas (Fig. 2). Results of the logistic regression analyses confirmed the importance of nest concealment of waterfowl nests against crow predation. The different predation patterns on waterfowl nests observed in the two years (Fig. 6) follow the change in the importance of mammalian predators (Fig. 2). This holds also true for passerine nests in 1990 (Fig. 6). However, the decrease of the 1989 passerine nest losses with time presumably resulted from vegetation growth, which provided better camouflage, although this was not supported by the logistic regression analyses (Table 17). The increase of waterfowl nest losses in the upland habitat of natural areas probably reflected higher density of mammalian predator later in the season (Fig. 2). Small predators such as blue jays, red squirrels and chipmunks were present in the forest throughout the season and their constant activity appears to be reflected in similar passerine nest losses through time.

The predation patterns observed in the marsh habitats were generally similar in all areas. Waterfowl nest losses increased with time in urban, agricultural and natural areas. Because avian predation was very low on these nests, mammals were probably responsible for most of the predation events. Crow predation on nests located in the marsh habitat was unimportant, presumably because of the dense vegetation at water level (Jones and Hungerford, 1972; Picman, 1988; Sullivan and Dinsmore, 1990) and aggression by blackbirds towards these predators (Picman, pers. comm.). The increases in predation rates with time were directly associated with decreasing water level in the marshes. Deep water prevented mammals from invading the marsh habitats. As the marshes dried out, the "water barrier" no longer prevented mammals from foraging in the marsh habitats (see also Giroux, 1981). The increase in mammalian predation on waterfowl nests in the three areas is demonstrated in Figure 2. Mammalian predation on passerine nests follows the same patterns (Fig. 3). However, predation rates did not increase accordingly in urban (Fig. 5) and agricultural areas (Fig. 7). Nest losses were constant in time in these two areas. A large proportion of passerine nest losses in the marsh habitat of urban and agricultural areas were attributed to avian predators. This is related to the presence of nesting marsh wrens and grackles in these marshes. In natural areas, where no marsh wrens nested, mammals were responsible for the observed predation. Early avian predation on passerine nests could result from the presence of transient marsh wrens during their migration period.

Changes in predator number in time and corresponding predation pressures have been noted in several studies. The arrival of young later in the season was probably the cause of increased predation rate in old-field habitats due to the addition of young snakes to the population (Zimmerman, 1984). Higher nest losses to crows were associated with the additional food demands of feeding their young (Götmark et al., 1990). Mammalian activity near a waterfowl nesting area increased after their young were born (Raymond, 1983). Movement pattern changes by mammals can also influence the predation patterns. Raccoons are important nest predators (Greenwood, 1981) and were present in all marshes. Use of wetlands by raccoons has been noted to increase as the season progressed (Fritzell, 1978). Predation on red-winged blackbird nests was more important later in the season for marsh-nesting populations (Goddard and Board, 1967; Caccamise, 1978) and for upland-nesting populations (Dolbeer, 1976). Nest losses to large mammals in several open-nesting bird species increased with time in a variety of habitats (Best and Stauffer, 1980). These observations are consistent with the results obtained from this study. However, other studies reached contradictory results on the change of predation rate with time where nesting success either remained constant (Gates and Gysel, 1978; Martin, 1987; Salathé, 1987) or increased with time (Gottfried and Thompson, 1978; Crabtree et al., 1989). It is difficult to generalize the predation patterns over a wide geographic range because predators, and hence the predation patterns, show geographic variations (Francis, 1971). It is more important to describe the predation patterns and their causes on a more local basis. Weatherhead and Robertson (1977) reached the same conclusions when explaining the contradictory results obtained by several authors on the relationship between nest height and nesting success of red-winged blackbirds.

The change of predation rates with time is related to an increase in mammalian predation. This change may be associated with an increase in predator density. It could, however, also be a consequence of the predators becoming more efficient at finding the nests. After having found some nests, the predators can form a search image for the nests and concentrate their searching effort on that type of prey. This phenomenon was of concern in many previous studies (Tinbergen et al., 1967; Robertson, 1973; Sonerud and Fjeld, 1987). In general, predation rates on waterfowl nests was higher in 1990 than in 1989 in the three areas, whereas is was similar on passerine nests (Table 3). This can also be explained by higher predator density in 1990, or by long-term memory in their searching patterns. Greater predation rates in successive years was observed for corvid predation on artificial nests (Sonerud and Fjeld, 1987; Willebrand and Marcström, 1988). Lenington (1979) reported that higher predation on red-winged blackbird nests in the years following the first field season is widespread in several marsh-nesting populations. This pattern was more variable for upland-nesting populations. She concluded that human activity around the nests could explain these results.

Comparison between waterfowl and passerine nests

Waterfowl and passerine nests data were not pooled together in any analysis because the structure of these two nest types was distinct and offered predators different stimuli (Martin, 1987). Differences in patterns of predation on the two nest types suggest that waterfowl and passerine nests were under different predation pressures. I compared predation rates on waterfowl and passerine nests for all trials in the three areas. Overall, predation on passerine nests everywhere was greater or similar to that on waterfowl nests. These differences can best be explained by different predator communities present in the marshes, rather than by the physical nest parameters.

Water depth under the nest played a role in reducing mammalian predation. Water depth did not differ between waterfowl and passerine nest locations. In addition, nest camouflage was similar for all nests set up in urban, agricultural and natural areas. In certain cases, passerine nests were even better camouflaged than waterfowl nests but this did not affect their survival. The major cause of higher predation rates on passerine nests was probably that the small quail eggs can be destroyed by more predators. The presence of small predators in the studied marshes may have increased the predation pressure on passerine nests while not affecting the predation rates on waterfowl nests.

Ricklefs (1969) suggested that marsh-nesting passerines suffer higher nest losses to predation than waterfowl nests because of the smaller size of their eggs. In his experimental study of nest predation, Janzen (1978) observed that quail eggs were more readily destroyed than chicken eggs. Best and Stauffer (1980) argued that nests of larger birds were less vulnerable to predation by large mammals. These authors were, however, working with real bird populations where parental defense could play a role. My study further confirms this pattern of higher predation rates on small eggs than on large eggs.

Numerous small predators (blue jays, chipmunks, squirrels, mice) were present in the upland habitats of urban and natural areas while relatively few were observed in agricultural areas (Appendix 1). The presence of such predators in urban and natural areas is the main reason why passerine nest losses were greater or similar than waterfowl nests losses in these areas. In agricultural areas, large predators were predominantly the only predators operating in the upland habitat and waterfowl and passerine nests were depredated at the same rate.

Small predators in the marsh habitat of the studied marshes were mostly represented by avian predators. Marsh wrens were nesting in one urban marsh (Gatineau) and in all three agricultural marshes. Grackles were also nesting in high density in the two urban marshes. These birds were responsible for many predation events on passerine nests in the marsh habitat of these two areas. Passerine nests therefore suffered greater or similar losses than waterfowl nests in the marsh habitat of urban and agricultural areas. Predation rates on the two nest types in the marsh habitat of natural areas were similar presumably because few small predators were found in natural marshes.

In areas where small predators were found and where predation by large mammals was low early in the season, passerine nest losses were generally higher than waterfowl nest losses. As the season progressed, predation by large mammals increased and waterfowl nests suffered more. In July, when all the potential predators were present, the two nest types were under high predation pressure. Small predators were usually present throughout the season in areas where they were found. The predator community attacking passerine nests was more diverse and hence predation pressure on these nests should be high. However, passerine nests did not regularly suffer higher predation than waterfowl nests. Predation events were recorded every three days in 1989 and once a week in 1990. The majority of the predation events occurred before my first visit; the remaining nests survived the 13-day period. In a study of red-winged blackbird nesting ecology, Robertson (1973) found that a constant number of nests were depredated irrespective of nest density. He concluded that predator satiation could explained his observation. Under his hypothesis, a fixed number of predators can feed on a certain maximum number of nests, which would vary with predator density. This might explain why some nests were not attacked. However, this does not explain why, late in the season, predation on passerine nests was not higher than that on waterfowl nests (at that time, there were more potential passerine nest predators).

However, it is also possible that there were some locations in the studied marshes that were relatively free from predation. The predators' territories and home ranges cover a fixed surface of the habitats. Small patches of land can be outside the predators foraging territories and hence assure nest survival. Since waterfowl and passerine nest locations were 10 m apart, the overall surface covered by these "safe patches" would likely include similar numbers of the two nest types. If predator density increased with time, the area covered by those patches was reduced, but still included a significant number of nests. Even though camouflage did not differ between successful and depredated nests, the vegetation surrounding the nests offered some protection and nests located inside the predators' foraging territories could nevertheless have survived the 13-day period. This idea is hypothetical but provides a conceptual framework of what could have sometimes happened in the studied marshes.

Comparison between upland and marsh habitats

During this study, the nests were set up in every marsh in two different habitats: upland and marsh. The predation pressure acting on the nests will be directly related to the potential predators that can forage in these habitats. Lower nesting success observed in the adjacent upland in previous studies has been associated with more diverse predator communities inhabiting that habitat because some predators avoided the flooded portion of the marsh (Robertson, 1972; Picman, 1988). In this study, the presence of water seemed to prevent some predators from foraging in the marsh habitats because the drop in water levels in each area is generally associated with an increase in nest predation. Different predators were present in the three areas and their distribution within each area should determine if upland habitats will be safer than marsh habitats.

For all nests in urban areas, predation rates were similar in upland and marsh habitats. Mammals were responsible for most waterfowl nest losses in the marsh habitat. The presence of water thus did not prevent all mammals from foraging in the marsh. Raccoons may be important nest predators in shallow water areas of marshes (Urban, 1970). On the other hand, water depth at the nest locations cannot be totally ruled out as an important factor in preventing nest predation (Table 16). Predators on passerine nests were different in the upland and marsh habitats but nest survival in these habitats was similar. Blue jays, squirrels, chipmunks and garter snakes were the dominant small predators in the upland while marsh wrens and grackles were important in the marsh.

Survival of waterfowl nests was generally lower in the upland than in the marsh in agricultural areas. The "water barrier" argument also applies here because as the marshes dried out (Fig. 10), mammalian predation increased (Fig. 2). The breeding populations of marsh wrens found in all three agricultural marshes were the major differences in the predator communities acting on passerine nests in the upland and marsh habitats. Mammalian predators were generally more important in the upland and avian predators were relatively more important in the marsh. The sharp decrease in nest losses in the upland in 1989 was not followed by a similar pattern in the marsh where marsh wren predation was high throughout the season. This was the only case when nest predation was higher in the marsh habitat (Table 13). In 1990, passerine nest losses in the upland were high and constant which resulted in higher or similar predation rates in the two habitats. Small predators (possibly small rodents) were presumably the most important predators in the upland because a large proportion of the predation events could not be attributed to either mammalian or avian predators.

In natural areas, mammals were responsible for most of the predation on waterfowl and passerine nests. Small predators were generally confined to the upland habitats and water level was relatively high throughout the season (Table 8), hence hindering the predators' foraging activities in the marsh habitat. This could explain why predation rates were generally higher in the upland than in the marsh habitat for all nests.

The role of water in nest survival was noted in several studies (Robertson 1972; Shipley, 1979; Picman 1988; Sullivan and Dinsmore, 1990). Birds nesting on islands are better protected than those on the mainland (Young, 1968; Giroux, 1981). The water barrier acts in two ways. First, it prevents some predators, particularly large mammals, from foraging in deep areas of the marsh; and second, the vegetation may be unsuitable for some of the predators that occur in high density in the adjacent uplands. Water depth under the nest was directly related to the distance from the marsh edge at the nest location. In general, whenever there was a difference in predation rates on nests located in the upland and marsh habitats, one of these two variables (WD, DIST) played a major role in nest survival (Tables 16, 17). Nest location within a given area was therefore critical for its survival.

Comparison between areas

Numerous predation studies have shown that different predators live in different areas (Gottfried, 1978; Janzen, 1978; Zimmerman, 1984; Picman, 1988; this study). In general, predator diversity is lower in areas where the vegetation has been altered (Snow and Snow, 1963; Skutch, 1966). In agricultural areas, tall vegetation is lacking in upland habitats adjacent to marshes and vegetational diversity is therefore reduced, affecting predator diversity. On the other hand, urban development has profound effects on the reproductive success of nesting birds. Urbanization drastically reduces vegetation complexity in the areas adjacent to marshes, therefore, presumably also reducing predator diversity. Studies conducted in Europe, however, concluded that a higher density of generalist predators was related to human density and activity (Andrén et al., 1985; Angelstam, 1986). Wilcove (1985) also noted an increase in the number of some nest predators with urban development. The activities of humans and their pets (many of which are potential nest predators) disturbed nesting birds and reduced the reproductive success of both passerines (Klimstra and Stieglitz, 1957; Howard, 1974; Beissinger and Osborne, 1982) and waterfowl (Heusmann and Burrell, 1974; Montgomery et al., 1975). Ground-nesting passerine species are generally absent in urban areas (Howard, 1974; Beissinger and Osborne, 1982; this study). Large mammalian predators such as the raccoon adapt their behaviour to human presence and can increase their density in urban areas (Whitney and Underwood, 1952 from Schinner and Cauley, 1974; Cauley, 1974). Densities of squirrels and blue jays may also be increased by human activities. More and more people feed the animals in their backyards or in city parks and contribute to their survival. Domestic pets and rats could have been responsible for some nest destructions even though I recorded no direct proof of this. Human disturbance of the original habitat therefore can affect the predator community in two ways. First, predator density is reduced in clear-cut areas; and second, urban development can favor the proliferation of nest predators. My results support these conclusions. The predation rates were higher overall in urban and natural areas than in agricultural areas.

Waterfowl nests set up in the upland habitat of the studied marshes suffered similar predation rates in all three areas. As I noted earlier, predators were more abundant and/or diverse in urban and natural areas than in agricultural areas. On the other hand, crows were responsible for a significant number of predation events in agricultural areas and offset a possible lack of mammalian predators. Predation rates on waterfowl nests located in the marsh habitat of urban areas was the highest of all three areas. Mammalian predators accounted for the majority of nest losses in every area. Water levels in the marshes could explain the observed differences in predation rates. Although urban and natural areas are thought to support similar mammalian predator density and/or diversity, the water in natural marshes was deeper than in urban marshes. Foraging activities of mammals may therefore have been less intense in natural marshes. Similarly, agricultural marshes were shallower than natural marshes. Even if predator density was lower in agricultural areas, their movements would be facilitated by the shallow water relative to natural marshes. This could explain similar predation rates on waterfowl nests in these two areas.

In addition to the large predators found in every area, small predators were also more diverse in the upland habitats of natural and urban areas than in agricultural areas (Appendix 1). The predation rates described in Table 21 reflect these different predator communities operating on passerine nests in the upland habitats. Finally, passerine nests set up in the marsh habitats suffered highest predation in urban areas while natural areas provided the safest nesting sites for marsh-nesting passerines. Avian predators (marsh wrens, grackles) were responsible for a significant proportion of the nest losses in urban and agricultural areas, whereas avian predators were rarely encountered in natural areas. In addition, deep water in natural marshes prevented some mammalian predators from moving far into the marsh. Density and/or diversity of mammalian predators found in the adjacent uplands of urban marshes was higher than in agricultural areas and possibly added more pressure on nests in the marsh habitat of urban areas. Hence, birds and mammals were both important predators on passerine nests in the marsh habitat of urban areas while birds predominated in agricultural areas and mammals in natural areas.

Theoretical and practical implications

Because the fate of real nests was not monitored during this study, I cannot conclude that the predation rates observed on artificial nests apply to the nests of real birds. Previous studies showed that predation rates differed between artificial nests and real nests (Dwernychuk and Boag, 1972; Schranck, 1972) suggesting that comparing the factors responsible for predation on artificial and real nests would be hazardous (Salathé, 1987; Willebrand and Marcström, 1988). The presence or absence of adult birds at the nest might therefore influence nest success. Adult birds can defend their nests against predators through communal defense as it is the case in red-winged blackbird populations (Picman et al., 1988). On the other hand, parental presence can attract predators. Departure from the nest by incubating females increased nest predation (Hammond and Forward, 1956). Brown-headed cowbirds also rely on their hosts' activities to find the nest before removing an egg and parasitizing the nest (Thompson and Gottfried, 1976). I found several least flycatcher nests by listening to females begging for food while incubating (pers. obs.). These results suggest that while parental presence can improve nest success through communal defense, their behavior might also lead predators to their nests. The types of predators as well as the breeding birds found in a given habitat should determine if artificial and real nests will suffer similar nest losses under similar predation pressures.

This study was conducted during two nesting seasons. In general, the predation patterns observed were similar in the two years. If these trends were consistent over several consecutive nesting seasons, then predation should present a strong selective force. Because predation is the major cause of nesting failure in birds, this selective force should shape the nesting behavior of birds. If birds can assess the factors that might influence chances of nest predation, it is reasonable to assume that nest site selection will occur according to the predation pattern present in the area. By examining nest site selection, we should be able to establish which factors reduce nest predation. Several studies confirm the association between nest site selection and predation. Leonard and Picman (1986) concluded that spatial segregation between marsh wrens and yellow-headed blackbirds (Xanthocephalus xanthocephalus) was a direct result of the aggressive interactions occurring between the two species due to marsh wren predation. Fretwell (1972) noted that the nest density of open-nesting passerines was reduced in the presence of blue jays. Waterfowl nesting on islands have higher success than those on the mainland because some predators cannot cross the water barrier (Young, 1968; Giroux, 1981). Robertson (1973) observed that nest predation was lower in large red-winged blackbird colonies, possibly because of a predator satiation effect. The concentration of blackbird nests in a small area improved nest protection and might lead to polygyny (Wittenberger, 1976).

The birds found nesting in my marshes also demonstrated interesting nesting patterns. Marsh-nesting passerines (mostly red-winged blackbirds and common grackles) selected their nest sites in the deep water area of the marsh, often at the edge of open water. I also found several nests in small cattail patches that formed isolated islands. These birds were therefore nesting in the safest sites in the marshes. No ground-nesting passerines were observed in urban marshes suggesting that human and predator activities interfered with the birds reproductive duties (see Howard, 1974; Beissinger and Osborne, 1982). However, several species were nesting at the ground level in agricultural marshes where predation rates were lowest of all habitats. In natural marshes, both tree-nesting and ground-nesting birds were observed. Nests in trees were free of predation by large mammals while nests located on the ground could possibly escape detection by avian (blue jays) and small mammalian predators (squirrels, chipmunks). Thus predation is an important factor in shaping the nest site selection in birds, and perhaps other aspects of their social behavior.

Wetlands are disappearing in every part of the country because of human encroachments. This trend is espacially of concern in the Prairie Pothole area because the highest density of nesting waterfowl is found in that region and habitat losses are associated with a sharp decrease in waterfowl production. Nest predation also reduces markedly waterfowl production and one goal of the North American Waterfowl Management Plan is to increase nest success in that region (Canadian Wildlife Service and U.S. Fish and Wildlife Service, 1986). Attemps to control predator populations are a common practice and have sometimes proven to be very efficient (Byers, 1974; Duebbert and Kantrud, 1974; Duebbert and Lokemoen, 1980). The method employed in a predator control experiment must be carefully chosen to avoid killing non-target species. An adequate knowledge of the predator community and their temporal activity patterns is therefore necessary before conducting any predator control study. The identification of the predation patterns and their relative causes should be a prime objective in planning sound management policies aimed at increasing waterfowl production.

Habitat management can also ensure higher success for nesting waterfowl. Construction of artificial islands will provide secure nesting sites for ducks (Giroux, 1981). In marshes where water fluctuations can be controlled, water level should be kept high throughout the nesting season to prevent large mammalian predators from invading the marsh, therefore reducing the possibility of nesting failure due to predation.

CONCLUSIONS

The nest predation patterns in urban, agricultural and natural areas generally reflected the predator community inhabiting each area. The density and diversity of predators varied between areas. The change in predation rates with time, differential nest losses between waterfowl and passerine nests or between upland and marsh habitats, and variations in predation rates among urban, agricultural and natural areas could all be explained in terms of different predators communities in the three areas, different temporal activity patterns of predators and the reluctance of some predators to forage in the marsh habitats.

The density and distribution of artificial nests were different than those exhibited by the birds in my marshes. Hence, a comparison of predation rates between artificial nests and the real nests would be hazardous. My study, however, succeeded in identifying the causes of nest predation in a variety of habitats. The predation patterns described in this study would therefore reflect what is happening regarding predation on nests of birds nesting in marshes and adjacent uplands in southern Québec and southeastern Ontario regions.

The results obtained in this study indicate clear trends in nest predation patterns. However, to further improve our understanding of predation as a selective force, we need to conduct long-term predation studies and sample predation in other geographic regions.

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Appendix 1 : Possible predators and breeding birds living in the studied marshes in the 1989 and 1990 seasons.

MARSH	HUL	GAT	ANG	LAI	RAM	M.BL	CON	KAN
<u>PREDATORS</u>								
<u>AVIAN</u>								
Marsh Wren		X	X	X	X	X		
Blue Jay	X	X			X	X	X	X
American Crow	X	X	X	X	X	X	X	
Catbird	X			X	X			
Marsh Hawk			X	X	X			
Raven							X	
House wren					X			
Common Grackle	X	X	X		X			X
<u>MAMMALS</u>								
Raccoon	X	X	X	X	X	X	X	X
Skunk	X	X	X	X	X	X	X	X
Red Squirrel	X	X				X	X	X
Chipmunk	X					X	X	X
Small rodent	X	X	X	X	X	X	X	X
Mink		?	X	X	X	X		
Dog	X	X	X					
Red Fox	X		X	X	X			
Cats	X	X						
Rats	X	X						
Weasel	X				X		X	
<u>OTHERS</u>								
Water snake							X	X
Garter snake	X	X		X	X		X	

Appendix 1 : (Continued)

MARSH	HUL	GAT	ANG	LAI	RAM	M.BL	CON	KAN
BREEDING BIRDS								
Redwinged blackbird	X	X	X	X	X	X	X	X
Swamp sparrow	X	X	X	X	X	X	X	X
Marsh wren		X	X	X	X			
Black duck	X					X		X
Blue-winged teal	X	?	X	X	X			
Mallard	X	X	X	X	X	?	X	
Gadwall			?	?				
Hooded mergenser							?	
Common gallinule	X	?	X		X			
Sora				?				
Eastern kingbird	X	X	X		X			X
Yellow warbler	X	X	X	X	X	X	X	X
Common yellowthroat	X		X	X	X	X		
Song sparrow	X	X	X	X	X	X	X	
Common grackle	X	X	X		X			X
Virginia rail	X	X	X	X	X		X	X
Least flycatcher		X						X
Common snipe			X	X	X			
Alder flycatcher			X	X		X		
American Crow	X		X	?				
Savannah sparrow			X	X	X			
American bittern			X	?	X			
Bobolink			X	X	X			
Eastern meadowlark			X	X	X			
American robin	X	X			X	X	X	X
G.-crested flycatcher					X	X	X	X
Northern waterthrush							X	
R.-breasted grosbeak						X	X	X
Ruffed grouse						X	X	X
Ovenbird						X	X	X
W.-throated sparrow						X	X	X
Hermit thrush						X		
Wood thrush						X	X	X
Veery						X	X	X

Appendix 1 : (Continued)

MARSH	HUL	GAT	ANG	LAI	RAM	M.BL	CON	KAN
BREEDING BIRDS								
Cedar waxwing	X							
Green heron	?							
Tree swallow	X					X	X	X
Blue jay	?				X	X	X	X
House sparrow	X	X						
European starling	X	X	X				X	X
Killdeer		X		X				
Chipping sparrow		X					X	
American goldfinch			X	X				
Black tern				X	X			
House wren					X			
Winter wren							?	
Mourning warbler						X		
Chesnut-sided warbl.						X		
Nashville warbler						X		X
Yellow-rumped warbl.							X	X
Red-eyed vireo						X		X
Bl.-capped chickadee						X	X	
Mourning dove								X
Brown creeper							?	
Northern oriole		X						
Grey catbird					X			
Eastern wood pewee							X	
American woodcock							X	