

# NEST SITE SELECTION BY EARED GREBES IN MINNESOTA<sup>1</sup>

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**Abstract.** This study examined nest site selection within Eared Grebe (*Podiceps nigricollis*) colonies in terms of nesting synchrony, nearest-neighbor distances, vegetation, exposure, and nest success. Nests in 11 Eared Grebe colonies in Minnesota were initiated over a span of 11–45 days, with most nests in each colony initiated in <11 days. In each of six colonies studied, mean nearest-neighbor distance of the earliest nests was greater than that of the complete colony. Nearest-neighbor distance tended to decrease with an increase in emergent vegetation density. Early nests seemed to form the skeleton of a neighborhood, with later nests filling in or establishing other neighborhoods. In five of six colonies, clutch sizes were larger in earlier nests. No significant difference in egg volume between early and late nests was apparent in the two colonies studied. Early nests were more successful than were late nests in two of four colonies; center nests were more successful than were edge nests at only one of four colonies. Most nest destruction in this study was caused by waves generated by high winds; <2% of nests showed evidence of predation.

**Key words:** Eared Grebe; *Podiceps nigricollis*; *Podicipediformes*; habitat selection; nest-site selection; nesting synchrony.

## INTRODUCTION

Selection of a breeding habitat that meets the reproductive requirements of an animal is critical to its evolutionary fitness (Partridge 1978). Breeding habitat selection by birds probably takes place on several levels (Burger 1985). Among colonial birds, colony site selection and nest site selection are two major levels that are frequently studied (Birkhead and Harris 1985).

Among the colonial grebes, quantitative studies of nest site selection have been conducted on Western Grebes (*Aechmophorus occidentalis*) (Nuechterlein 1975) and on Silver (*Podiceps occipitalis*) and Rolland's (*Rollandia rolland*) Grebes (Burger 1974b). Studies of Eared Grebe (*Podiceps nigricollis*) habitat selection include a study of wetland selection by three grebe species in North Dakota (Faaborg 1976) and recently completed studies of wetland and colony site selection by Eared Grebes in British Columbia (Breault 1990) and in Minnesota (Boe 1991).

Eared Grebes nest over water on shallow, eutrophic wetlands that are particularly vulnerable to yearly fluctuations in water levels, including periodic natural lowering due to drought (Kanttrud et al. 1989). These dynamic water regimes

result in rapidly changing vegetation patterns, which probably contribute to the peripatetic nature of grebe colony formation (Cramp and Simmons 1977).

The objective of this study was to examine nest site selection within Eared Grebe colonies in terms of nesting synchrony, nearest-neighbor distances, vegetation, exposure, and nest success.

## STUDY AREA AND METHODS

I studied nest site selection by Eared Grebes in 11 colonies on nine wetlands in western and southern Minnesota (Fig. 1) from May–August in 1987–1989. These wetlands mark the eastern extent of the Eared Grebe breeding range in North America (Robbins et al. 1983) and the eastern edge of the prairie pothole region of the continent. Most of the wetlands are shallow and hypereutrophic (Heiskary and Wilson 1989), and frequent, high winds and high summer temperatures contribute to rapid evaporation rates (Adams 1988).

Terminology largely follows Gochfeld (1980) and Kushlan (1986): a colony site is the place where colonial nesting takes place, a colony is the collection of birds using the site, a subcolony is a cluster of birds separated from adjacent clusters by space or habitat variation, and a neighborhood is a cluster of birds whose members interact frequently with each other. I use the term colony to refer to either the nests or the birds present. A colony site is the location of a group

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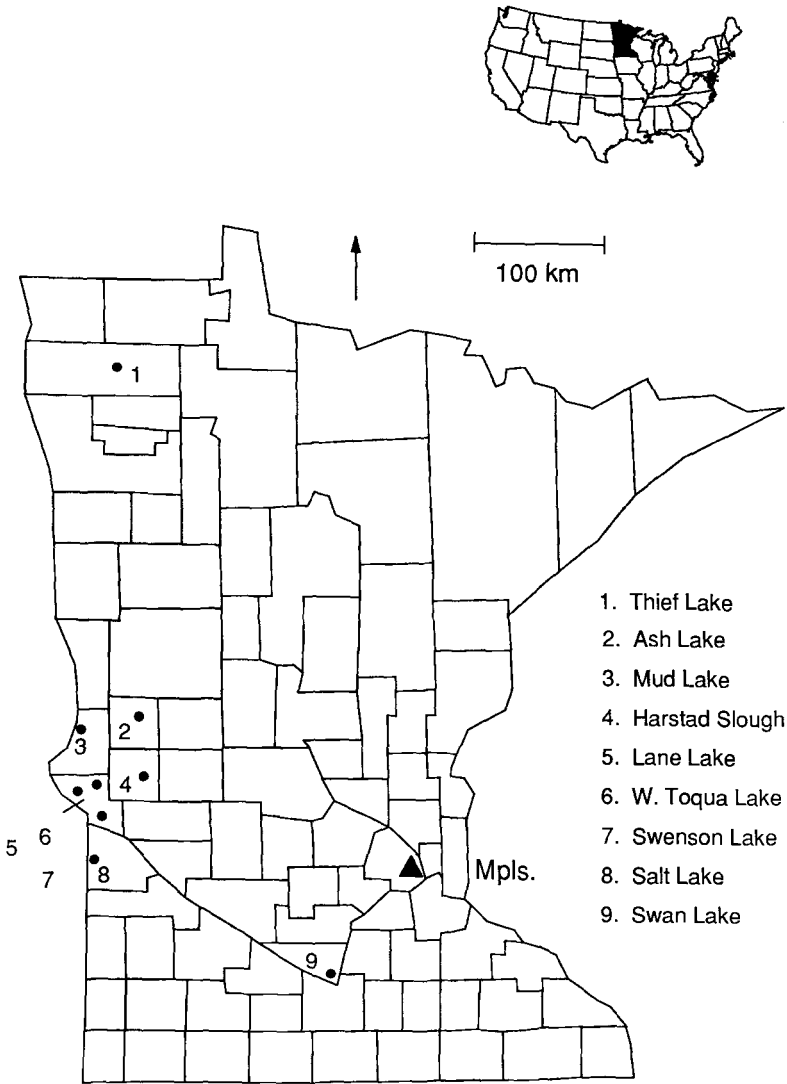


FIGURE 1. Map showing location of Eared Grebe breeding wetlands in Minnesota with colonies marked in 1987–1989.

of nests on a breeding wetland, and nest sites are the locations of nests at the colony site.

Colonies are identified by the name of the breeding wetland and the year. All nests in each colony were marked with uniquely numbered 2 m × 1 cm diameter steel posts placed immediately north of each nest. When nests were marked, water depth was measured on the west side of the nest with a calibrated wooden stick. At Harstad Slough in 1989, nests in both an original colony (I) and a probable re-nesting colony (II),

which nested at a different location after the original colony was destroyed by wind, were marked.

Eggs were numbered uniquely using a felt-tip marker. They were then floated (Westerkov 1950, Nuechterlein 1975) to determine stage of incubation, and their color was recorded. Lengths of flotation categories (Fig. 2) were determined using frequent checks (usually 1–3 day intervals) of 100 eggs found on the day of laying (chalky blue, unstained eggs). Length and breadth were measured to the nearest 0.1 mm with plastic cal-

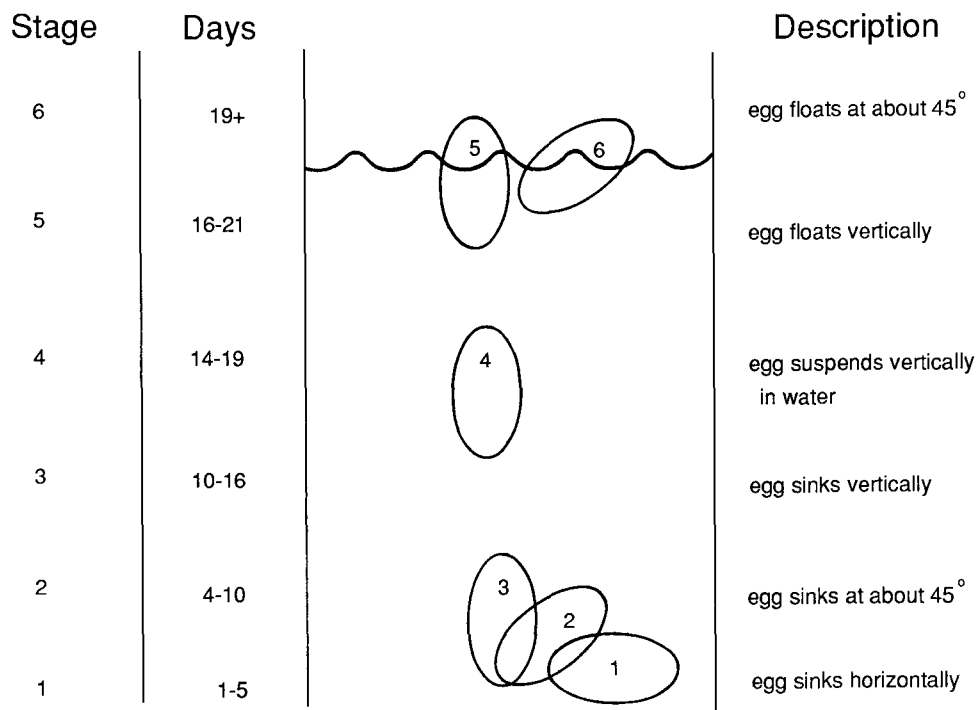


FIGURE 2. Stages of incubation of Eared Grebe eggs determined from flotation of 100 fresh eggs.

ipers at all or most nests in the two West Toqua colonies.

Intervals between nest checks varied and depended upon the distance from other colonies, size of the colony, and status of other marked colonies. Number of checks ranged from two (one after discovery of the colony, one near hatching) to six (Table 1). Number of nests, vegetation type at the colony site, and phase of incubation when the colony was discovered varied (Table 1).

Nest sites were marked photogenically and photographed from the air to determine nest placement. After nest abandonment, nest marking posts were fitted with gallon plastic milk bottles that had been spray-painted fluorescent orange. Low level (71 to 630 m above ground level;  $\bar{x} = 179$  m) 35 mm aerial photographs of these "bottle colonies" were taken from a small, fixed-wing aircraft with a belly camera mount. Prints or Mylar overlays of nest sites were enlarged to scales that allowed labelling with nest numbers. Bottles on the aerial photos were matched with their nest numbers by taking the aerial photo to the colony site or by using nearest-neighbor distances and directions recorded when the nests

were marked. Once nest numbers were matched with bottles on the photo, I determined the scale using ground distances measured between selected nests.

Map Image Processing Software (MIPS) (MicroImages, Inc. 1990), a geographic information and computer-assisted design system, was used to determine x-y coordinates for each marked nest in 10 colonies. Then, a program written by D. H. Johnson using SAS (SAS Institute 1987) statistical software was used to calculate nearest-neighbor distances. Nearest-neighbor distances were calculated for several stages of colony development and were compared for colonies in several vegetation types. I tested further for the effects of social attraction in nest site selection by comparing the incubation stage of the oldest egg in each nest to that in its nearest neighbor in three colonies with late stage incubation data available for them. Because late stages are shorter, they give better resolution of age differences between nests. A Spearman rank correlation was calculated for nests in each of those colonies.

Egg volume was calculated using Hoyt's (1979)

TABLE 1. Number of nests, vegetation at colony site, phase of incubation (E[arly] = oldest egg in stages 1–2, M[iddle] = stage 3, L[ate] = stages 4+) of most nests when colony marked, and number of nest checks in marked Eared Grebe colonies.

Colony	Nests	Vegetation	Phase	Checks
Swenson 87	19	algal mat	E	4
W. Toqua 87	73	dead cattail ( <i>Typha</i> spp.)	E	4
Salt 88	15	pondweed mat ( <i>Potamogeton</i> spp.)	E	4
Swan 88	325	bulrush island ( <i>Scirpus acutus</i> )	E	2
Thief 88	583 <sup>1</sup>	bulrush islands/ pondweed mats	E	3
W. Toqua 88	121	dead cattail	E	5
Ash 89	97	cottonwood ( <i>Populus deltooides</i> )/willow ( <i>Salix amygdaloides</i> and <i>S. interior</i> )	M	2
Harstad I 89	29	dead cattail	E	5
Harstad II 89	88	dead cattail/coontail mat ( <i>Ceratophyllum demersum</i> )	E	6
Lane 89	18	bladderwort ( <i>Utricularia vulgaris</i> )/algal mat	L	4
Mud 89	147	dead goosefoot ( <i>Chenopodium rubrum</i> )	M	2

<sup>1</sup> Original colony.

equation and Preston's (1969) bicone and asymmetry values for grebe eggs. Clutch size was considered the maximum number of eggs recorded in a nest at one time. Since parents and young abandon the nest shortly after hatching, a nest was considered successful if shells without membranes (Girard 1939) were present or if at least one egg was in a late stage (stage 5 or 6, Fig. 2) of incubation on the last nest check. Nest initiation date was determined by using Fig. 2 and setting the date of the nest check as the middle of the stage of incubation recorded on that date. Platforms (nests without eggs) were not included in statistical analyses. Number of nests included in analyses varies slightly due to the presence of platforms and loss of data during fieldwork.

Based on nest initiation dates, nests on each colony map were divided into early, peak, and late nests, with approximately equal numbers in each group (Appendixes A and B). Clutch size, egg size, nest success, and exposure (edge or center) were compared in early, peak, and late nests in several colonies.

Perimeter nests were defined as those with no other nests within a 120° arc around the nest (Appendixes A and B). Once perimeter nests were defined, I used MIPS to calculate the area of the colony. Large colonies ( $\geq 50$  nests) were then divided into three concentric groups of nests (edge, intermediate, and center) with approximately equal numbers of nests in each group (Appendix A). To maximize contrasts, I used only edge and center nests in comparisons. In small colonies ( $< 50$  nests; Appendix B) and in one linear, large colony (West Toqua 87, Appendix A), only edge and center nests were designated. An unusual pattern of nest placement in one large, nonlinear colony (Ash 89, Appendix A) led to a colony map in which all edge nests were also perimeter nests and most remaining nests were designated as center nests to equal approximately the number of edge nests. At West Toqua 87, two discrete subcolonies were formed and were considered separately when designating edge and center nests, but for other analyses, subcolonies were combined. At West Toqua 88 (Appendix A), also with two subcolonies, only the large subcolony was divided into edge, intermediate, and center nests because of sample size limitations in the smaller subcolony.

At some colony sites, emergent stem densities were measured following nest abandonment by counting stems in a 0.25 m  $\times$  0.75 m quadrat regularly placed at 0.75 m intervals along N-S and E-W transects. Nest placement in relation to dead cattail (*Typha* spp.) was studied at the Harstad Slough 89 colony sites using aerial photography. On both colony aerial photographs, I compared the percent cover of dead cattail debris in a 5 mm (1.4 m and 2.0 m ground distances) diameter circular template centered on the nest and in the same size circle centered on randomly selected points within the boundaries of the colony (a rectangle defined by the limits of nests) using an 8 $\times$  magnifying lens.

Although standard deviation of nest initiation dates provides more information on nesting synchrony (Gochfeld 1980), I use two measures of time span to illustrate nesting synchrony because of the infrequency of my nest visits and the estimation of nest initiation dates from categorical flotation data. Span was defined as the number of days between initiation of the first nest and initiation of the last nest in the colony. A second measure of span, 50% span, represents the minimum number of days during the peak nesting

TABLE 2. Median and span of nest initiation dates in 11 marked Eared Grebe colonies, based on flotation of the oldest egg in each nest.

Colony	Span		Days	Median	n	50% span <sup>1</sup>
	From	To				
Swenson 87 <sup>2</sup>	5/25	6/12	19	6/4	19	8
W. Toqua 87	5/29	7/6	39	6/8	71	9
Salt 88	6/30	7/21	22	7/9	14	10
Swan 88	5/22	6/27	37	5/31	320	5
Thief 88 <sup>3</sup>	6/6	6/16	11	6/13	583	1
W. Toqua 88	5/7	6/14	39	5/27	114	7
Ash 89	6/5	7/15	45	6/21	95	7
Harstad I 89 <sup>4</sup>	6/4	6/16	16	6/12	25	2
Harstad II 89	6/18	7/19	32	6/29	78	11
Lane 89	6/25	7/21	27	6/29	12	4
Mud 89 <sup>5</sup>	6/3	6/18	16	6/8	138	3

<sup>1</sup> Minimum number of days during peak nesting period in which 50% + 1 nests established.

<sup>2</sup> Colony destroyed in thunderstorm 6/16.

<sup>3</sup> Colony destroyed in storm about 6/25.

<sup>4</sup> Colony destroyed by high winds 6/19.

<sup>5</sup> Colony abandoned nests late in incubation, probably due to low water levels.

period in which 50% + 1 nests were established (adapted from Gochfeld 1980).

Because of small sample sizes, I did not conduct statistical tests on most small colonies ( $n = 4$ ). For some large colonies ( $n = 6$ ), I used one-way analysis of variance (ANOVA) to test for significance of differences in clutch size and egg size among early, peak, and late nests. Duncan's multiple range test was used to make paired comparisons when an ANOVA showed significant differences ( $P < 0.05$ ). I used Student's  $t$ -tests to compare clutch size and egg size in edge nests and center nests.  $G$  tests were used for comparisons involving nominal data. Spearman rank correlations and parametric tests were run on a microcomputer using Statistix (NH Analytical Software 1986), and  $G$  tests were run using Lotus 1-2-3 (Lotus Dev. Corp. 1984). Because of the complexity of Thief 88 (nests were distributed among 44 bulrush islands and 2 surface mats), that large colony is excluded from most analyses in this manuscript.

## RESULTS

The number of nests in colonies marked in this study varied widely, from 15 to over 580 nests. The three smallest colonies nested on surface mats of filamentous green algae, sago pondweed (*Potamogeton pectinatus*), or bladderwort (*Utricularia vulgaris*). A variety of dead or living emergent species anchored nests at the remaining colonies (Table 1).

TABLE 3. Mean and SD of nearest-neighbor distances (m) in several stages of colony development (E[arly], P[eak], L[ate];  $n$  = number of nests) in six Eared Grebe colonies and nest densities of complete colonies.

Colony	Stage	n	$\bar{x}$	SD	Nests/100 m <sup>2</sup>
Swan 88	E	75	1.23	1.08	
Swan 88	L	315	0.85	0.30	41.3
Ash 89	E	16	6.21	9.80	
Ash 89	L	93	0.78	0.46	14.2
West Toqua 87	E	17	6.56	5.01	
West Toqua 87	P	49	4.53	3.45	
West Toqua 87	L	70	5.16	4.97	3.0
West Toqua 88	P	47	2.93	4.61	
West Toqua 88	L	119	2.60	2.93	8.0
Mud 89	E	30	2.37	1.32	
Mud 89	L	147	1.60	0.58	16.0
Harstad II 89	E	25	3.25	2.89	
Harstad II 89	P	52	2.98	1.80	
Harstad II 89	L	88	3.18	2.20	2.8

## NESTING SYNCHRONY

Colonies with the shortest span of nest initiation dates were destroyed by storms or abandoned early because of low water levels (Table 2). Although destroyed early, the large number of nests established in a short time at Thief 88 portrays the frenzy of activity observed at the colony site. Among colonies not destroyed or abandoned early ( $n = 7$ ), correlations of colony size with the span of nest initiation dates ( $r_s = 0.63$ ,  $P < 0.10$ ) and the 50% span ( $r_s = -0.36$ ,  $P < 0.50$ ) are not significant.

## NEAREST NEIGHBORS AND NEST DENSITY

Colonies in green emergent vegetation tended to have shorter nearest-neighbor distances than did those in dead emergents or on surface mats (Fig. 3). In most colonies, distances of nearest-neighbor nests decreased as the colony progressed through later stages of development (Table 3). Swan 88, with the greatest emergent stem density of colony sites in this study ( $\bar{x} = 144$  stems/m<sup>2</sup>,  $SD = 84$ ), also had the greatest nest density and one of the smallest mean nearest-neighbor distances (Table 3). For all three colonies tested, the stage of incubation of the oldest egg in each nest and the stage of the oldest egg in its nearest neighbor were positively correlated ( $r_s = 0.36$ – $0.68$ ,  $P < 0.001$  for each, Table 4).

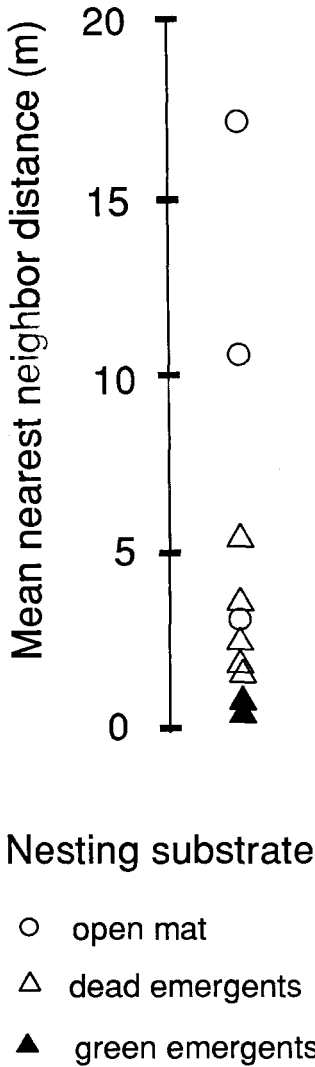


FIGURE 3. Nesting substrate and nearest-neighbor distances (m) of Eared Grebe colonies marked in 1987–1989.

**SMALL COLONIES**

Three of the four small colonies (Swenson 87, Salt 88, and Lane 89) nested on surface mats of algae or submergent macrophytes; the fourth (Harstad I 89) nested in cattail stubble. Two of the four (Swenson 87 and Harstad I 89) were destroyed about midway through incubation by a storm and high winds. Nesting success at the remaining two colonies (Lane 89 and Salt 88; Appendix B) was 39% and 33%, respectively. Among the four colonies, eggs in only one nest were predated. At each nest check, one or a few

TABLE 4A–C. Frequency distribution of incubation stage (1–6, H = hatched) of oldest egg in each nest and in its nearest neighbor at W. Toqua 88 on 10 June (A), W. Toqua 87 on 26 June (B), and Mud 89 on 21 June (C). Spearman rank correlations are given below each subtable.

Nest inc. stage	Nearest neighbor inc. stage						
	1	2	3	4	5	6	H
1		1					
2		4	4	3	1		
3		3	7	1	1		
4	2	4	3	5	2	1	2
5				4	3	4	2
6				1	2	3	1
H				2	1	1	7

$r_s = 0.68, P < 0.001, n = 71.$

Nest inc. stage	Nearest neighbor inc. stage						
	1	2	3	4	5	6	H
1							
2			1			1	
3			3	3	1	2	
4	1		2	7		3	
5			2	1	1	7	
6			1	3	6	11	3
H					1	1	2

$r_s = 0.46, P < 0.001, n = 63.$

Nest inc. stage	Nearest neighbor inc. stage				
	1	2	3	4	5
1	9	5	5	1	1
2	6	15	7	5	2
3	4	9	18	13	3
4		2	17	6	
5		2	2		1

$r_s = 0.36, P < 0.001, n = 133.$

nests were found emptied or sunken, suggesting abandonment. Nests require frequent upkeep to maintain their integrity, and a light wind may generate sufficient wave action to empty an abandoned nest.

**LARGE COLONIES**

*Vegetation.* Emergent stem densities varied widely among and within colony sites. Mean density of bulrush at the Swan 88 colony site was 144 stems/m<sup>2</sup> (SD = 84), mean density of dead goosefoot at the Mud 89 colony site was six stems/m<sup>2</sup> (SD = 7), mean density of dead cattail at the West Toqua 88 colony site was 8 stems/m<sup>2</sup> (SD = 11), and willow and cottonwood density at the Ash 89 colony site was 10 stems/m<sup>2</sup> (SD = 10).

TABLE 5. Successful (+) and unsuccessful (0) early, peak, and late nests in four large Eared Grebe colonies.

	Colony							
	W. Toqua 87		W. Toqua 88		Swan 88		Harstad II 89	
	+	0	+	0	+	0	+	0
Early	23	0	34	1	95	18	12	13
Peak	23	1	32	9	80	15	12	12
Late	20	4	30	8	89	24	5	21
<i>G</i>	6.231		8.094		1.420		1.300	
<i>P</i>	<0.03		<0.01		<0.25		>0.50	

Nest sites had more dead cattail debris than did random points at both Harstad Slough colony sites (colony I:  $t = -3.85$ ,  $df = 66$ ,  $P = 0.0003$ ; colony II:  $t = -3.85$ ,  $df = 174$ ,  $P = 0.0002$ ).

*Early, peak, and late nests.* Two of the four large colonies analyzed showed a significant difference in success among early, peak, and late nests (Table 5). The two West Toqua colonies showed significant differences despite having relatively few unsuccessful nests in each colony. Swan 88, also a very successful colony, showed no significant difference in the distribution of unsuccessful nests among early, peak, and late nests. Two of the large colonies, Ash 89 and Mud 89, were omitted from these analyses. Ash 89 was probably very successful, but the final nest check was delayed, and it is likely that shells were gone from some nests by the time they were checked. Mud 89 was abandoned prematurely, probably because of low water levels. A colony check planned for about the time of hatch found empty nests. As at Ash Lake, some shells may have been lost during the unknown number of days between colony abandonment and the final nest check. However, based on the approximate timing of nest abandonment, it is not likely that most eggs at Mud Lake hatched.

In all colonies except West Toqua 88, one-way ANOVA showed a significant difference in clutch

size among early, peak, and late nests (Table 6). In most cases, paired comparisons showed that clutches of late nests were smaller than were those of early and peak nests. Egg measurements were also taken at West Toqua 87 and West Toqua 88. At West Toqua 87, one-way ANOVA showed no significant difference ( $P = 0.34$ ) in egg volume among early ( $n = 23$ ,  $\bar{x} = 20.05$  cm<sup>3</sup>), peak ( $n = 24$ ,  $\bar{x} = 20.04$ ), and late ( $n = 23$ ,  $\bar{x} = 19.56$ ) nests. Similarly, no significant difference ( $P = 0.31$ ) was found among early ( $n = 23$ ,  $\bar{x} = 20.00$ ), peak ( $n = 23$ ,  $\bar{x} = 20.40$ ), and late ( $n = 23$ ,  $\bar{x} = 20.01$ ) nests at West Toqua 88.

Only the largest of the six colonies studied, Swan 88, showed a significant difference in the spatial distribution of early, peak, and late nests, with a greater proportion of early nests in the center than on the edge (Table 7).

*Edge and center nests.* Of four colonies tested, only Swan 88 showed a significant difference in success ( $P < 0.001$ ; Table 8) and clutch size ( $P = 0.001$ ; Table 9) between edge and center nests. No significant difference ( $P = 0.40$ ) in egg volume was found between edge ( $t$ -test;  $n = 36$ ,  $\bar{x} = 19.76$ ,  $SE = 0.224$ ) and center ( $n = 34$ ,  $\bar{x} = 20.02$ ,  $SE = 0.206$ ) nests at West Toqua 87 or between edge ( $n = 25$ ,  $\bar{x} = 20.71$ ,  $SE = 0.330$ ) and center ( $n = 28$ ,  $\bar{x} = 20.64$ ,  $SE = 0.281$ ) nests at West Toqua 88 ( $P = 0.86$ ).

TABLE 6. Comparison of clutch size in early, peak, and late nests in six marked Eared Grebe colonies using one-way analysis of variance. Differences between means followed by the same letter were not significant (Duncan's multiple range test).

Colony	Early			Peak			Late			<i>F</i>	<i>P</i>
	<i>n</i>	$\bar{x}$	Var	<i>n</i>	$\bar{x}$	Var	<i>n</i>	$\bar{x}$	Var		
W. Toqua 87	23	4.09 A	0.27	24	3.63 B	0.42	24	3.25 C	0.54	10.03	0.001
Swan 88	113	3.22 A	0.30	95	3.07 A	0.28	108	2.52 B	0.65	36.20	0.001
W. Toqua 88	35	3.49	0.67	41	3.07	1.17	38	3.16	0.68	2.05	0.131
Ash 89	33	3.24 A	1.13	37	3.03 AB	0.42	25	2.64 B	0.66	6.79	0.002
Harstad II 89	31	2.97 A	1.83	28	3.00 A	0.89	26	2.27 B	1.01	3.63	0.030
Mud 89	41	3.47 A	0.56	49	3.20 A	0.67	48	2.44 B	0.72	19.95	0.001

TABLE 7. The number of early, peak, and center nests that were edge (edg) or center (cen) nests in six Eared Grebe colonies.

	W. Toqua 87		Swan 88		W. Toqua 88 <sup>1</sup>		Ash 89		Harstad II 89		Mud 89	
	Edg	Cen	Edg	Cen	Edg	Cen	Edg	Cen	Edg	Cen	Edg	Cen
Early	12	11	23	43	7	13	12	17	5	11	12	15
Peak	10	14	24	26	12	10	18	15	7	7	13	21
Late	14	10	57	28	12	7	19	13	14	6	18	13
<i>G</i>		1.37		16.09		3.33		2.10		5.52		0.98
<i>P</i>		>0.50		<0.001		<0.25		>0.25		<0.10		>0.50

<sup>1</sup> Large subcolony only.

#### NEST ABANDONMENT AND DESTRUCTION

*Weather and predation.* Waves generated by high winds with or without rain or hail were responsible for the destruction of at least 1,030 of 2,370 (44%) nests examined or marked in this study.

During nest checks, only 36 eggs in 31 nests showed any signs of predation, resulting in an overall nest predation rate of <2%. No colony had a nest predation rate greater than 3%. No evidence of mammalian predation was observed. American Coots (*Fulica americana*) appeared to be responsible for most egg predation and were observed harassing grebes during both colony establishment and hatching. They appeared to be attempting to appropriate grebe nests for use as roosting platforms.

Franklin's Gulls (*Larus pipixcan*) and Forster's Terns (*Sterna forsteri*) were also observed harassing grebes (swooping low over grebes on the water and forcing them to "crash-dive") and roosting on temporarily abandoned grebe nests, but no evidence of egg destruction by these species was observed. Harassment by Black-crowned Night-Herons (*Nycticorax nycticorax*) may have contributed to early abandonment of the colony at Mud Lake.

*Investigator disturbance.* During nest checks, grebes congregated within sight of the colony site. Occasionally, a bird returned to the nest to check eggs, cover or re-cover eggs or incubate for a short time, then left again. When I left the colony,

most birds returned immediately (within 5 min) to their nests. If possible, visits were kept short, but I monitored the level of disturbance to the group and altered the length of a visit accordingly.

Birds off their nests during nest checks were often harassed by coots, but during most colony checks, coots did not venture into the colony. However, coots occasionally pecked a few eggs, and my disturbance may have contributed to this predation. Yellow-headed Blackbirds (*Xanthocephalus xanthocephalus*) seemed to search nests for invertebrates while grebes were off their nests during nest checks at Swan Lake. One fresh, small peck was observed in one egg immediately after a blackbird left the nest.

#### DISCUSSION

##### NESTING SYNCHRONY

Synchronous breeding may improve food finding through social foraging (Ward and Zahavi 1973, Emlen and Demong 1975), while predator swamping, predator confusion, and collective defenses of the young are three potential anti-predator advantages of reproductive synchrony (Ims 1990). Darling (1938) suggested that increased social stimulation in larger colonies led to earlier laying and increased synchrony, resulting in decreased predation and increased success of larger colonies. Since the presentation of Darling's hypotheses, biologists have been examining bird colonies for support for those hypotheses, with equivocal results (Gochfeld 1980, Ryder 1980). Burger (1979), for example, studied Herring Gull (*Larus argentatus*) colonies and found that, up to a critical size, the standard deviation of nest initiation date was negatively correlated with colony size, while Knopf (1979), studying American White Pelicans (*Pelecanus erythrorhynchos*), found synchrony independent of colony size.

TABLE 8. Successful (+) and unsuccessful (0) edge and center nests in four Eared Grebe colonies.

Colony	Edge		Center		<i>G</i>	<i>P</i>
	+	0	+	0		
W. Toqua 87	7	19	11	13	1.38	<0.25
Swan 88	72	36	89	8	20.48	<0.001
W. Toqua 88	26	5	28	2	1.39	<0.25
Harstad II 89	34	2	32	5	1.38	<0.25



TABLE 9. Comparison of clutch size in edge and center nests in six Eared Grebe colonies.

Colony	Edge			Center			<i>t</i>	<i>P</i>
	<i>n</i>	$\bar{x}$	SE	<i>n</i>	$\bar{x}$	SE		
W. Toqua 87	36	3.75	0.10	37	3.41	0.16	1.80	0.073
Swan 88	104	2.62	0.01	97	3.04	0.01	-3.70	0.001
W. Toqua 88	31	3.00	0.18	30	3.43	0.13	-1.93	0.056
Ash 89	42	3.00	0.12	42	2.79	0.18	0.98	0.334
Harstad II 89	26	2.39	0.25	24	2.71	0.22	-0.97	0.338
Mud 89	43	2.98	0.15	49	3.10	0.13	-0.64	0.532

In this study, the frenzy of nest-building activity observed and the establishment of most nests in all successful colonies in <11 days suggest a moderate to highly synchronous nest establishment strategy. In most colonies, however, there were one or two nests that were established well ahead of the main group, and often there were late nests started well after most nests.

Nesting synchrony in some colonies may have been associated more with weather conditions than with differences in social stimulation. For example, recurrent, small scale nest washouts probably lengthened the span of nest initiation dates at Harstad II 89, while drought conditions and decreasing water levels may have hastened nest abandonment and discouraged later nesting at Swan 88 and West Toqua 88. Decreasing water levels probably spurred early abandonment at Mud 89, and high winds or storms destroyed the Harstad I 89, Swenson 87, and Thief 88 colonies, thereby truncating the span of nest initiation dates for those colonies. At Ash 89, an extraordinarily secure and protected colony site, late clutches were laid in hatched-out platforms, effectively extending the span of nest initiation dates for this colony.

By restricting their mobility, nesting increases the vulnerability of most birds to predation. The small size, weak call, and evasive response of Eared Grebes to disturbance by most potential predators (diving or swimming away to a safe distance) make their nests especially vulnerable. The frequency with which grebes nest near noisier, more aggressive colonial birds (Durango 1954; Burger 1984; Fjelds  and Jensen, unpubl. manuscript) suggests that such antipredator strategies are important to their survival.

Certain antipredator advantages may bring grebes together, and breeding synchrony, itself a successful antipredator strategy, may, in some cases, be forced upon them by the ephemeral nature of the colony site. Windstorms were the

principal cause of nest destruction in this study, but they occur sporadically and at unpredictable intervals. If a group of birds establishes nests as soon as other conditions (e.g., food, vegetation) are met, they may be able to lay, incubate, and hatch eggs before damaging wind occurs, vegetation changes, or the food supply decreases.

Grebes capture food on lakes on which they nest; these lakes are eutrophic, and available evidence suggests that they have abundant invertebrate food sources. Although general information concerning the best feeding areas is probably available to observant birds, it seems unlikely that social foraging is the driving force behind nesting synchrony in grebes.

#### VEGETATION

Characteristics of the vegetation at the colony site may also dictate patterns of nest site selection. In this study, the decrease in nearest-neighbor distance with increasing vegetation density suggests that distance or visual protection from neighbors may be important in nest site selection by Eared Grebes. Within a colony, nests may be placed to decrease intraspecific interference.

Nests were closer together in dense than in sparse vegetation in studies of Yellow-eyed Penguins (*Megadyptes antipodes*) (Sheldon and Davis 1989), Laughing Gulls (*Larus atricilla*) (Thebeau and Chapman 1984), island nesting ducks (Lokemoen et al. 1984), Black-headed Gulls (*Larus ridibundus*) (Burger 1976), and Franklin's Gulls (*Larus pipixcan*) (Burger 1974a). This suggests that sites were selected to give visual protection from neighbors. However, in other studies (Burger 1974b, Becker and Erdelen 1981) selection of sites favoring visual protection from neighbors was not demonstrated.

Vegetation provides stability to nests and is important in the survival of a nest. The pattern of vegetation may dictate the shape of the colony. At Harstad II 89, nests were placed on cattail

debris (stubble and floating rhizomes) in preference to a dense mat of coontail (*Ceratophyllum demersum*) that surrounded the debris. Rather than filling in a broad area, nests were established progressively around the circular band of cattail debris, hence the similarity in nearest-neighbor distances as the colony developed.

#### NEAREST-NEIGHBOR DISTANCES

Nearest-neighbor distances among island nesting ducks (Lokemoen et al. 1984), Franklin's Gulls (Burger 1974a) and Double-crested Cormorants (*Phalacrocorax auritus*) (Siegel-Causey and Hunt 1986) decreased as the season progressed. Decreased levels of aggression later in the nesting cycle may explain such "filling in" of late nests among early nests (Burger 1974a, Lokemoen et al. 1984, Kilpi 1988). Oring (1969) found an increased tolerance to close neighbors among Gadwalls (*Anas strepera*) as the season progressed and drake aggressiveness decreased.

The longer nearest-neighbor distances among early nests in some colonies in this study suggest that early nests form the skeleton of a colony and that later nests fill it in. However, the patterns of nest establishment (Table 4, Appendix A) seem to indicate that nests in most colonies are established by neighborhoods. As a colony ages, later nests fill in "bare spots" in and between the neighborhoods. Increased tolerance as laying progresses to incubation may allow some late nesters to nest closer to early nests than another early nester might have.

#### EARLY, PEAK, AND LATE NESTS

In many species, early nesters are often older birds that generally lay larger clutches and have higher productivity than do late nesters (Gochfeld 1980), and young birds may lay smaller eggs than do older birds (Saether 1990). A significant difference in clutch size between early and late nests was apparent in five of six large colonies in this study. Although no data on age of the grebes in this study are available, the difference suggests that earlier nesters may have been more experienced birds. However, no significant differences in egg volume were detected among early, peak, and late nests at either of the West Toqua Lake colonies. A larger sample size may be needed to overcome the effects of individual variation in egg size.

The similarity of reproductive success between early and late nests may be due in part to the

conservative, somewhat insensitive measure of success used in this study. Detection of a difference in reproductive success between early and late nesting pairs in most colonies may require information about the number of eggs hatched and the quality of the young.

#### EDGE AND CENTER NESTS

Some studies of other colonially nesting species have found differential success between center and edge nests (Coulson 1968, Dexheimer and Southern 1974, Montevecchi 1978), while other studies have found no difference (Knopf 1979, Podolsky 1980, Ryder and Ryder 1981, Kilpi 1988). In this study, only the Swan Lake colony showed a difference in temporal distribution, clutch size, or success between edge and center nests. This may be due to the non-centrifugal nest establishment pattern of most other colonies. In most colonies, nesting in synchronous neighborhoods appeared to be more important in colony patterning than was vying for center nest sites. At Swan Lake, however, the dense emergent vegetation beds provided a visual barrier from even close neighbors, and early nesters established nests closer together than they did in other colonies, in a sense forming a smaller, more compact skeleton that was quickly filled in by other early nests. With the interior of the bulrush island saturated, later nesters may have been limited to the periphery of the colony, leading to a centrifugal nest establishment pattern.

#### CONCLUSIONS

Patterns of Eared Grebe colony establishment and nest site selection are intimately associated with vegetation patterns at the colony site. The diverse colony establishment patterns observed in this study reflect the greatest variety of nesting substrates selected as colony sites. In spite of this diversity, there seem to be a few threads that connect the establishment patterns of colonies.

Vegetation density seems to dictate the mean nearest-neighbor distance found in a colony. Colonies seem to establish by neighborhood, and, as the colonies age, the skeleton formed by the earlier nests is filled in by later nesters. This type of colony establishment usually seems to do away with the hierarchy of center versus edge nests. Nesting synchrony seems firmly under the influence of the weather; drought conditions may hasten abandonment of a colony site, thereby increasing synchrony, while weeks of calm weather

and a secure colony site may encourage late nesters, effectively decreasing synchrony.

The variety of colonies and the variability in nest success seen in this study reinforce the importance of broad geographic and temporal coverage in studies of particular species. The marking of individual birds would also contribute much toward a greater understanding of nest site selection by Eared Grebes. However, capturing grebes is difficult and disruptive to the colony, and, due to the shifting of colony sites from year to year, grebes marked in one year may nest on a different wetland the following year. Until an efficient, field-proven method for identifying individuals, or at least the sex and age of a bird, becomes available, significant pieces of information about Eared Grebe colony establishment will remain missing from the puzzle.

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## APPENDIXES A AND B

Symbol colors indicate early (white), peak (gray), or late (black) nests. Symbol shapes indicate successful (circles) and unsuccessful (triangles) nests and platforms (nests without eggs; asterisks). Perimeter nests, which define the edge of the colony, are joined by lines. In all large colonies but one, edge, intermediate, and center nests are separated by dotted lines. The arrow indicates north.

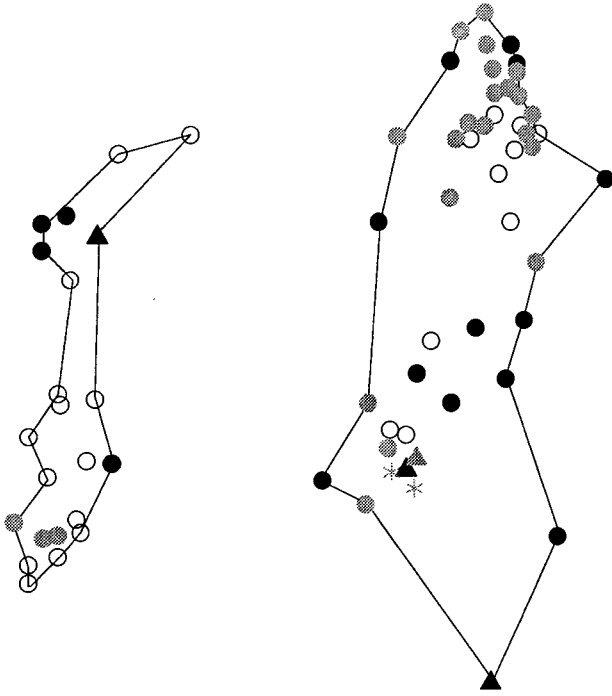
### APPENDIX A. Large colonies.

- Figure A1. Location of nests in West Toqua 87.  
 Figure A2. Location of nests in Swan 88.  
 Figure A3. Location of nests in West Toqua 88.  
 Figure A4. Location of nests in Ash 89.  
 Figure A5. Location of nests in Harstad II 89.  
 Figure A6. Location of nests in Mud 89.

### APPENDIX B. Small colonies.

- Figure B1. Location of nests in Swenson 87.  
 Figure B2. Location of nests in Salt 88.  
 Figure B3. Location of nests in Harstad I 89.  
 Figure B4. Location of nests in Lane 89.

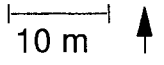
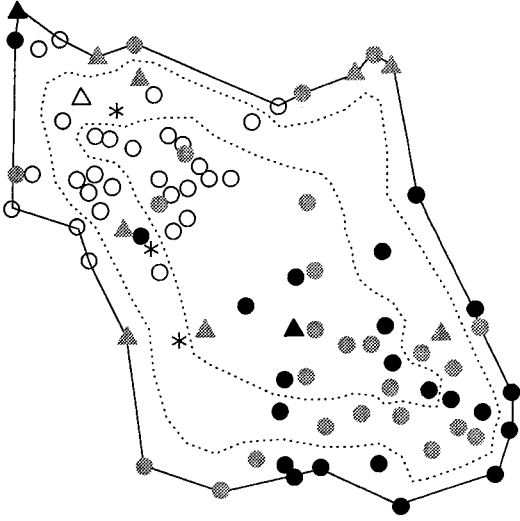
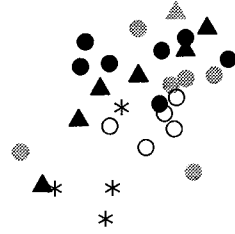
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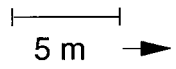
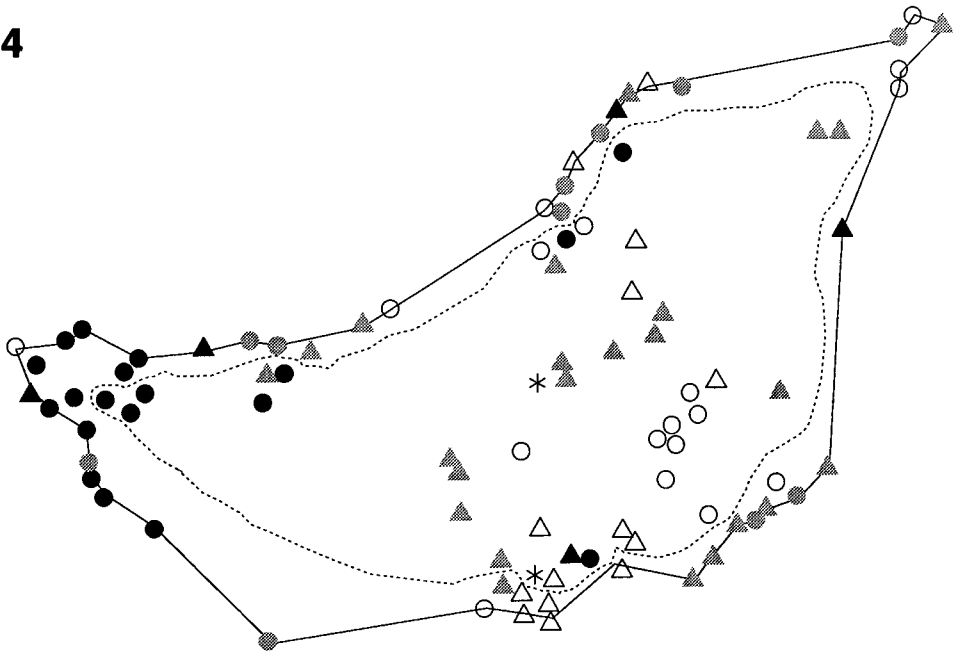
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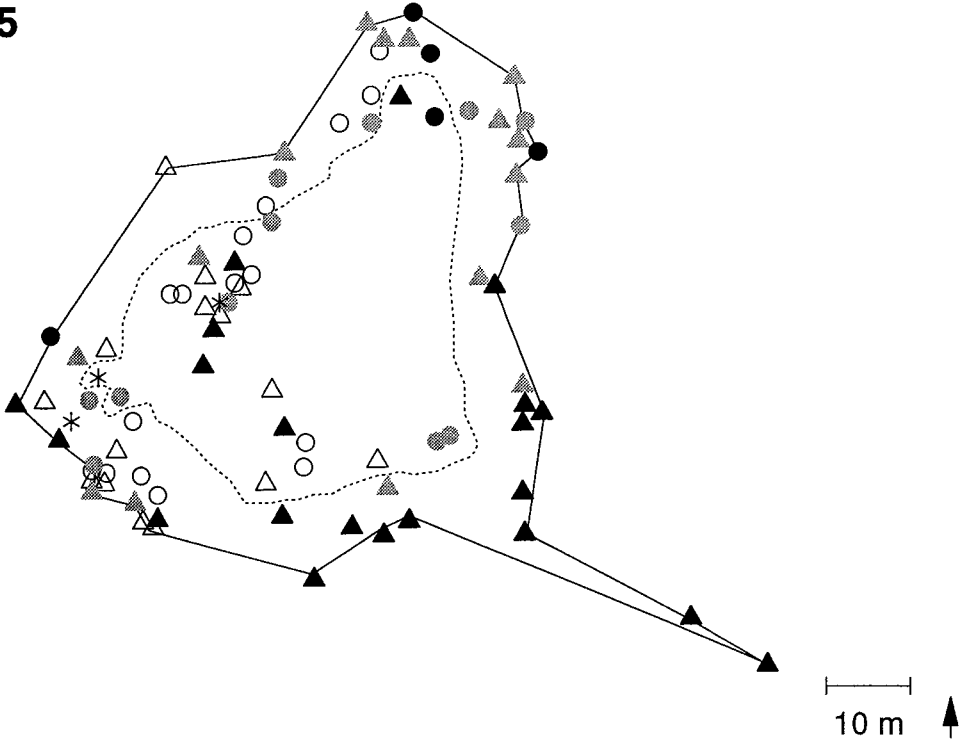
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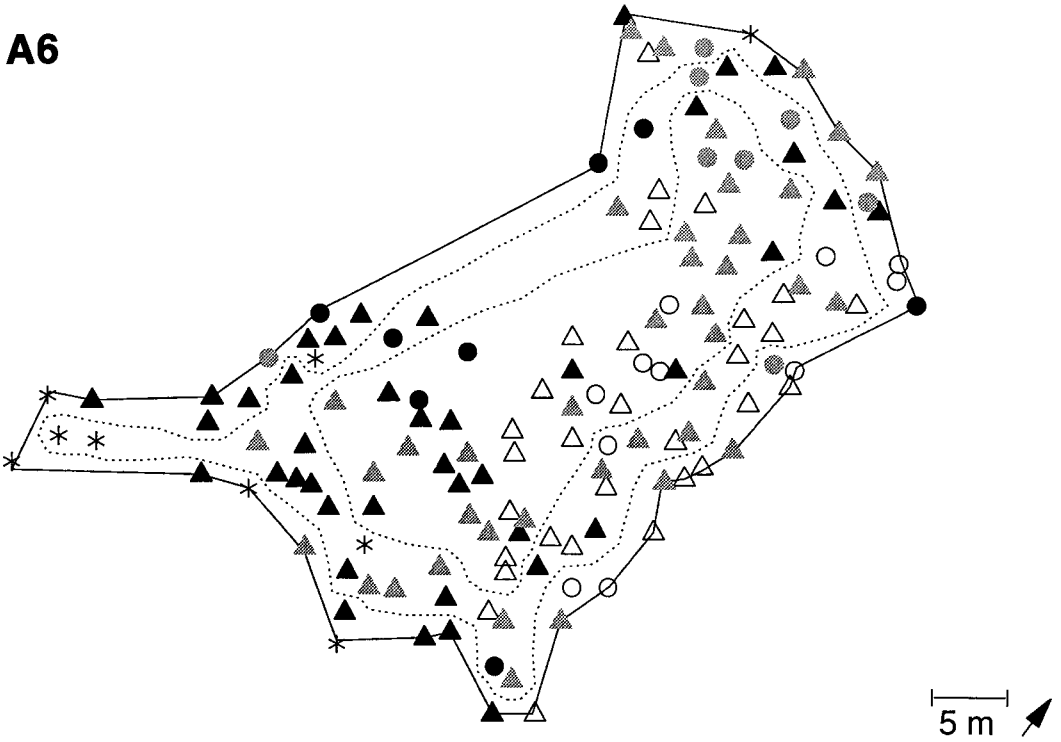
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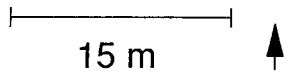
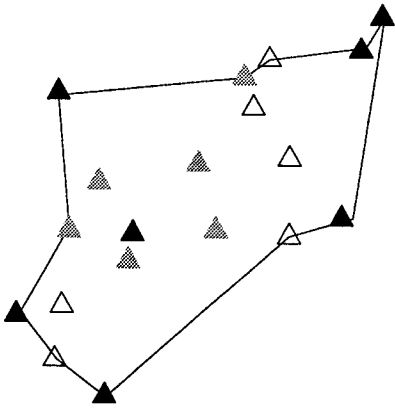
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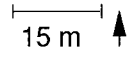
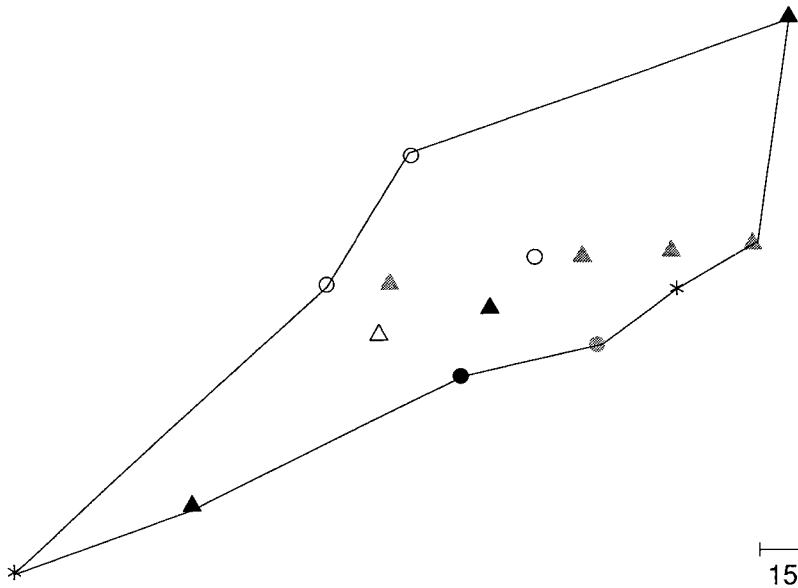
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**B1**

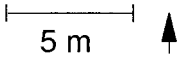
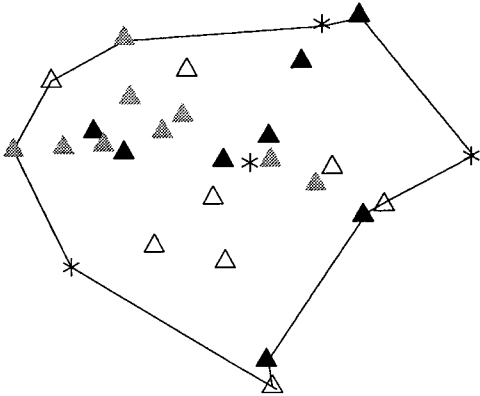


**B2**





**B3**



**B4**

