Harwood 4439

A short-term ecological study of a small breeding population of Redwing Blackbirds (*Agelaius phoenicius)* in a heavily-impacted urban marsh

SUMMARY: A small marsh (approx. 1 hectare in area) which sustains a minimal breeding population of redwing blackbirds was studied during the interval between arrival of redwings on the marsh in early spring , and the beginning of actual breeding activities, in mid-May of 1991. A map of old-nest distributions was constructed. Water depth below the nest was observed to be the most important physical habitat characteristic, other than the presence of cattails, determining distribution of nests. Other factors, such as proximity of heavy human activity, density of emergent vegetation, distance from edges, availability of insect prey, and presence of other species such as starlings and muskrats, did not appear to be important. Territorial behaviors of male redwings strongly reflected the distributions of old nests, possibly because most successful males returned to their territories of previous years. Neither evidence of abundant predators in the marsh, nor increasingly heavy human impacts seemed to deter territorial establishment or breeding behavior. Old male birds (OM's) grew increasingly aggressive as the season progressed, but were often observed in close proximity with no sign of aggressiveness throughout the study period. Females and immature males (IM's) flocked together until the final week of observations, when total segregation took place. General behavioral observations included indifference to disturbance by everything from starlings to dumptrucks; communal foraging with a possible division of labor between the sexes; precocious song-spread behavior by IM's; sexual chasing; and mate selection behavior by females.

by Garth Harwood
for Dr. Alexander Cruz
EPOB 5750, Ornithology
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CONTACT:
Home 440-8148
Office 492-2584
POB 1374
Boulder CO 80306

Copy 2: to City of Boulder (CO) Open Space Program

Introduction: Breeding behavior among red-wing blackbirds ("redwings") has been intensively studied from the time of nest-building onwards, but comparatively little is known about the patterns leading from migratory arrival at the breeding ground, to the point of nest-building and actual reproduction. This study has been designed to add to the general body of knowledge regarding this phase of redwing ecology, as well as to observe and critique various findings by other researchers.

Research questions for this study included:

1) How old nest densities related to physical-habitat characteristics;

2) Whether territorial behaviors of the birds reflected patterns of old nest distributions;

3) What additional environmental factors, such as human impacts, influence early breeding-season behavior;

4) How winter flocks separated at the commencement of breeding;

and 5) What general patterns of activity could be observed during this interval.

It was originally hoped that current nest-building might also be observed, and

density patterns compared with those evident from old nests of previous breeding seasons; however, nest-building for the 1991 breeding season had not yet begun as of the termination of this project.

What follows, given the wide scope of this introductory study, is a necessarily brief series of discussions of the ways in which my observations appear to address each research question. In Appendix 2, occasional "Interaction Detail" sections will more fully describe particularly intriguing observations, using excerpts from field notes where appropriate. Appendices I-III include maps, summarized field notes with excerpts, and species lists.

I. Distribution of old nests with respect to physical-habitat characteristics.

Erckmann *et al.* (1990) recently determined that over 90% of redwing nests survive between breeding seasons, allowing their use as reliable indicators of habitat-use patterns of the previous season. Many possible indicators of optimal nest sites are not available, or are reduced, at the time when nest sites are chosen by female redwings, so old nests might seem to be one of the likeliest cues. However, the work of Erckmann *et al.* (1990) did not support this hypothesis, indicating that other cues may be more important.

Dominant physical and behavioral qualities of older male redwings were long thought to be of primary importance to females when selecting nest sites. Larger, bright-red epaulettes, combined with high levels of aggressiveness and larger body size, were thought to win females for the males with these characteristics, whose choices of nest sites were then constrained by the territory held by such males.

However, most recent work on this question indicates that habitat quality is at least as important to the females as male traits are - that is, females may be choosing the habitat primarily, and consorting with whichever male happens to hold it. Eckert and Weatherhead (1987a) tested the older theories and found both epaulette size and body size to be insignificant as determiners of competitive success, and in further investigations concluded that there is "only a weak correlation between male competitive ability and territorial quality" and recommended that the two factors should be treated independently when modelling mate choice, and therefore, nest-site selection (Eckert and Weatherhead 1987b, 1987c.)

Aggressiveness is undoubtedly a factor of some significance, but just how much

is not clear. In a study designed to measure the importance of holding a territory with regard to increased male fitness, Bray et. al. (1975) vasectomized a number of dominant males without removing them from their territories. Despite their infertility, 69% of the clutches laid within "their" territories were fertile.

If neither male traits nor old nests account for nest-site selection, then what does? My observations suggest that the primary factors at this study site are physical habitat characteristics, and especially, optimal water depth. Male territorial displays are of probable importance, but I surmise that these may in fact be indicating something rather more like "See how hard I fight for this place over here? Come and see why!", rather than a simple "Look at me!".

By walking a series of transects of 5m spacing across the narrower direction of the marsh, I was able to closely survey the entire site for old nests and map this information along with various physical habitat parameters.

Of 38 old nests and 1 currently-active nest found in the marsh, only 10 (25.6 %) were sited outside of the 2 small areas of deeper water that are found at the extreme southern tip of the marsh, beside Valmont Road (nest-area 1), and in a narrow band along the northwest edge (nest-area 2, see site map, Appendix I). If nests exhibiting two or more non-standard characteristics, such as incorporation of woody stems for support, being unusually high, or use of different nest materials, are excluded, this number is only 4 of 39, or 10.3%. I believe this to be the more reliable figure, as these nests may well belong to other bird species. Nests within the high-density areas were remarkably consistent in height and construction (avg. height above water = 18"; constructed of coarse grasses and/or cattail [ct]).

Water depth was identified as the most important single factor as other explanations are demonstrably unlikely. (Water depths of 2"-8" are present at both nest areas, and are the only parts of the marsh with these depths. Greater water depths do not occur in this marsh.)

Distance from human activity is clearly unimportant. Valmont Road is a heavily-traveled, main artery for Boulder traffic, often sounding a continuous roar at the study site. Yet nest-area 1, the single densest area for redwing nests, is within 25m of the road, while the greater part of the marsh is virtually uninhabited.

Orians (1980) and others have suggested that differences in density of emergent vegetation -i.e., cattails - and distances from edge areas are important to nest-site selection. I did not see convincing evidence of this. Nest-area 1 has low ct density, in

accordance with Orians' model, but nest-area 2 is extremely dense in ct, and nevertheless, contains a similar density of nests.

Edges can be defined in two pertinent ways; as the boundary between the marsh and upland areas, or as the boundary between variant patches of habitat within the marsh. In classic models of redwing territoriality, redwings are said to prefer interior portions of marshes (for predator avoidance), and outside edges of denser vegetation patches. Marsh/upland boundary areas were strongly chosen over interior sites in this case, sometimes to the point where a human could reach out and touch a redwing nest from dry ground. Yet not all edges were so chosen; again, only those of the optimal water-depth range were occupied. There is stronger support for the patch-edge concept, however. While no clear pattern was evident at nest-area 1, nest-area 2 shows an obvious pattern of nests sited at the interior edge of the optimal water-depth band, where it meets drier, slightly less dense patches.

Availability of close food resources for the feeding of young is another important siting factor discussed by Orians (*op cit.*). As "central-place foragers", redwings should choose nest locations requiring the least energy expenditure per foraging round-trip, and will thus cluster around areas of high food availability. Once again this was not apparent at this study site. Aquatic insect larvae, which comprise the bulk of redwings' diets elsewhere, were little in evidence anywhere on this marsh. Many ct stalks were home to a type of small insect larva, however, and heavy foraging for these was often observed (to be discussed in greater detail later.) Such foraging always took place at the portions of the marsh farthest from the greatest nest density (see map). Although it is possible that the inhabited areas are more productive later in the season, the evidence collected thus far contradicts the standard CPF model.

Presence of other species generally appeared to have no impact on the redwings I observed. Throughout the study period I witnessed countless intrusions of other animal species into the marsh with no reaction whatsoever on the part of the redwings, with the single exception that my own approach within 10m usually caused flight. A very active starling colony bordered nest-area 2, bringing the two species into almost continuous contact, yet not once was any direct interaction observed. (Indeed, despite the variety of bird species seen at the site, only two or three interspecies interactions were ever witnessed, a kestrel-flicker- starling triad, and the mobbing of a buteo by the kestrels which were nesting among the starlings.)

For all of the reasons listed above, it seems that water depth may provide the single most important cue for nest-site selection. But, why deeper water? Protection from hydrophobic predators that are effectively deterred by only a few inches of water may be the answer. Numerous potential predators have been observed, including raccoons, foxes, several types of rodents, and other birds. Snakes were not seen, but are probably present, and are considered a locally important predator (Cate Ortega, *personal communication*). Snakes and foxes seem the likeliest predators to be deterred by these water depths, but the ultimate determination of their relative importance as predators is material for another study.

II. Territorial behavior in relation to old nest distributions.

During my first few field outings, before I began the mapping process, I was mystified by the seemingly-maladaptive concentration of effort by older male redwings in marsh-edge areas, and especially at the narrow tip closest to both Valmont Road and to the new fill & construction associated with the City's extension of Pearl Street. At every time of day, in every weather, certain OMs could be found intently guarding small trees and adjacent cattails at this "least appealing" location (indeed, not one female was ever seen in this vicinity until pair formation began in earnest at the very end of the study.) Similarly, my attempts to discover areas of high nest density by walking directly through "most appealing" sites, which also had the highest female activity, came up with nothing.

Systematic mapping explained a great deal. To focus on nest-area 1, which was simpler to observe due to its smaller size and lack of complication by flock-foraging in combination with territorial behavior, it became apparent after mapping actual nest distributions that this was indeed the portion of marsh most worth defending, as it had previously attracted the most females for nesting.

The relatively even spacing of marsh-edge trees, attributable to the artificial character of the vegetational community, gave the older male redwings a very efficient means for parceling out the territories among themselves. According to Nero (198_), redwing territories run about 60 feet to a side on the average, but in highly irregular shapes. Thus, if each OM held one marsh-edge tree (or two or three, if close together), and a chunk of adjacent cattails (which is about 100 feet across at this section of marsh), there would be room for 9 or so territories in this section. The

site map shows the trees held by OMs 1-9 in relation to nest distributions, and indicates cases in which a territory holds two or three guard trees. As might be predicted from this distribution, territorial behavior was considerably more intense at trees 1-5 than at the others in this series.

Because I did not band birds for this study, it was impossible to tell if the same individuals held these territories throughout the study period. Even so, it was clear that these were the most vigorously defended territories on the marsh, and after mapping the area, it was also clear that the pattern I was observing was a strong correlation between territorial behavior and old-nest distributions. At times, early in the study, I could not help but feel compassion for the individuals which held them, as the large flocks foraged enthusiastically a long distance away, and the few OMs with these "prime" territories sat hour after hour on their tiny perches, displaying away and interacting only with pugnacious intruders.

IV. Seasonal segregation of genders and male age classes

It has already been noted that nothing seemed to put the redwings off from their territorial and sexual behaviors, so I will proceed to the fourth research question, regarding the separation of wintertime flocks into the patterns observed during the height of the mating season.

Very little change was seen during the early part of the study period. After 4/14 a few signs of impending change appeared, but may or may not have been signs of progressive segregation. Things remained subtle until the last several weeks, when large changes seemed to occur all at once. On April 14 I observed a segregated perching pattern of females and IMs on the same small trees (see excerpted field notes from 4/14, Appendix 2.)

Still, by April 23 I saw no change from a pattern I had become very familiar with, namely the activity I call "flock-foraging" (see excerpt from field notes for 4/1, Appendix 2). Hundreds of females were mixed together with immature males (IMs) in a ratio of about 5:1. Then, on April 28, I noticed a great change in the degree of precocial behavior on the part of the IMs. They were still accepted with the foraging flock, but spent much more time than before drifting into OM territories, displaying, and being chased off (the OMs were almost lazy about performing this chore, as though they did not feel any real threat.) On several occasions, I did see OMs make

violent contact with IMs, including one occasion on which I was mystified by the long interval the two spent quietly down in the rushes (see 2nd excerpt from field notes of 4/28).

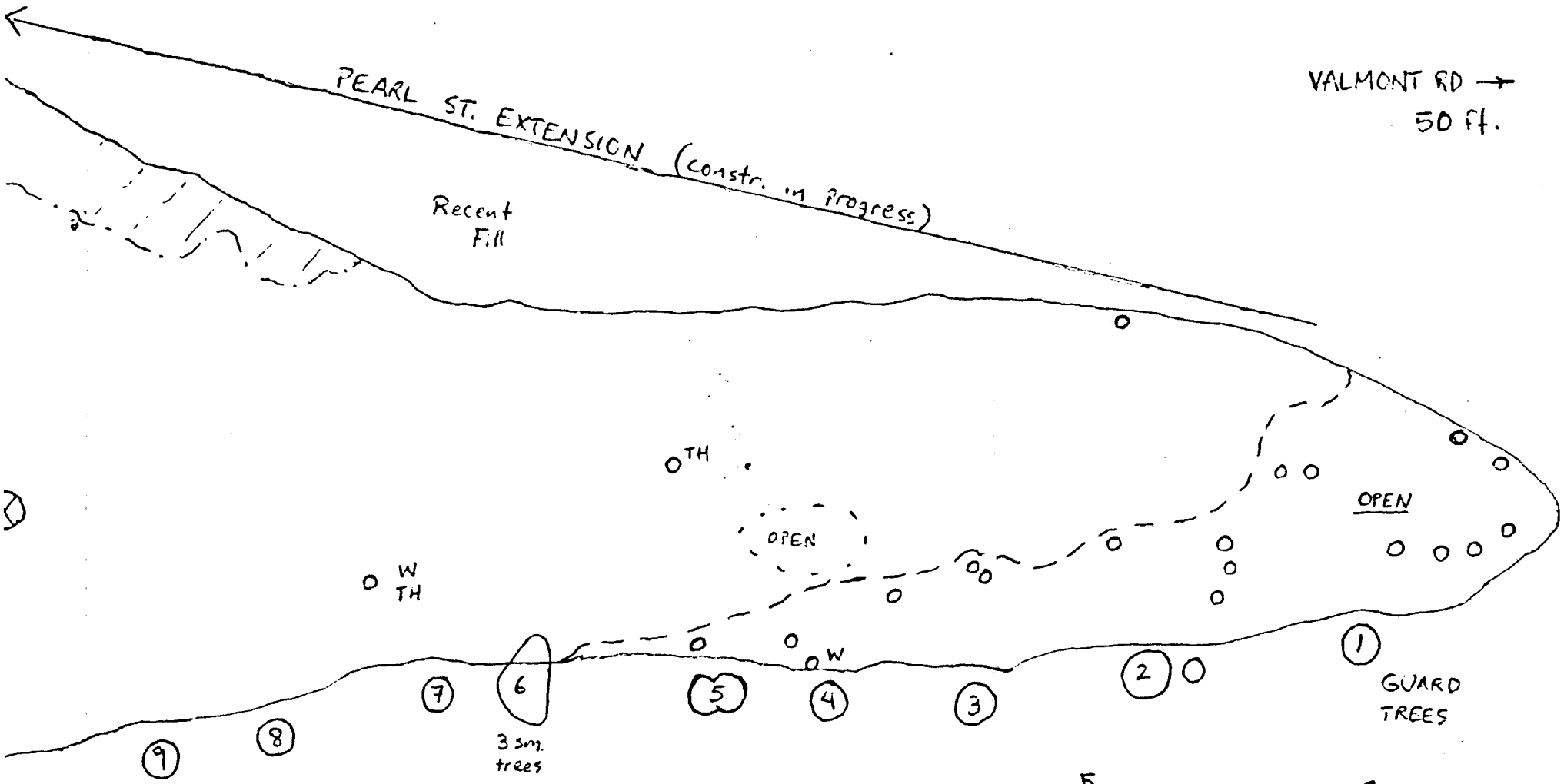
On my next visit (May 5), I was surprised to see that total segregation of the IMs and the females had occurred. Ten IMs were observed foraging together at the pond, (a site where I only rarely saw redwings), and despite the presence of over 100 females in a dense flock, foraging in the usual way, not one IM was among them. This pattern was to persist throughout the visit and until my next and last visit, on May 9, at which time no IMs were seen on the marsh (actually, I made a recreational visit to the site on 5/15 and saw no IMs then, either.)

Moreover, on both May 9 and May 15, females were no longer in the large flocks I had been used to seeing, but were either solitary or in smaller groups of up to 10 individuals. The first solitary female was seen on 5/5 on one of the nest-area one territories (terr.#2), which was also the first sighting of any female in that general area. By May 15, solitary females were a common sight throughout the marsh.

While these observations of flock segregation may be incomplete and unsatisfying in certain ways, (what happened in the 4/28-5/5 interval, anyway?), they do at least indicate the rough timing and general pattern of the segregation process that results in the patterns of breeding season groupings outlined by Nero (198_), in which females are grouped unevenly according to patchy habitat, and possibly male, quality. IMs, meanwhile are ostracized for the season, as they take a year longer than females to reach full sexual maturity.

V. General patterns of activity observed.

Appendix 2 contains a summarization of field notes containing the most important observations of each outing. Most activity patterns fit into the discussions above, but a few deied classification and are presented as detailed excerpts from field notes for the reader's interpretation.



NEST-AREA ONE

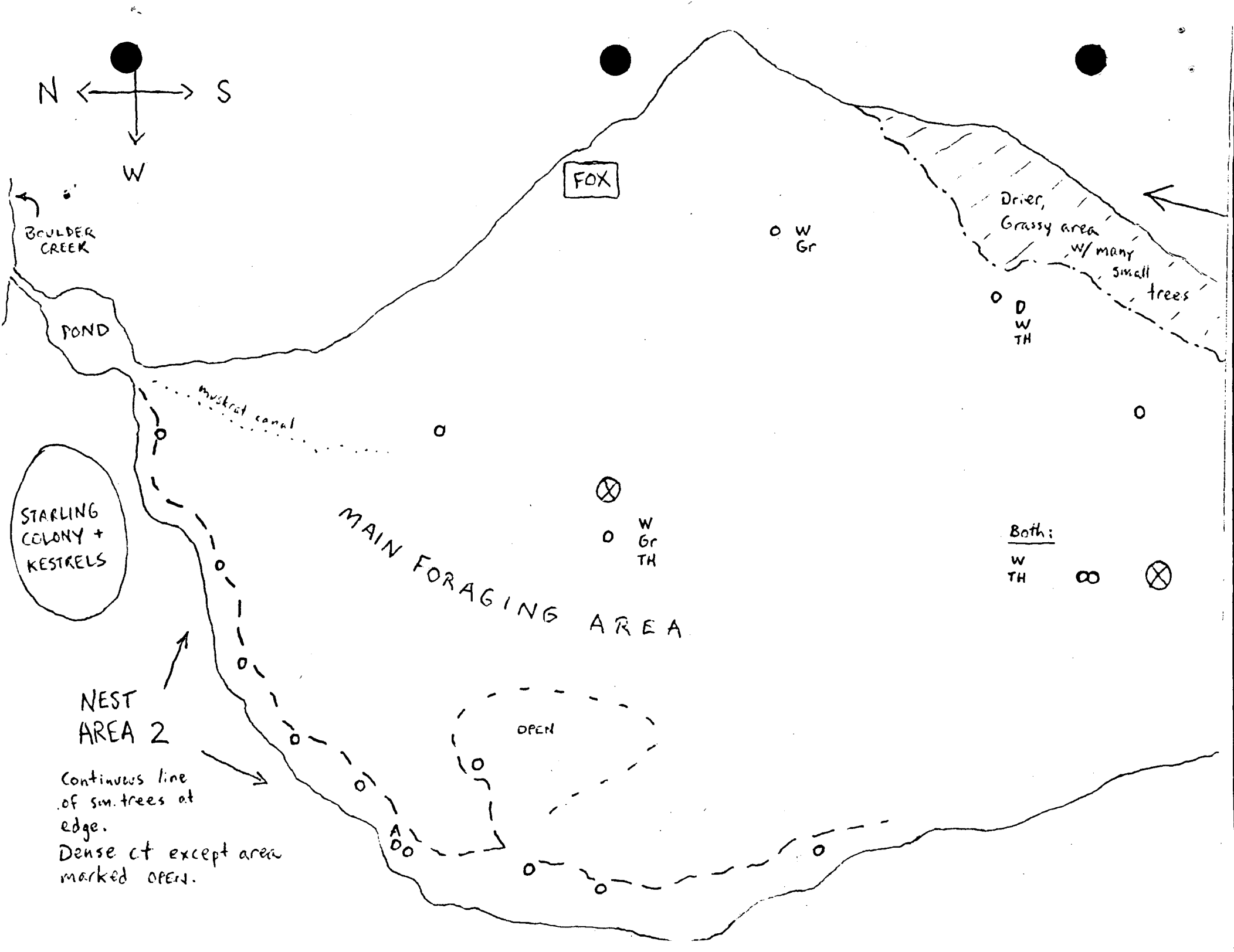
Open. Water depth 2"-8".

KEY

D = Downy nest material
Gr = Fine grass " " .
W = Nest support w/woody stem
TH = Too high above water/soil
O = Nest location
⊗ = Island Tree

SCALE:

1 cm = 5m
(1:500)


N
S
W
FOX
BOULDER CREEK
POND
muskrat canal
STARLING COLONY + KESTRELS
MAIN FORAGING AREA
NEST AREA 2
Continuous line of sm. trees at edge.
Dense ct except area marked OPEN.
OPEN
W
Gr
Drier, Grassy area w/ many small trees
D
W
TH
W
Gr
TH
Both:
W
TH

Appendix 2

Summarization of field observations

Observations made on all field days:

1. OM-OM territorial-defense behaviors:
- Chasing
- Song-spread displays
- Guarding/perching at same spot at all times
2. Flocking of females
3. Flocking of IM's
4. Obliviousness to any & all other species (except my direct approach <5m)

Feb 24 - First outing - mid-day (weekend) "Just Scoping"

-Many males present, but not "on territory" - mostly in tall trees at creek.
-Scanned marsh for nests - none observed.
-Pearl St. construction inactive, but clearly has impacted marsh since last breeding season (I visited several times last spring and noted differences).

3/22 Fri, 6 AM: First day of "real" study.

-Several inches of fresh snow. No sag in RW activity! Many OMs present, vigorously displaying.
-Some OMs seem to have distinct territories already - repeated song-spread (s-s) displays from same locations.
-Most active male area: narrowest end, very close to Valmont Rd.
-Most common display site: small trees bordering cattails, 1-2m above ct.
S-S displays most frequent, intense in sm. trees (some in farther tall tr.)
Displaying birds often within 20m of one another - some <10m.
FEMALES present - in large flocks - fat end of marsh. (Close to, but not with OMs.)
Crossed marsh at 3 points looking for nests. None spotted.
OTHER SPECIES: Canada Goose, house sparrow, dark-eyed junco, starling, magpie,

deer, muskrat.

INTERACTION DETAIL: OM-OM chasing. From field notes:

Aggressive territorial behavior: One of first OMs seen left sm tree in panhandle area to chase another - perched above #2 in tall tree @2min., displaying every 10-15 sec. until #2 (not displaying but singing weakly) left for more distant tall tree. #1 chased #2 there and repeated pattern of first tree (why did #2, arriving first, choose a low perch?) #2 leaves again after shorter stay. #1 chases #2 clear out of view in distance, hovers, returns to orig. tree.

4/1; 6 AM

Usual male displaying at typical sites (sm. trees by ct.)

Large female flock present. Some subgroups appeared to contain OMs, IMs, and females. Little aggression or display behavior apparent within these subgroups. Flock appears to be engaging in group activity down low in cattails (later ID'd as "flock-foraging" for larvae inside ct stalks).

OTHER SPECIES: Canada goose, magpies, northern flicker, starlings, song sparrow, deer, muskrat, rabbit.

INTERACTION DETAIL: (1) Female-flock foraging. From field notes:

(Actual excerpt is from 4/28): *Bug-ridden cattails! Answer to mystery of flocks descending from view for long periods? (This behav seen by mixed fem/IM flocks on every visit [except 2/24 and after 5/5]). Had noted busy rustling w/much noisemaking by these lg groups but could not see reason. Investigate & find lg # of reeds "peeled", always between 8"-20" on each stalk (peels go up and down, leaving fringed array at both ends). Some interior places completely exploited - behav never seen at edges. Noise a danger - prev detection of preds? Many stalks have lg number of exit holes, <2mm dia. Cutting in I see nondescript, sm insect larvae tunneling w/in lvs. No birds actually seen peeling ct - too low.*

Guarding by OMs? Looking back on this pattern later I realized there were always OMs at the top of ct stalks or in small trees near these feeding groups, a pattern I first attributed to sexual motives. But whether or not that is true, it serves as a good division-of-labor between the OMs and mixed flocks, because the OMs stay up above when the females drop down low and begin making noise. Thus they are in

position to warn of danger - as they often did at my approach. Typical pattern of mixed flock settling in to this pattern: 1. Flock arrives suddenly on marsh & perches on ct tops or all in 1 or 2 small trees. 2. After a few minutes inspection, all drop low out of view. 3. A few OMs drift to area from various places during inspection stage, remain behind when others drop.

4/6; 6:30 AM

Usual display behavior & sites, OMs.
Female flocks present.
Single old nest spotted, near water's edge at narrow end.
OTHER SPECIES: Kestrel - Starling interaction observed: both entering/leaving same cavity in tall cottonwood within starling colony along stream. 2 kestrels present; many starlings. RWs unaffected.

4/14; 1:30-6 PM. Began transect survey (see map).

Female flock present, 4-600 individuals, engaging in same "flock foraging" behavior first observed on 4/1.
Very noisy in flock! Squeaks, honks, a few s-s calls.
Mapping process reveals locally dense nests, esp. at extreme tip of marsh.
Immediately discover that 20m gridlines are ridiculous for reliable nest locating in heavy ct; modify to 5m - it's going to take a while.
INTERACTION DETAIL: Partitioning of perch trees by gender.
After foraging a mixed female/IM flock emerged from ct and all @100 individuals perched in 2 adjacent small trees. Noticed a distinct subgroup pattern according to gender. Neither height nor any other feature of trees seemed to determine the pattern, but each branch was distinctly all female or all IM - no mixing. First sign of impending flock segregation?

4/16; 2 PM. Survey continuing.

Typical OM terr. behavior in progress.
Female/IM flock in group-foraging mode. Flock comes and goes periodically; no

discernible stimulus for movements.
Very few nests located in this central section. Boring work.
All nests located today were non-standard in materials, height, or both (see map).

4/23; 5:30-8 PM. Plugging away at transect.

Typical OM terr. behavior in progress.
Female/IM flock in group-foraging mode. Engaging to watch. Will allow approach within 20m without departing or changing behavior.
- Wide, boring transects.
- One std nest located as "deep" water trough appears along creekside edge of marsh (see map).
OTHER SPECIES: Usuals + common grackles as new arrivals.

4/28 All day (10AM-6PM). Finish transect.

- Familiar male territorial/mixed-flock foraging behaviors in progress throughout day. Working close to foraging flock. Investigate reason for intense rustling & discover "peeled" cattails w/larvae inside.
- Distinct pattern in nest locations is revealed - much denser ct here than at other high-nest density area, but all nests are inside narrow trough of deeper water.
- New cattails now at avg. 8" height.
- Males (both age classes) spend time w/ foraging flock but mostly stay above. Beginning to think of this as a guarding behavior - not mating.
- Big increase in precocial s-s behavior by IMs. Usually chased away from flock, always from territory perches by OMs.
- Chasing not vigorous - could even be called lazy. IMs allowed to remain with flock often as not.
INTERACTION DETAIL: Unusual OM-IM interaction. From field notes:
Wild OM-IM interaction! 2 males seen flying together in "chase" pattern away from gen. area of foraging flock, (still of mixed fem/IMs.) Both land in ct near me, w/in 1m of each other - descend out of view. I wait...10 min later no sign at all, no noise or sightings. Gone? I approach ct and OM exits as I begin to make noise. Perches on ct at same spot, displays 2-3x then leaves marsh. Still no IM. I approach. IM exits from

10m. Perches but doesn't display. Then goes directly to join fem flock 20m away! Neither male shows signs of struggle. No response of OM to this mvmt of the IM.
OTHER SPECIES: Fox (seen last year as well), rabbits, rodent young, rainbow trout (as prey), butterflies, grasshoppers, small fishes, 5 black-crowned night herons, all usual bird species EXCEPT flickers (driven out by starlings?). Kestrels seen copulating. Song sparrows especially active.

5/5, 3:30 PM. Heavy rain most of last 36 hours.

- No noticeable change in water level of marsh.
- OMs present in most of guard trees, but absent most of time.

SEVERAL DRAMATIC CHANGES:
- First full-contact aggression witnessed among OMs. Numerous instances.
- IMs are separate! Group of 10 at pond feeding on their own (no groups seen feeding here before.) No evidence of aggressive IM-IM interactions.

Female flock still in ct, no IMs among them. A few OMs stay near flock.
- First female seen at narrow end of marsh. Solo, in one of most consistently occupied guard trees. Descends to ct nearby & stays until I approach. No evidence of nest-building in area. (Note that despite 2 months of observation, & hundreds of females observed, this is the first time *any* female has been seen in this part of marsh - despite incessant OM activity and highest density of old nests.)

OTHER SPECIES: Grackles, night herons now standards. New: Common yellowthroated warbler, barn swallows overhead, house finches, probable American bittern overhead, unknown buteo (circling slowly overhead/low; vigorously mobbed by kestrels & driven off.) Muskrat & fox activity heavy (3 sep. sightings of foxes - more than 1 in marsh?)

5/9; 6 AM. Last visit.

- New ct's now avg. 16-18"
- No OMs at usual terr's at narrow end. Some s-s going on, but from fat end of marsh or creekside.
- No IMs seen anywhere on marsh.

- Large # females present, but in much smaller groups than usual - single up to about 10 indiv's. OMs are with these groups or nearby.
- Intersexual song answering? Single pair in tree 3, several exchanges.
- Sexual chasing is everywhere; not seen before. Much more vigorous and acrobatic than intra-gender chasing. Much of it "pointless" - broken off in middle, or distracted by other birds of either gender.

INTERACTION DETAIL: Intense sexual interactions. From field notes:

@7 fem close together at ct tops. One OM chases fem - very swift, acrobatic, energetic. (Nero:"sexual chasing"). 2nd OM chases first OM, who breaks away from sexual chasing. 3rd, 4th OMs join in, swooping low over group of females, all 4 making plays at fems and each other - busy, intense, confusing. Numerous "unexplained" trips into ct - often m&f together. Nero says this is where most copulation occurs - but in mixed groups?

--3 OMs chase single fem below view - all stay down for >1min.

--Fem chases OM to remote part of marsh - near me - did not see copulation but suspect it.

OTHER SPECIES: Raccoon seen for first time (BOLD). Single flicker seen, but not at former "nest area" where 2 were always to be found. Common yellowthroat is back. Pair of lesser goldfinches busy in a small tree at marsh edge. First yellow-headed blackbird seen, flying quickly over marsh & gone.

APPENDIX 3:

SPECIES LISTS: SIGHTINGS AT BOONDOGGLE MARSH

** = Seen on all, or nearly all outings*

AVIAN SPECIES

*Great blue heron**
*Black-crowned night heron**
American bittern
*Song sparrow**
Lesser goldfinch
Common yellowthroat
Yellow-headed blackbird
Common grackle
Barn swallow
House sparrow
House finch
Darkeyed junco
*Starling**
Unid. buteo
*Black-billed magpie**
*Canada goose**
*Northern flicker**
*American Kestrel**
*Unid. duck**

OTHER SPECIES

Raccoon
*Red fox**
*White-tailed deer**
*Rabbit (swamp species?)**
*Muskrat**
*Unid. fish**
Rainbow trout (as prey)
*Unid. rodent - 6 yg,, many nests**
*Unid. frog**
Butterflies
Grasshoppers
Mosquitoes

References Cited

Bray, O.; J.J. Kennelly, and J.L. Guarino 1975. Fertility of eggs produced on territories of vasectomized red-winged blackbirds. The Wilson Bulletin 87:2 June 1975.

Eckert, C.J. and P.J. Weatherhead 1987a. Owners, floaters, and competitive asymmetries among territorial redwing blackbirds. Anim Behav 35:1317-1323.

Eckert, C.J. and P.J. Weatherhead 1987b. Male characteristics, parental quality andthe study of mate choice in the redwinged blackbird. Behav Ecol and Sociobiol 20:43-52.

Eckert, C.J. and P.J. Weatherhead 1987c. Competition for territories in redwinged blackbirds: is resource-holding potential realized? Behav Ecol and Sociobiol 20.

Erckmann, W.J., L.D. Beletsky, G.H. Orians, T. Johnson, S. Sharbaugh and C. D'Antonio 1990. Old nests as cues for nest-site selection: an experimental test with red-winged blackbirds. The Condor 92:113-117.

Nero, R.W. 198_. Redwings.

Orians, Gordon H. 1980. Some adaptations of marsh-nesting blackbirds. Princeton University Press, Princeton, NJ.