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THE UNIVERSITY OF ALBERTA

Factors Regulating the Breeding Population, Reproductive Success and Mating System of House Wrens (*Troglodytes aedon*) at Beaverhill Lake, Alberta

by

Michael S. Quinn

A Thesis
submitted to the Faculty of Graduate Studies and Research
in partial fulfilment of the requirements for the degree
of Master of Science

Department of Forest Science
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Date: 20 April 1989

Probably we have no other familiar bird keyed up to the same degree of intensity as the house wren. He seems to be the one bird whose cup of life is always overflowing. The wren is habitually in an ecstasy either of delight or of rage. He probably gets on the nerves of more people than any other of our birds. He is so shrilly and overflowingly joyous, or else so sharply and harshly angry and pugnacious -- a lyrical burst one minute, and a volley of chiding, staccato notes the next. More restless than the wind, he is a dynamo of bird energy.

--- John Burroughs

THE UNIVERSITY OF ALBERTA

FACULTY OF GRADUATE STUDIES AND RESEARCH

The undersigned certify that they have read, and recommend to the Faculty of Graduate Studies and Research for acceptance, a thesis entitled **FACTORS REGULATING THE BREEDING POPULATION, REPRODUCTIVE SUCCESS AND MATING SYSTEM OF HOUSE WRENS (_Troglodytes aedon_) AT BEAVERHILL LAKE, ALBERTA**

submitted by **Michael S. Quinn**

in partial fulfilment of the requirements

for the degree of **Master of Science**

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Date: 17 April 1989

Dedication

I appreciatively recognize the patience and kindness of my wife, Jenny. Her words of encouragement made my work infinitely more bearable and it is to her that I dedicate this thesis.

ABSTRACT

The breeding density, reproductive success, and mating system of House Wrens (Troglodytes aedon) were monitored at Beaverhill Lake, Alberta. Nestboxes were made available to wrens in dense willow vegetation and open poplar forest. House Wrens preferred to nest in the more dense vegetation. The abundance of invertebrate prey was positively correlated with breeding density. Wrens in the habitat with the most abundant food initiated egg laying earlier in the season and fledged heavier young than in the other habitats. Intraspecific nest-content destruction and predation by weasels were responsible for a high number of nest failures in the denser vegetation. Low predation rates in the more open poplar areas may have been due to the ability of wrens to detect and repel intruders.

House Wrens were polygynous in 27.1% of all matings for which the mating status was known (15.7% of the males polygynous). Polygyny occurred asynchronously with no overlap between the nestling period of the primary and secondary females. The high incidence of polygyny may be compensatory for the males to make up for the lack of second clutches.

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I wish to thank Dr. G.L. Holroyd for his many ideas and encouragement throughout my research and for allowing me the independence to pursue the many facets of this project. I am also grateful to Dr. Holroyd for his willingness to involve me in a variety of projects unrelated to my thesis, but extremely valuable in providing a well-rounded educational experience.

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INTRODUCTION

A. BREEDING DENSITY AND REPRODUCTIVE SUCCESS

1. Factors that Regulate Populations

The question of what factors regulate the density and reproductive success of a breeding population is central to the study of population dynamics. Further, ecologists seek to determine the relative importance of each factor. No single factor can be identified as most important in regulating all populations (Ricklefs 1982). The controversy surrounding which factors regulate populations has probably generated more discussion than any other concept in population ecology (Elseth & Baumgardner 1981).

Population ecologists have generally classified factors that influence populations as being either density dependent or density independent. The latter are those factors associated with the physical environment and do not vary in intensity with changing population densities (Andrewartha & Birch 1954). Therefore, density independent factors do not provide a regulatory function. Weather is the factor most often given as an example of being density independent.

Density dependent factors are those which have a stabilizing effect, acting to increase populations when densities are low and vice versa, returning them to an equilibrium level (Nicholson 1933). Food resources, predators and pathogens are often cited as density dependent factors.

The separation between the two types of factors is not always clear. Smith (1961) argued that weather may act in a density dependent manner. For example, if shelter sites are required by a population for protection from weather, and these sites are limited, then the percentage of a population destroyed by a severe weather event becomes greater with increasing density.

The extent to which various factors regulate the numbers of breeding birds has been of considerable interest to ornithologists (Lack 1966). The density dependent effects of regulatory factors have been reported widely in the bird literature (McCleery & Perrins 1985). For example, studies of the Great Tit (Parus major) illustrate the inverse fecundity-density relationship through a decrease in clutch size (Perrins 1965, Lack 1966), a higher rate of nest predation (Krebs 1971, Dunn 1977), and greater nestling mortality (Dhont 1977) with increasing population density.

2. Suitable Nest Sites for Cavity-Nesting Birds.

A primary factor limiting the breeding populations of some secondary cavity-nesting birds is the availability of suitable nest sites (von Haartman 1957, Holroyd 1975, Pinkowski 1979, Minot & Perrins 1986). Through the provision of a surfeit of nest sites, in the form of nestboxes, it is possible to establish a breeding bird population limited by some other factor(s) (i.e. food, space, cover). The use of nestboxes facilitates investigations related to population regulation through the potential for manipulation of breeding density. Nestboxes also allow the investigator relatively easy access to sampling a variety of parameters related to reproductive success.

The majority of long-term studies related to passerine population dynamics have been based on species that breed in nestboxes (Kendeigh 1941, Lack 1966, Kluyver 1971, Perrins 1979, Alatalo & Lundberg 1984). Researchers must take caution in interpreting the results of such studies, as they may bear little relevance to natural populations, especially at artificially inflated densities. Nestboxes may also impact various breeding parameters such as laying date, clutch size and breeding success (East & Perrins 1988).

3. Food Availability

The availability of food is widely recognized as an important factor in the regulation of bird populations. The question is, how often, if ever, are avian populations limited by food (Newton 1980).

Lack (1954, 1966) proposed that mortality outside the breeding season is the primary factor affecting the number of birds in the subsequent breeding season. Further, Lack suggested that variability in mortality is due to fluctuations in the food supply, and is density dependent. Lack recognized that his hypothesis was founded mainly on circumstantial evidence and called for researchers to initiate longer-term studies and to gather more experimental, rather than observational, evidence.

The strongest support for Lack's hypothesis comes from experiments, involving food provision outside of the breeding season, that result in an increase in breeding density (Krebs 1971, van Balen 1980, Smith et al. 1980, Jansson et al. 1981). The magnitude of the effects of such studies varies with the natural food abundance.

Available food could also limit the number of birds through regulation of reproduction (Lack 1968, von Haartman 1971, Immelmann 1971). Since reproductive effort requires a large energy expenditure, food supply will ultimately be a factor in the reproductive success of an individual.

The most basic level of proximate control imposed by local food supply on a potential breeding bird is whether or not to breed (Drent and Daan 1980). There is evidence that some raptorial rodent predators fail to breed in years of rodent scarcity (Galushin 1974, Phelan & Robertson 1978, Smith et al. 1981). However, it has also been suggested that food is superabundant for some birds in the breeding season (Morse 1978, Rosenberg et al. 1982). For many species, food availability will probably fall between the two extremes and be a dominant factor in determining where to breed, when to breed, and how much to invest in offspring.

Experiments that involve manipulation of the food resource during the breeding season provide the best evidence for the role of food in limiting the size of breeding bird populations (Table 1). Fifteen of the 19 (79%) studies that reported laying date, showed an advancement of clutch initiation following food provision before the onset of laying. Earlier commencement of egg-laying may lead to a longer breeding season and thus the potential for raising more than one brood. Furthermore, early season breeders may have increased fitness resulting from greater experience of the offspring before winter/migration (von Bromssen & Jansson 1980).

All of the food enhancement experiments in Table 1 report one or more positive effects on the reproductive success of the species examined. This evidence strongly supports the food limitation hypothesis, but it is difficult to establish a causal link. Factors such as predators, territorial control or other social interactions may act separately or in conjunction with food in limiting populations (Newton 1980).

TABLE 1. Summary of the effects of supplemental food on reproduction of several bird species.

Reference	Species	Food Provided	Advanced Laying	Larger Clutch	Other Effects
Arcese & Smith 1988	Melospiza melodia	W,B	+	+	1,3,5
von Bromssen & Jansson 1980	Parus montanus	W,B	+	N	(1)
von Bromssen & Jansson 1980	P. cristatus	W,B	+	N	(1)
Davies & Lundberg 1985	Prunella modularis	W,B	+	N	1
Dijkstra et al. 1982	Falco tinnunculus	W,B	+	(+)	0
Ewald & Rohwer 1982	Agelaius phoeniceus	B	+	N	9,10
Harper 1984 *	Erithacus rubecula	B	N	+	0
Hill 1988	Fulica americana	B	N	N	7,8
Hochachka & Boag 1987	Pica pica	B	+	N	2
Hogstedt 1981	P. pica	W,B	+	+	2,4,8
Horsfall 1984	Fulica atra	B	N	0	11
Jones 1973	Parus major	W,B	N	N	0
Kallander 1974	P. major	B	+	0	6
Knight 1988	Pica pica	B	+	N	13
Miller et al. 1970	Lagopus lagopus	W,B	(+)	0	2,6
Newton & Marquis 1981	Accipiter nisus	B	(+)	+	12
Smith et al. 1980	Melospiza melodia	W	+	N	0
Swanberg **	Nucifraga caryocatactes	-	0	+	0
Wimberger 1988	Agelaius phoeniceus	B	+	0	9
Yom-Tov 1974	Corvus corone	W,B	+	N	4,6

* cited in Davies and Lundberg 1985
** cited in Lack 1954

W = winter
B = breeding season
\+ = positive effect
N = no effect
0 = not reported or not applicable
()= inconsistent or weak effect
1 = increased number of nesting attempts
2 = increased number of fledlings
3 = shorter re-nest interval
4 = increased hatching success
5 = lower nest parasitism
6 = increased fledling survival
7 = increased fledging weight
8 = increased egg weight
9 = increased polygyny
10= increased predation
11= lower within-clutch variability in egg mass
12= increased female weight
13= increased nesting density

4. Habitat Structure

Habitat structure, especially vegetation structure, has been widely implicated as an important factor in the regulation of bird populations. MacArthur and associates (MacArthur 1958, MacArthur & MacArthur 1961, MacArthur, MacArthur & Preer 1962, MacArthur, Recher & Cody 1966) found composition and diversity of bird communities consistently related to foliage profiles based on vertical vegetation density (see also Willson 1974, Terborgh 1977). Shugart and James (1973) reported changes in bird species composition with successional changes in vegetation structure. Such studies suggest that birds may be limited by the availability of suitable nesting environments defined by vegetation structure.

Readily available multivariate statistical software packages have recently allowed researchers to collect and analyze data from a greater variety of structural features representing both vertical and horizontal directions. Ordination and classification techniques, usually principal components analysis and discriminant function analysis respectively, are used to generate new axes in the form of linear combinations of the original variables. Although these methods may identify structural features that correlate well to the density of certain bird species, they do not tell us what it is about the structural variable that the bird is responding to (Cody 1985).

Holmes et al. (1979) attempted to interpret forest vegetation structure in terms of its influence on the foraging behavior of insectivorous birds. Cody (1981) suggested that an insectivorous forest bird has a fixed morphology and limited behavioral flexibility that defines its ability to find, capture and handle arthropod prey more effectively in some vegetation structure types than in others. Bird species often exhibit strong preferences for foraging in certain tree species and may in fact, be limited in the ways which they can capture arthropod prey in different foliage types (Holmes & Robinson 1981, Robinson & Holmes 1982). Robinson and Holmes (1984) hypothesize that,

> "the primary role of vegetation structure is to provide a set of opportunities and constraints that influence how and where birds perceive and obtain their arthropod prey. These opportunities and constraints, in turn, are a function of the differences in architecture and in the types and abundances of available arthropods that occur between plant species. The resulting foraging environment ultimately determines which bird species can successfully exploit and survive in a particular habitat and, as a consequence, influences bird community structure and species diversity."

Preference for a foraging substrate, however, does not necessarily indicate limitation. For example, Ovenbirds (Seiurus aurocapillus) forage primarily in the forest understory, but have been observed feeding in the lower canopy of conifers in response to an outbreak of spruce budworm (Choristoneura fumiferana) (Zach & Falls 1975). The range of foraging opportunities that a bird species is able to exploit will vary with the degree of morphological and behavioral specialization.

The role of vegetation in providing a foraging substrate is only one measure of its importance. Vegetation structure may also be critical in providing thermal and protective cover, suitable nesting locations and perch sites.

The flexibility of many bird species to apparently drastic habitat alteration is evidenced by the results of several vegetation manipulation studies. Beaver (1976) found little impact on bird populations of Sierra Nevada forests following the use of herbicides in the understory. Similarly, Emlen (1970) recorded few changes in bird populations following severe fire in Florida pine forests and Franzeb & Ohmart (1978) reported little change in bird diversity after selective logging in mixed-wood forest. Bird species may not be strictly limited to the habitats in which they are normally found, but may simply avoid other habitats because of previous experience, competitive exclusion or in the case of cavity-nesters, the lack of suitable nest sites.

B. MATING SYSTEMS

Verner and Willson (1969) examined 291 species of passerines and only 14 (5%) were regularly polygynous (defined as 5% or more males polygynous). Orians (1961) identified that polygynous passerines breed in habitats where nest site availability is limited. It would be expected that secondary cavity-nesters occurring in areas of restricted nest availability should exhibit polygynous mating systems, if other factors do not limit them to monogamy. A single male may protect more than one nest site in a territory (or be polyterritorial) and may thereby serve as a potential mate for more than one female. This has been shown to be true for Great Tits (Kluyver 1951), Pied Flycatchers (*Ficedula hypoleuca*; Alatalo & Lundberg 1984b), and House Wrens (*Troglodytes aedon*; Kendeigh 1941).

Lack (1968) attributed the low percentage of polygyny in passerines to the need for male parental care to complete the breeding cycle; the "male parental care hypothesis". The need for such male parental care may be a product of food availability. Armstrong (1955) found that the European Wren (*Troglodytes troglodytes*) may have up to 50% polygynous matings in areas of high food abundance and be strictly monogamous in areas of low food abundance. In the cases where *T.troglodytes* exhibits a 50% rate of polygyny, many of the females are observed to care for the young without the assistance of the male.

Food availability is only one of the components that determine the quality of a territory. It is not known what combination of environmental and behavioral factors a female uses as criteria for selecting a mate and his associated territory and nest site. However, the relative quality of a male's territory is thought to limit his ability to assist two or more females to successfully raise young (Verner & Willson 1969, Orians 1969) resulting in a threshold that limits the opportunities for polygyny. The polygyny threshold can be defined as the point at which the difference in two males' territories is great enough that a female could rear as many young alone or with limited assistance in the better territory than she could with full assistance in the poor territory (Verner & Willson 1969).

Weatherhead and Robertson (1980) presented another possible factor influencing the occurrence of polygyny. The "sexy-son hypothesis" is an expansion of the polygyny threshold hypothesis with the difference being a separation of male territory quality and individual male qualities. If females are more attracted to males that exhibit attributes not necessarily related to territory quality, then females that select and mate with these males may have lower reproductive success than females on the best quality territories. If the male progeny of the females mated to the males with the "sexy" traits inherit the qualities of the father, then these "sexy-sons" should leave more offspring because they can attract more females. In this way, the female is able to leave more descendants.

Subsequently it was argued that polygyny was a male strategy to maximize the number of progeny by dominating high quality habitat and more than one female (Emlen & Oring 1977). However, if the first, or alpha, female produces fewer offspring as a result of the addition of another female, it is in the interest of the alpha female to keep the male monogamous. This argument has given rise to the hypothesis that female aggression limits the frequency of polygyny (Wittenberger & Tilson 1980, Hannon 1984).

The deception hypothesis proposed by Alatalo & Lundberg (1984) suggests that a second female is attracted to a male's territory without being aware that the male is previously mated, thus selecting the male based on territory quality and male behavioral and/or physical characteristics. The process of deception may be facilitated by the timing of advertising by the male for a second female. Aggression by the primary female might be eliminated if the secondary female is attracted during incubation by the primary female.

The above arguments can be summarized as follows. A species will be monogamous if both parents are required to successfully raise young. If two adults are not required, then the frequency of polygyny will be determined by some or all of the following: the quality of the habitat, the attractiveness of the male, or the aggression displayed by the female. The relative importance of these factors as variables that control polygyny is under active investigation, however, the quality of the habitat is accepted as a primary factor for many species (Wittenberger & Tilson 1980). The difficulty is in the determining which factors are used by the birds to judge habitat quality and which factors are important in determining breeding success.

C. APPROACH

In this study, data are presented on the breeding density, reproductive success and mating systems of House Wrens. Research was guided through the investigation of the following hypotheses and associated predictions and assumptions.

Hypothesis 1. The availability of suitable nest sites is the primary factor limiting the breeding density of House Wrens.

Prediction 1A. The breeding density of House Wrens can be increased through the provision of artificial nest sites.

Prediction 1B. The House Wren will nest in an area where no natural cavities exist if nest boxes are provided, given that other resources required for breeding are present. Specifically, it is predicted that House Wrens will nest in a shrub willow habitat that is enhanced by the provision of nestboxes.

Hypothesis 2. When nest sites are not limited, House Wrens will nest preferentially in areas that provide resources for the greatest reproductive success.

Prediction 2A. Food abundance will be positively correlated with nesting density and reproductive success.

<u>Prediction 2B.</u> There will be a measurable difference in habitat structure between occupied and unoccupied nest sites.

Hypothesis 3. Density dependent regulation in the form of predation and intraspecific interaction will be observed in the areas of highest nesting density.

Hypothesis 4. Polygynous mating is expected to occur when the difference between the territories of two males is sufficient that a female is able to produce more young on the superior territory, with little or no parental care, than she could on the inferior territory with full male parental care. (The Polygyny Threshold Hypothesis; Verner & Willson 1966).

<u>Prediction 4A.</u> Polygynous males will produce more young than monogamous males. This prediction is based on the assumption that an individual will seek to maximize its reproductive output.

<u>Prediction 4B.</u> Polygyny will occur more frequently on higher quality territories. This prediction will be tested under the assumption that food availability and vegetation structure are good indicators of territory quality.

METHODS

STUDY AREA

I studied House Wrens in an area 72 km east of Edmonton, Alberta on the southeast shore of Beaverhill Lake (53° 24' N; 112° 31' W)(fig.1). According to the classification by Rowe (1972) the area is Aspen Grove within the Boreal Forest Region.

Balsam poplar (Populus balsamifera) is the dominant overstory species with a minor inclusion of trembling aspen (P. tremuloides) on the drier sites. The transition zone between the forest and waterline is dominated by dense willow (Salix spp.) and young aspen and balsam poplar. This dense transitional shrub zone is composed mainly of vegetation <2.5 m in height and <7.5 cm diameter at breast height (dbh), completely lacking in suitable nesting cavities for House Wrens. Henceforth, I will refer to the forested P. balsamifera / P. tremuloides area as poplar forest, while the shrub zone will be denoted as willow scrub.

The study area was composed of four grids containing 210 nestboxes (figs. 2a & 2b). Two small grids (24 and 23 nestboxes) were located on the west side of Lister Lake and two larger grids (71 and 92 nestboxes) on the east side of Lister Lake. Grid A contained 23 nestboxes in poplar forest,

Fig. 1 Location of Study Area

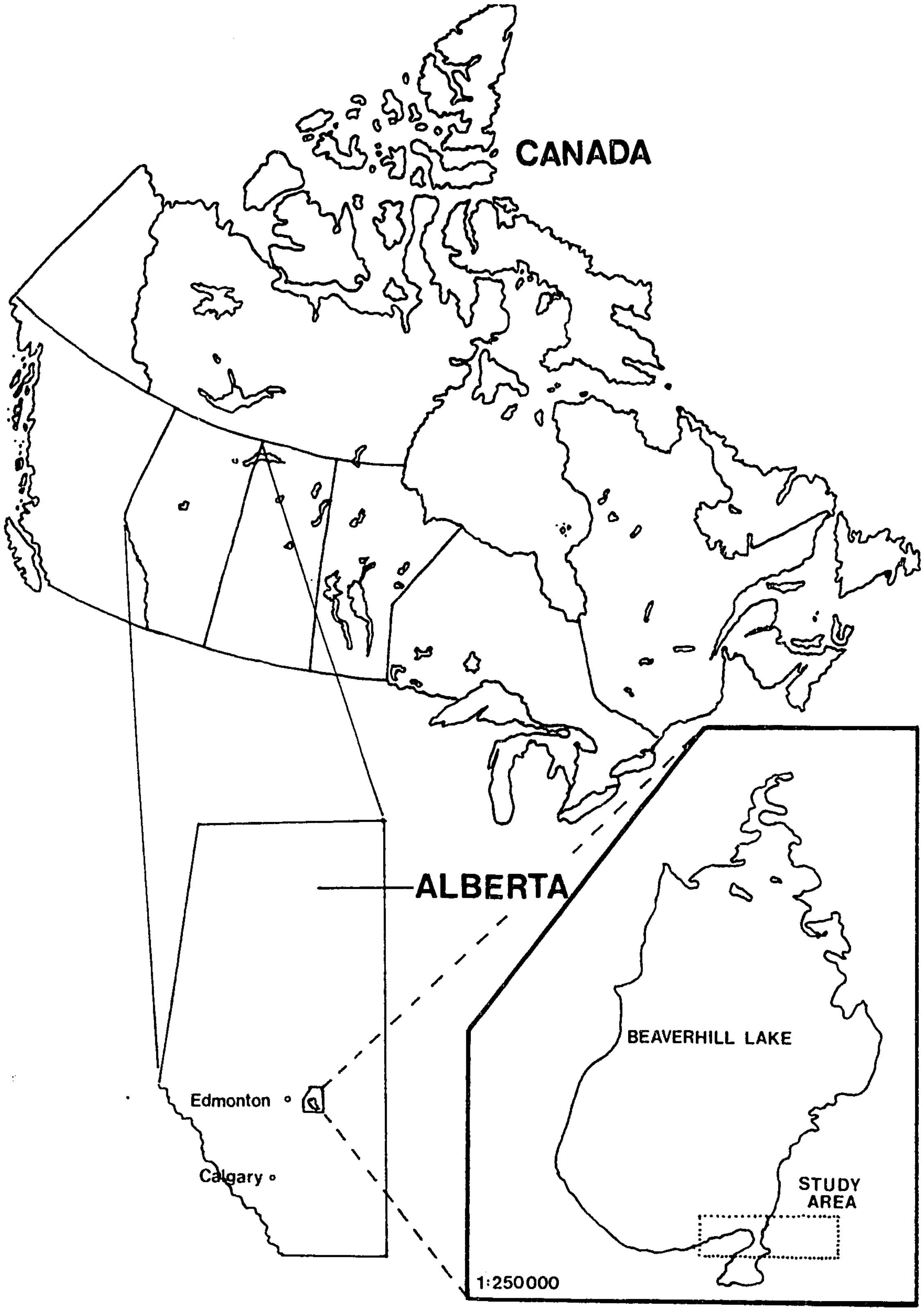


Fig. 2a Map of study area for House Wrens at Beaverhill Lake, Alberta (west)

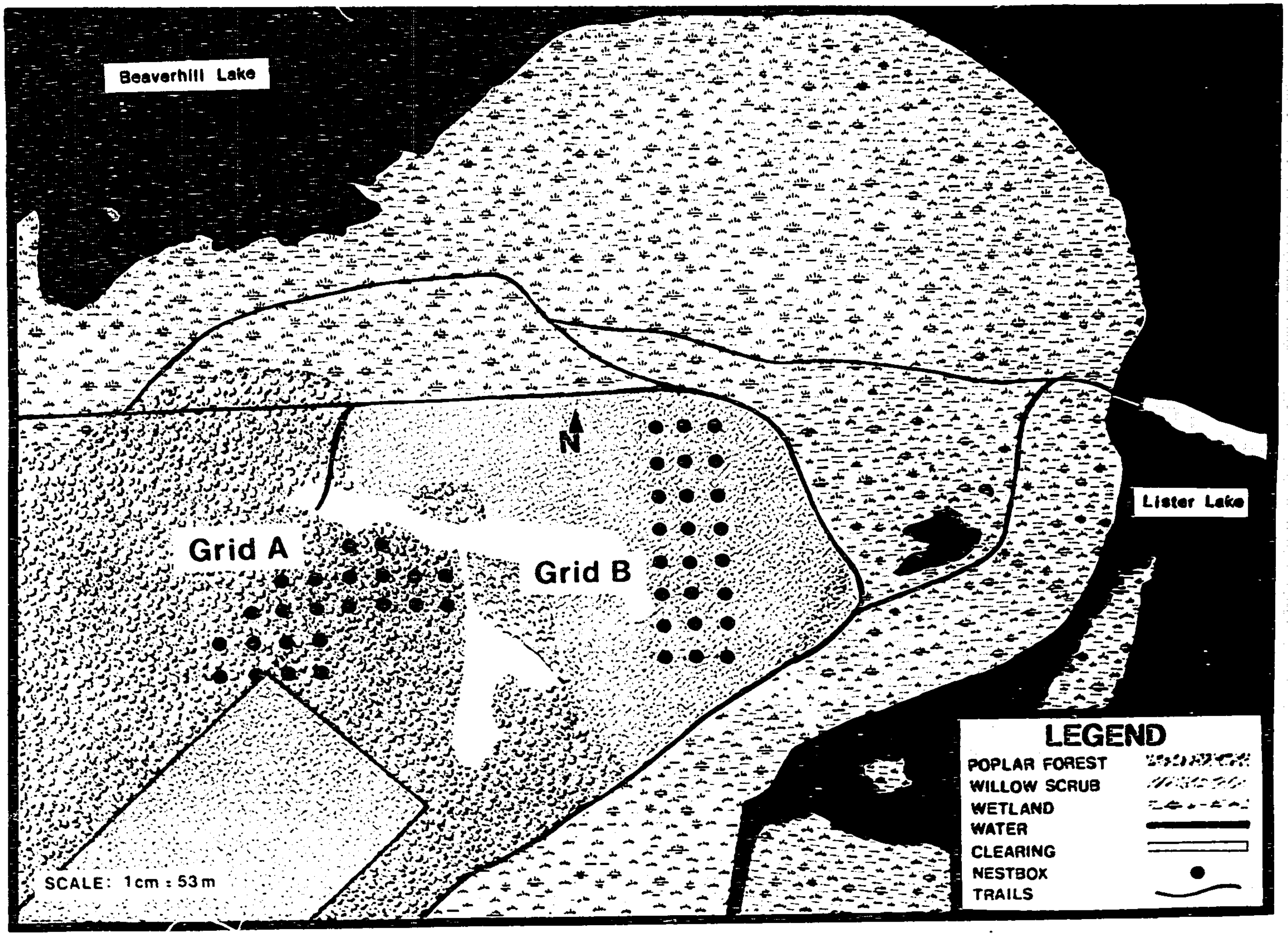
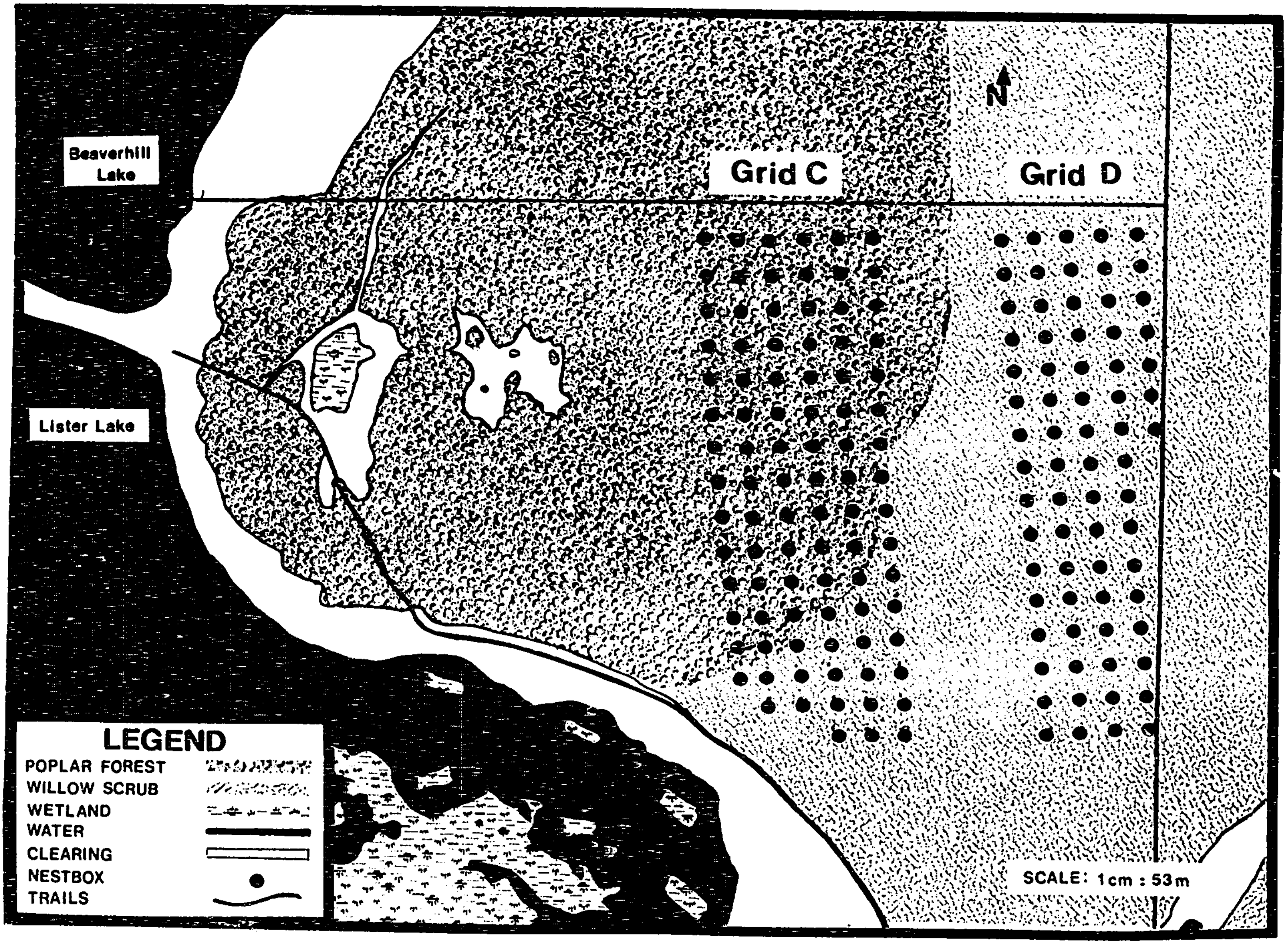


Fig. 2b Map of study area for House Wrens at Beaverhill Lake, Alberta (east)



grid B contained 24 boxes in willow scrub, grid C contained 92 boxes, 68 in poplar and 24 in willow, and grid D contained 71 boxes in willow. The east and west areas were 1.5 km apart. The distance and the presence a water body between the east and west grids served to minimize movement of wrens between the areas. Grids on the same side of Lister Lake were separated by 150 m. A control grid of equal size and similar vegetation structure, but lacking in nest boxes, was established for each experimental grid. The control grids were marked with flagging tape and were adjacent to each experimental grid (directly west of grids A, B, and C and north of grid D).

The nest boxes were nailed to trees in the poplar forest, and wired to clumps of stems or wooden posts in the willow scrub. The distance between ground level and the nestbox entrance-hole ranged from 1.0 to 1.5 m and aspect varied. The distance between boxes within a grid was 30 m. The average territory size for House Wrens is 0.56 ha (Kendeigh 1941). The 30 m spacing used in this study created a box density of 4 boxes per average territory size to permit high nesting density.

An attempt was made to capture and mark all House Wrens in the study area in 1986 and 1987. Birds were caught by using mistnets or a simple trap-door mounted on the front of the nestbox. Capture of adults occurred primarily after commencement of incubation to minimize the risk of abandonment. All birds trapped were weighed to the nearest 0.1 gram with a 30 gram Pesola spring scale and measured for wing chord and tail length to the nearest 0.5 mm. Each House Wren was individually marked with a combination of a U.S. Fish and Wildlife aluminum band (size 0) and colored leg bands for later recognition. The characters used to identify the sex of adult birds were the presence of a brood patch on the female and a cloacal protuberance on the male. Nestlings were banded 8 days after hatching.

BREEDING POPULATION AND REPRODUCTIVE SUCCESS

Nestboxes were monitored daily throughout the 1986 and 1987 breeding season with every nestbox being checked at least once every three days. The following data were recorded or calculated for each nestbox: stage of nest development, date of first egg, clutch size, date of hatching, brood size, date of fledging and number of young fledged. All terminations in the breeding cycle, such as predation or abandonment, were noted. In 1988, only the occupancy of the boxes was recorded. No data were collected for grid 2 in 1988 as the boxes were not cleaned and repaired in time for settlement.

Control areas were searched for nesting pairs of House Wrens by walking transects of the same spacing as the experimental grids. If a wren was seen or heard, an attempt was made to locate the nest site. If a bird was seen or heard on only one day and no nest was found it was assumed that the bird was not breeding in the grid.

The total number of nesting attempts (defined as at least one egg being laid in a nest) was calculated for each grid. Tests for significant difference between the number of nesting attempts in each area were made using 2 x 2 contingency tables and the G-Test. The Williams' correction was applied to minimize type I error (Sokal & Rohlf 1981, p.736). The proportion of attempts that resulted in fledged young was also compared between areas with the G-Test.

The characters used to compare reproductive success between areas were clutch-size and number of young fledged. The Mann-Whitney U-Test was used to determine the statistical significance of differences between grids. A regression of clutch-size on date of first egg was calculated to test for a seasonal decline in clutch-size. Such seasonal declines have been noted for other passerines (Arcese & Smith 1988) and necessitate division of the breeding season into periods for more accurate comparison. Data between years did not differ significantly and were pooled to increase the sample size for the computation of the regression.

Nestlings from at least five broods in each grid were weighed daily in 1986. I attempted to weigh nestlings from broods that were initiated at the same period of the breeding season and had the same number of young. It was necessary to weigh nestlings from both 1986 and 1987 to obtain an adequate sample size for east poplar. Only nestlings that survived through to fledging were included in the analyses. In all, 133 nestlings from 21 broods (6.33 +/- 0.19 young) were successfully weighed.

Nestlings were weighed every morning between 0700 and 1000 where possible, commencing on the first morning after hatching. Nestlings were placed in a small nylon bag and weighed to the nearest 0.1 g with a Pesola spring scale. Each bird within a brood was given individual markings on the legs with non-toxic colored pens until the eighth day after hatching, at which time the marking was replaced with aluminum and color bands. Birds were not handled after 12 days of age to avoid premature fledging.

Data were pooled to test for fit to the logistic equation (Zach 1982) using a numerical procedure for estimating unknown parameters in sets of nonlinear equations by the least squares method (SAS 1985). Data for each individual area were then transformed and a linear regression was used to compute the intrinsic growth rate and the asymptotic weight simultaneously for the logistic equation (Crossner 1977). The regression equations for each area were tested for significance with a t-test. The regressions were then compared to test for differences in nestling growth between areas. Since the growth rate and asymptote were calculated simultaneously differences between regressions may be due to either one or a combination of the two. Weight of nestlings on days 1, 6 and 12 were also compared between areas with a t-test.

VEGETATION STRUCTURE

I sampled vegetation variables in the four study areas in an attempt to quantify vegetation structure. The plot size (0.04 ha) and variables were those first suggested by James and Shugart (1970) and modified by Noon (1981). The sampling design was chosen because it was believed to measure vegetation structure characters that are proximally, and perhaps ultimately, important in determining the population density and reproductive success of House Wrens. The variables were adapted to best fit the vegetation conditions of the study area and are presented in table 2 (see Noon 1981 for sampling procedures).

The number of plots was determined through a preliminary survey in the west poplar area consisting of five samples that measured the total number of poplar stems hectare^{-1}. Using the equation described by Freese (1962), a sample size of 8 was derived from the variance estimate of the pilot survey and a sampling criterion of being within 10% of the population mean 90% of the time. Therefore, 8 plots were located in each of the west willow and west poplar grids. The east grids were given proportional coverage resulting in 25 and 20 plots in the east willow and east poplar respectively. Plot locations were selected prior to the 1987 field season using random

TABLE 2. Vegetation variables measured in the 4 study areas at Beaverhill Lake, Alberta.

VARIABLE	DESCRIPTION
TOT1	total stems/plot 3.1-6.0cm dbh
TOT2	total stems/plot 6.1-9.0cm dbh
TOT3	total stems/plot 9.1-12.0cm dbh
TOT4	total stems/plot 12.1-15.0cm dbh
TOT5	total stems/plot 15.1-18.0cm dbh
TOT6	total stems/plot 18.1^{+}cm dbh
STEMHA	total stems $\text{hectare}^{-1} > 3.1$cm dbh
CANCO	% canopy cover
GRDCO	% ground cover
GRASS	% of ground cover in grasses and sedges
FORB	% of ground cover in forbs
LITR	% of ground cover in litter
POPSHR	% of shrubs that are poplar
WILSHR	% of shrubs that are willow
SHRDEN	total stems $\text{hectare}^{-1} < 3.1$cm dbh
CB1	number of squares >50% obscurred 0.0-0.3m
CB2	number of squares >50% obscurred 0.3-1.0m
CB3	number of squares >50% obscurred 1.0-2.0m
CB4	number of squares >50% obscurred 2.0-3.0m
PQ	distance to nearest stem in each quarter / 4
TRAGE	tree age
SHRAGE	shrub age

number generation that corresponded to a numbered grid placed over a map of each experimental grid.

Summary statistics for each parameter were compiled for the random survey to compare the means of each parameter between grids. Student's t-tests were performed on all variables to assess the significance of difference between means. Where the variances of any variable were unequal (as revealed by the F-test), the t'-test (Sokal & Rohlf 1984) was used instead of the Student's t-test.

The univariate analyses yield important information related to individual variables, but ignore the covariance structure of the variables (Morrison 1967). Therefore, I used the multivariate technique of principle component analysis (PCA) to identify the major axes of variation in the vegetation structure between areas. PCA summarizes the variation contained in the original set of variables in a smaller set of transformed variables. The principle components are linear combinations of the original variables that explain progressively smaller amounts of the total variation within the original data set. PCA was carried out using the SPSSx FACTOR program.

Along with a random vegetation structure sample, I also sampled the vegetation around each nestbox. Plots were identical to the random plots with the addition of 3 new variables: 1 & 2) the horizontal density of vegetation directly in front of the nestbox was measured from 5m and 10m away using a coverboard (40 cm x 40 cm with 16 squares), and 3) whether or not a nestbox was on the edge of the grid.

The samples around each nestbox were divided into two groups based on whether or not the box had been used by wrens. Vegetation samples at nestboxes that were used all three years (or 2 years in west willow) were grouped together for comparison with samples at boxes that were never used by wrens. This separation was based on the assumption that boxes used in all three years represent the sites most preferred by wrens and vice versa.

The two groups were subjected to discriminant function analysis (DFA) in order to identify the variables that were most important in contributing to the statistical separation in the groups. DFA provides a linear function that weights and combines the original data in such a way as to separate the groups as statistically distinct as possible. In this way it is possible to identify vegetation structure components that may be important to breeding House Wrens. Step-wise DFA was employed using the SPSSx Discriminant program.

ARTHROPOD ABUNDANCE

Invertebrates were sampled from 2 points within each of the 4 grids in 1987. Samples were collected one day week^{-1} between 1000 and 1300 hrs. for ten weeks, beginning on May 27. The points were randomly selected prior to the field season and were different each week. Sampling at a point consisted of thirty 180^0 sweeps of a standard 27 cm diameter net using approximately constant speed and force. Ten sweeps were taken at ground level, 1 m and 2 m above ground level. These sampling heights were chosen based on observations of wren foraging height. Samples were transferred from the net to alcohol for later analysis.

The second component of the arthropod sampling involved the placement of 2 commercially available "sticky-traps" (Aeroxon^R, 66cm x 4cm) at the sampling point. One of the traps was placed vertically along the bark surface of a tree or shrub and the other horizontally along a branch. The sticky traps were put up on the same day and at the same locations as the sweep net sampling. The traps were checked and removed after 48 hours.

Invertebrates from both methods were pooled, identified to Order and organized into 3 mm size classes. Weekly biomass (dry weight) was estimated for each size class using a general weight vs. length relationship for insects ($W = 0.0305 L^{2.62}$; Rogers et al. 1976).

To determine what prey items were being used by the wrens, I collected samples from collared nestlings and examined adult and nestling faeces. A total of 124 samples from collared nestlings were collected from 1986 and 1987. Thirteen droppings from adult birds and 48 droppings from nestlings were examined under a dissecting microscope for identification of prey remains. Remains were identified using a reference collection from the invertebrate sampling and published literature on bird faeces examination (Ralph et al. 1985, Moreby 1988).

POLYGYNY

I determined male House Wrens to be polygynous if they were observed feeding females or young at more than one nest. Males that were seen defending a second nestbox resulting in a female raising young without male assistance were also considered polygynous. Males were considered to be polygynous only if there was some overlap between the nesting periods of the primary and secondary nests. Males that initiated second matings following the success or failure of a first brood were not considered to be polygynous.

Vegetation density made it impossible to observe wrens travelling between boxes, therefore, it was necessary to color-band males to determine their breeding status. Since most males were caught after they started feeding young (they rarely enter the nestbox during incubation), the breeding status of males whose nests failed before hatching was usually unknown.

The timing and outcome of all known polygynous cases were recorded for 1986 and 1987. Primary and secondary nests were observed to determine the extent of parental care. The number of polygynous matings was compared to the total number of nesting attempts to give an estimate of the incidence of polygyny.

Comparisons of mean clutch size and number of young feldged were made between monogamous, primary polygynous and secondary polygynous females to determine whether or not there were any differences in reproductive success. Data for the nests where mating status was confirmed in 1986 and 1987 were used for the comparisons. Nesting attempts from the east willow grid in 1987 were not included due to complications that arose from heavy predation. Mann Whitney U-Tests were employed to test for statistical significance of any differences.

RESULTS

BREEDING POPULATION AND REPRODUCTIVE SUCCESS

In 1986, 1987 and 1988 there were 74, 90 and 55 nesting attempts respectively by House Wrens in all areas (Table 3). There were significantly fewer nest attempts in the east poplar as compared to the other areas in all years (Table 4). The only other significant difference was a greater occupancy in the east willow as compared to the west willow in 1987.

The timing pattern of clutch initiation in the west willow and poplar areas in 1986 and 1987 is represented in figure 3. Figure 4 presents the same information for the east grids. The west poplar area exhibited a similar pattern in both years, while the willow area had fewer nest attempts in the early season of 1987 as compared to 1986. The east grids had a similar settlement pattern in both years with more nesting attempts in 1987.

In 1986 there were no significant differences between any of the areas in the proportion of nests resulting in fledged young (Table 5). In 1987, however, both poplar areas had significantly greater success than both willow areas (G-Williams', $P<0.01$).

There were 3 nests of House Wrens found in the control areas over both years. A nest was found in each of the poplar

TABLE 3. Nesting attempts by House Wrens at Beaverhill Lake, Alberta.

	Number of Nesting Attempts (Percent of Available Sites Occupied)			
Grid	1986	1987	1988	Total
West Poplar	10(43)	14(61)	9(39)	33(48)
West Willow	14(58)	9(38)	------	23(48)
East Poplar	5(7)	8(12)	7(10)	20(10)
East Willow	45(47)	59(62)	39(41)	143(50)
Total	74(35)	90(43)	55(26)	219(36)

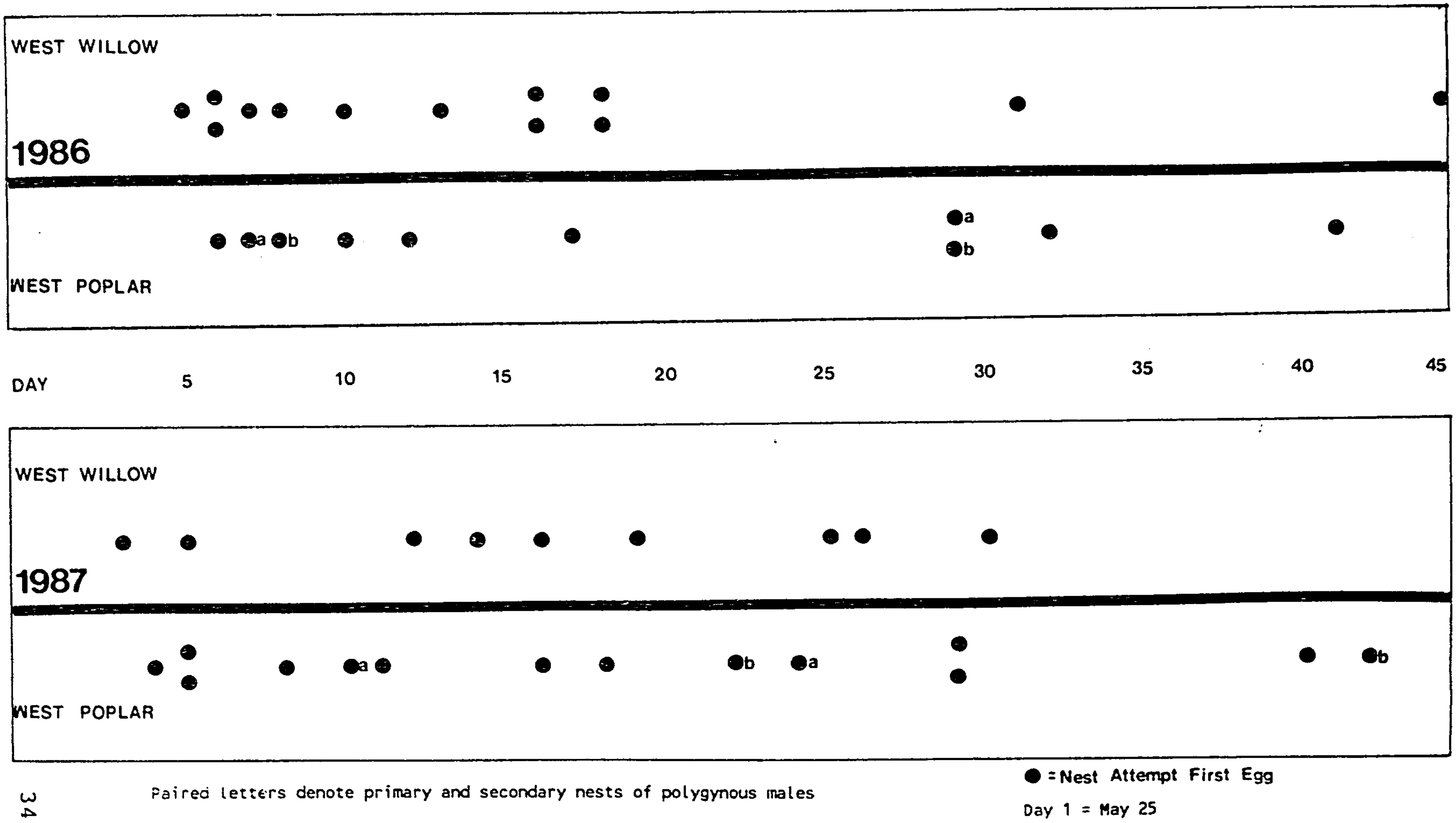
TABLE 4. Summary of tests for significant difference between occupation of willow and poplar areas by House Wrens at Beaverhill Lake (G-Test Williams').

GRID	YEAR	AREA		
		East Willow	East Poplar	West Willow
West Poplar	1986	0.110 NS	13.578^{**}	1.009 NS
	1987	0.040 NS	19.916^{**}	2.590 NS
	1988	0.633 NS	8.369^{**}	--------
	All	0.587 NS	41.743^{**}	0.607 NS
West Willow	1986	0.905 NS	24.443^{**}	
	1987	5.126^{*}	6.752^{**}	
	1988	--------	--------	
	All	3.049 NS	30.028^{**}	
East Poplar	1986	33.418^{**}		
	1987	46.709^{**}		
	1988	28.595^{**}		
	All	107.682^{**}		

* $P<0.05$

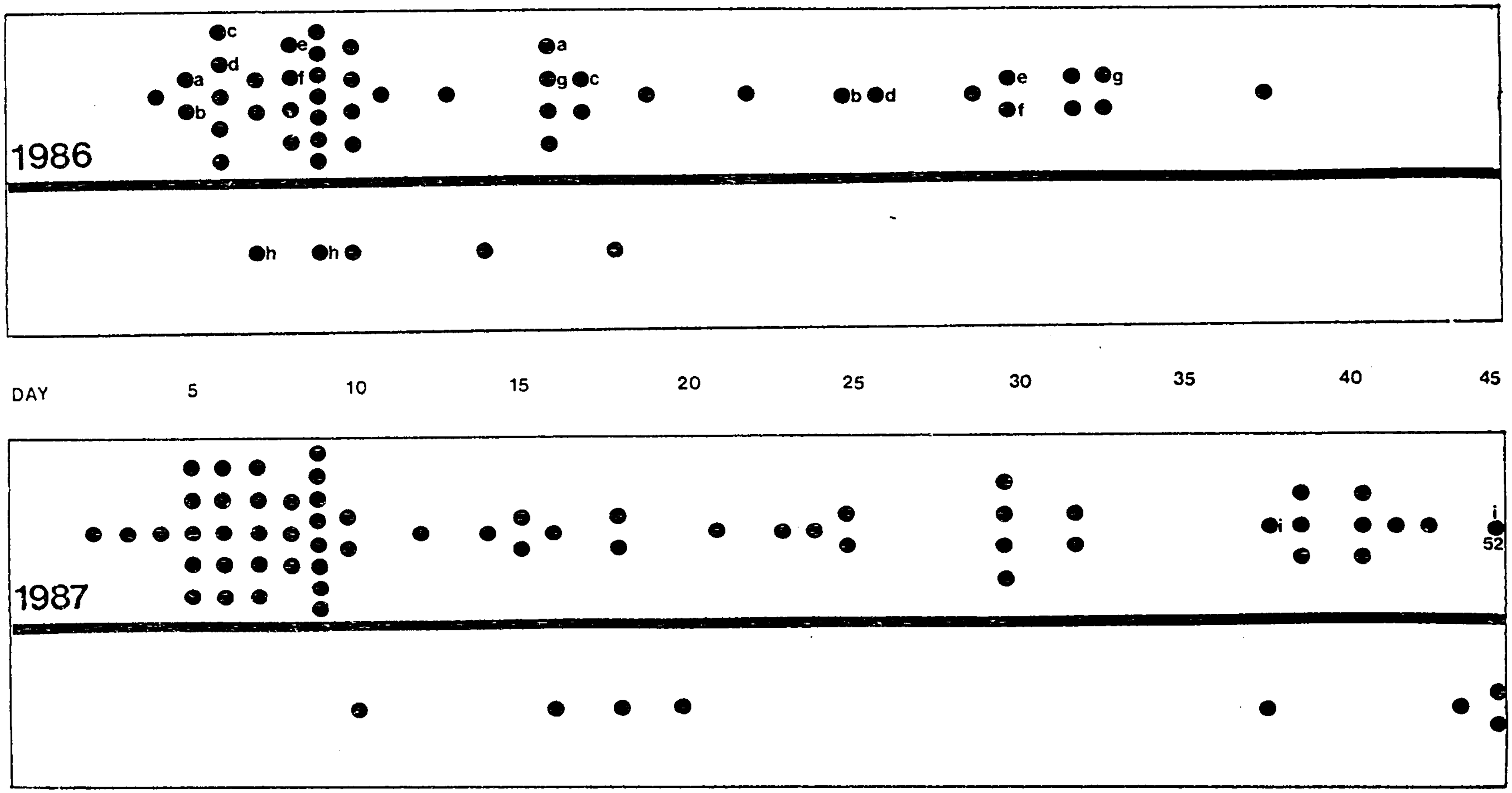
** $P<0.01$

Fig. 3 Timing of clutch initiation by House Wrens in the west willow and poplar grids in 1986 & 1987



Paired letters denote primary and secondary nests of polygynous males

Fig. 4 **Timing of clutch initiation by House Wrens in the east willow and poplar grids in 1986 & 1987**



Paired letters denote primary and secondary nests of polygynous males

● = Nest Attempt First Egg

Day 1 = May 25

TABLE 5. Number of House Wren nest attempts resulting in fledged young at Beaverhill Lake, Alberta.

Grid	Year	# Nests Occupied	# Nests Successful	%Nests Successful
West Poplar	1986	10	8	80
	1987	14	14	100
West Willow	1986	14	12	86
	1987	9	2	22
East Poplar	1986	5	4	80
	1987	8	8	100
East Willow	1986	45	30	67
	1987	59	16	27

controls in 1986 and one in the west poplar control in 1987. In addition, a nest of a Mountain Bluebird (Sialia currucoides) and a Black-capped Chickadee (Parus atricapillus) were found in natural cavities in the east poplar control in 1986 and west poplar control in 1987 respectively. No nests were found in natural cavities in any experimental grid in any year.

Predation on House Wren nests was recorded in neither of the poplar areas in 1986 and 1987. Failure to fledge young resulted from abandonment of nests before hatching in two instances, while the third case was apparent starvation of nestlings. One of the clutches was abandoned for unknown reasons and the other may have been due to infertile eggs (the female incubated for 20 days). The case of starvation occurred in the east poplar in 1986.

The high rate of nest failure in the willow areas was primarily due to three factors; intraspecific nest-content destruction, predation by weasels (Mustela erminea), and abandonment before the onset of incubation for unknown reasons. Intraspecific egg-breaking and infanticide was implicated in the loss of 3 nests in 1986 and 9 nests in 1987 (for further details see Quinn & Holroyd 1989). Weasel predation accounted for the loss of 1 nest in the east willow in 1986 and 26 in 1987. There were no losses to weasels in any other grid.

There was also evidence of a high post-fledging mortality in the east willow area. A Sharp-shinned Hawk (Accipiter striatus) pair nested on the west boundary of the east willow grid in 1987 and 1988. Examination of the hawk nest at the end of the season in 1987 yielded 14 color bands from banded nestlings and a large number of juvenile House Wren feathers.

The regression of clutch-size on time of breeding indicates a significant decline in the number of eggs laid as the seasons progressed ($t=10.93$, $P<0.01$; fig.5). The decline indicates that comparisons of clutch-size between areas is most accurately done for nests initiated at the same period of the breeding season. Therefore, clutches initiated between day 1 and day 15 were compared for 1986, and day 1 to 20 in 1987, allowing for comparison within a similar period while maintaining adequate sample sizes. Small sample sizes made it impossible to compare later nests.

In 1986, wrens in the west willow had a significantly higher clutch-size than wrens in both the east poplar ($U=-8$; $P<0.05$, Mann-Whitney U-Test) and the west poplar ($Z=2.46$; $P<0.05$). There were no other significant differences in clutch-size or number of young fledged in either year (Table 6).

The first clutches were initiated in the east willow in both years. In 1986 the first egg in the east willow was laid 1 day before the west willow, two days before the west poplar, and three days before the east poplar. In 1987 the first egg

FIG. 5

SEASONAL DECLINE IN CLUTCH–SIZE
OF HOUSE WRENS AT BEAVERHILL LAKE, ALBERTA
(N = 132)

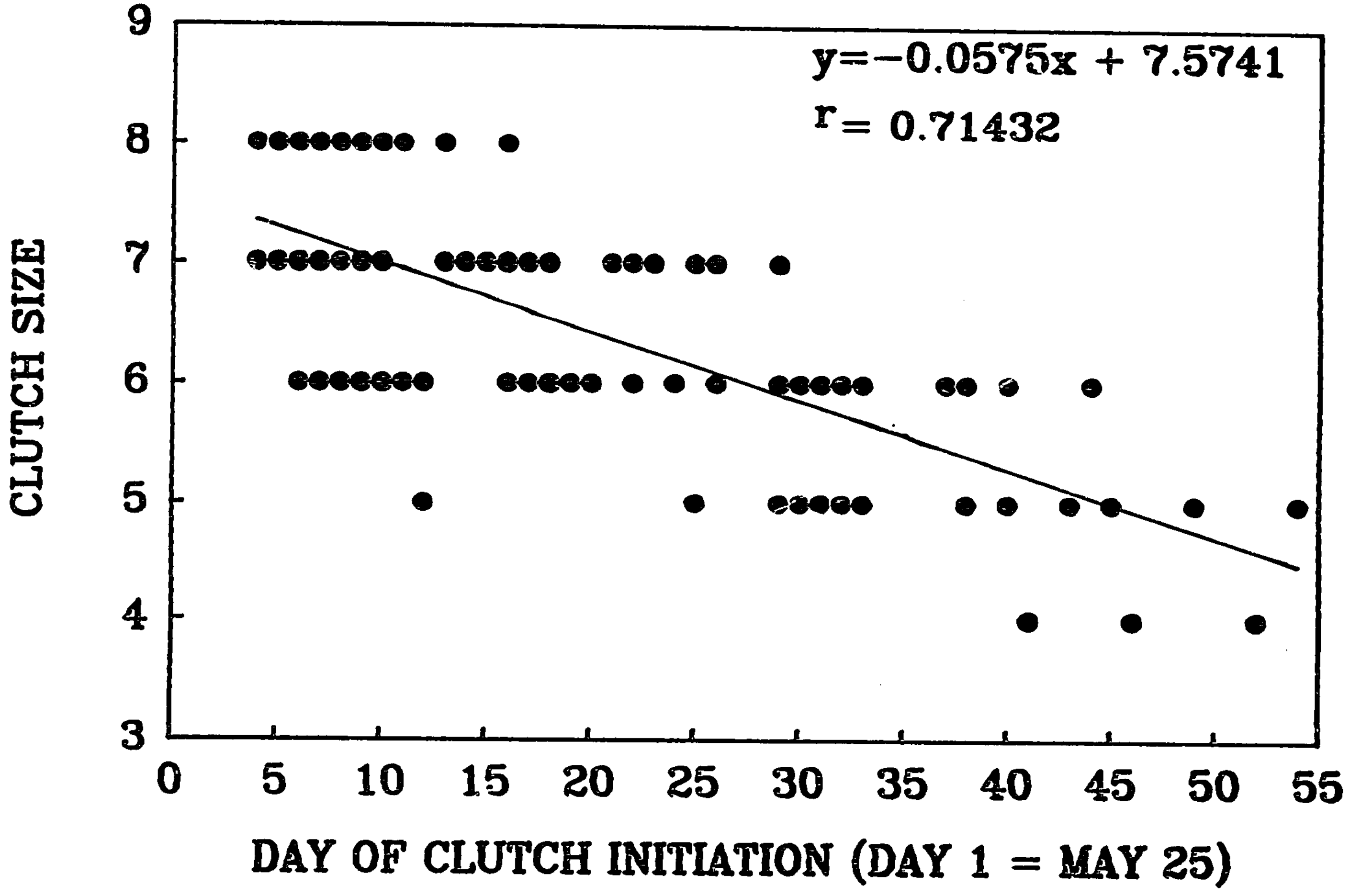


TABLE 6. Mean clutch-size and number of young fledged by House Wrens from clutches initiated between day 1 and 15 in 1986 and between day 1 and 20 in 1987.

	1986		1987	
Grid	Clutch Size (N)	Fledged Young (N)	Clutch Size (N)	Fledged Young (N)
West Poplar	6.75 (4)	6.00 (4)	7.12 (8)	6.62 (8)
West Willow	7.71 (7)	5.83 (6)	6.75 (4)	6.00 (2)
East Poplar	7.25 (4)	6.67 (3)	7.00 (4)	6.25 (4)
East Willow	6.92 (26)	6.56 (18)	7.00 (21)	6.00 (10)

in the east willow was laid 1 day before the west willow, two days before the west poplar and 8 days before the east poplar.

The nonlinear regression of nestling weight on age produced a highly significant fit to the logistic equation ($F=732,118$, $P<0.01$) with an asymptote A of 10.8 g and a growth-rate constant K of 0.51 day^{-1}(fig. 6). The transformed growth data for west poplar, west willow, east poplar and east willow all resulted in significant linear regressions ($t=58.63$, $t=44.98$, $t=40.87$, $t=54.94$; $P<0.01$ respectively, Table 7).

Comparison of the regressions indicate that the slope for east willow was significantly different than that of west willow ($F=15.34$, $P<0.01$) and east poplar ($F=11.58$, $P<0.01$). Slopes were not different, but levels of regression differed between east willow and west poplar ($F=56.62$, $P<0.01$). These differences are due to the greater weight obtained by nestlings in the east willow prior to fledging than in the other three areas. A comparison of weights on the 12th day after hatching shows that nestlings from east willow broods were significantly heavier than those from west poplar ($t=10.8$, $P<0.01$), west willow ($t=10.33$, $P<0.01$) and east poplar ($t=11.06$ $P<0.01$) (Table 8).

The nestlings from west willow broods were significantly heavier than those from west poplar ($t=4.49$, $P<0.01$), east poplar ($t=6.65$, $P<0.01$) and east willow ($t=7.82$, $P<0.01$) on

FIG.6 MEAN WEIGHT (standard deviation) OF HOUSE WREN NESTLINGS FITTED TO LOGISTIC EQUATION. (N=135)

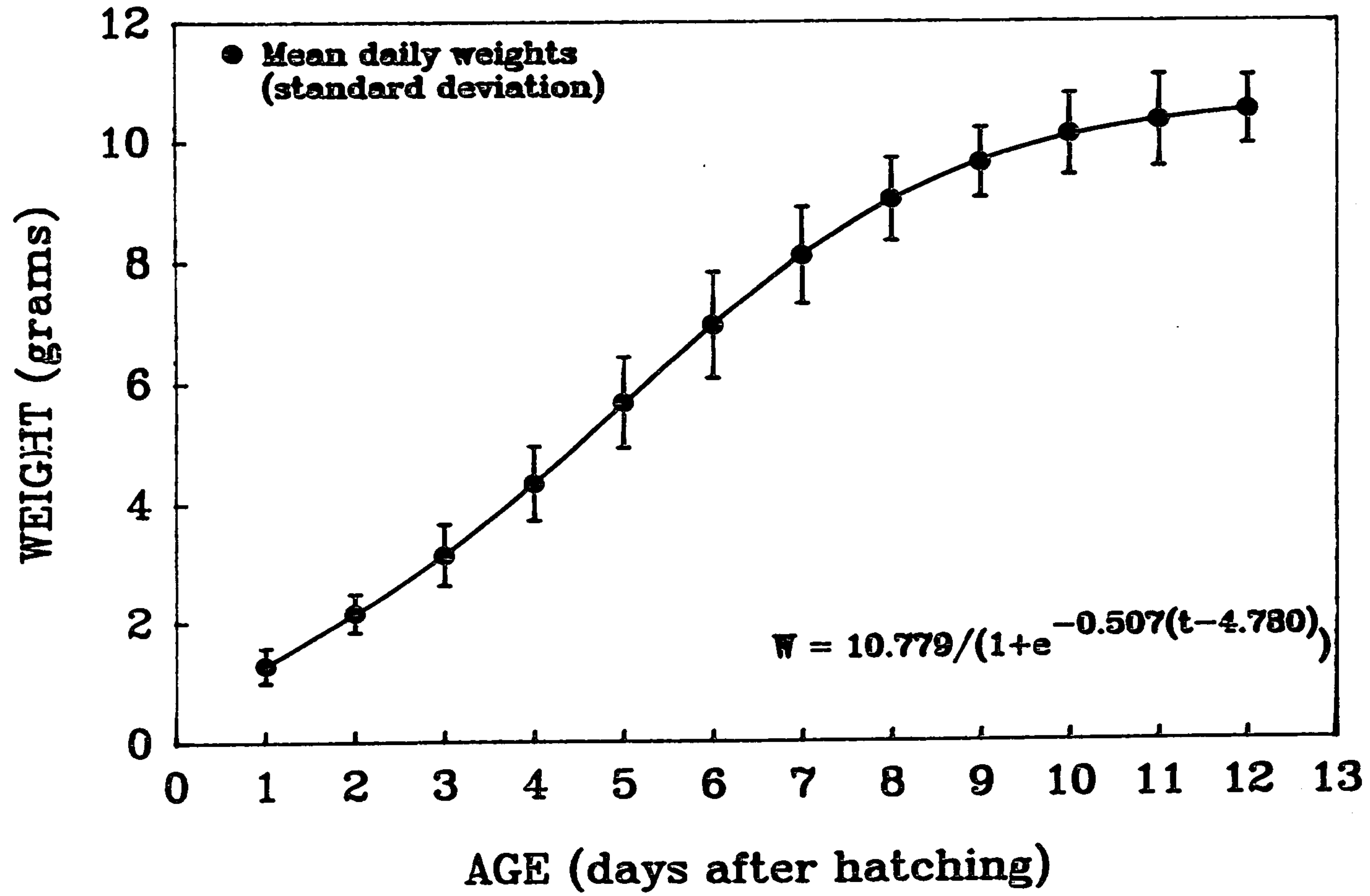


TABLE 7. Results of linear regression of transformed growth data for House Wrens at Beaverhill Lake, Alberta.

Variable	West Poplar	West Willow	East Poplar	East Willow
slope	-0.0496	-0.0529	-0.0526	-0.0473
SE	(.00085)	(.00118)	(.00129)	(.00086)
y-intercept*	0.5238	0.5413	0.5433	0.5372
SE	(.0502)	(.0589)	(.0586)	(.0539)
x-intercept**	10.56	10.23	10.33	11.36

* y-intercept = intrinsic growth rate from logistic equation

**x-intercept = asymptotic weight from logistic equation

TABLE 8. Mean weights (standard errors) of nestling House Wrens on days 1, 6 & 12 at Beaverhill Lake, Alberta.

	WEIGHT (g)			
Day	West Poplar	West Willow	East Poplar	East Willow
1	1.15(.06)	1.50(.06)	1.06(.02)	1.32(.04)
6	6.83(.09)	7.39(.12)	6.00(.07)	7.46(.10)
12	10.23(.06)	10.14(.08)	10.29(.05)	11.24(.07)

the first day after hatching. However, west willow nestlings are lightest at time of fledging.

VEGETATION STRUCTURE

The vegetation survey based on randomly selected plots yielded statistically significant differences between all study areas (Tables 9 & 10). Both poplar areas differed greatly from both willow areas in most vegetation structure parameters. The west poplar area was characterized by open balsam poplar forest with a mean density of 3867.5 stems/ha. The east poplar area was similar in overall stem density (x=3907.7 stems/ha), but differed significantly in age-class structure. There were more stems in the 9.1-12.0cm and 12.1-15.0cm classes in the west poplar reflecting a significantly older stand (37 vs. 31 years). The east poplar area had more ground cover due primarily to a heavier inclusion of grasses and sedges. There were also more shrubs in the east poplar, especially near the area margins.

The west willow area was void of stems >3.0cm dbh and consisted of a high density of willow and poplar shrubs (x=183,043 stems/ha). There were some tree-size stems in the east willow area and the density of shrubs was significantly less than the west willow (x=75,278 stems/ha). The difference in shrub density was due to the dispersion of shrubs rather

TABLE 9. Results of the random vegetation survey at Beaverhill Lake, Alberta.

VARIABLE	MEAN (Standard Error) FOR EACH VARIABLE			
	West Poplar(WP)	West Willow(WW)	East Poplar(EP)	East Willow(EW)
TOT1	62.625 (6.3385)	0.625 (0.6250)	76.077 (8.9008)	7.750 (4.1285)
TOT2	44.875 (4.4055)	0.000 (0.0000)	49.615 (4.8019)	6.125 (2.3570)
TOT3	33.625 (3.6151)	0.000 (0.0000)	21.462 (3.5637)	2.833 (1.0762)
TOT4	12.125 (2.2236)	0.000 (0.0000)	6.923 (1.1573)	2.167 (1.3620)
TOT5	4.500 (1.4015)	0.000 (0.0000)	0.615 (0.4875)	0.542 (.02083)
TOT6	0.625 (0.3239)	0.000 (0.0000)	0.615 (0.2412)	0.125 (0.0690)
STEMHA	3867.5 (759.8)	78.1 (78.1)	3907.7 (391.0)	440.2 (191.0)
CANCOV	55.8 (2.9)	93.5 (2.2)	56.0 (3.7)	67.6 (1.3)
GRDCOV	55.1 (2.4)	82.2 (2.1)	74.7 (1.4)	84.7 (1.5)
GRASS	37.5 (2.5)	59.4 (5.0)	62.7 (2.2)	65.0 (3.6)
FORB	24.4 (4.7)	26.2 (4.5)	12.7 (1.8)	20.4 (3.6)
LTR	34.4 (1.8)	14.4 (2.9)	23.1 (1.3)	13.3 (1.5)
POPSHR	0.00 (0.00)	23.75 (8.06)	30.77 (4.42)	3.33 (1.49)
WILSHR	100.00 (0.00)	76.25 (8.06)	69.23 (4.42)	96.67 (1.49)
SHRDEN	3867 (760)	183043 (27226)	12669 (1153)	75278 (5038)
CB1	4.64 (0.71)	14.28 (0.52)	8.65 (1.04)	14.59 (0.21)
CB2	6.21 (1.01)	31.21 (2.73)	11.60 (2.28)	30.31 (1.25)
CB3	7.61 (2.00)	41.92 (3.02)	16.62 (2.55)	39.71 (2.00)
CB4	9.24 (2.43)	26.10 (3.65)	19.78 (3.24)	36.33 (2.47)
PQ	2.06 (0.20)	0.87 (0.11)	1.33 (0.10)	1.18 (0.15)
TRAGE	36.62 (0.80)	------------	30.92 (1.52)	31.43 (1.18)
SHRAGE	10.62 (0.62)	11.88 (1.02)	17.15 (1.00)	19.21 (0.94)

TABLE 10. Tests for statistically significant differences between vegetation variables from the random vegetation survey at Beaverhill Lake, Alberta.

VARIABLE	COMPARISONS BETWEEN VARIABLES					
	WP vs.			WW vs.		EP vs.
	WW	EP	EW	EP	EW	EW
TOT1	P<0.01	NS	P<0.01	P<0.01	NS	P<0.01
TOT2	P<0.01	NS	P<0.01	P<0.01	NS	P<0.01
TOT3	P<0.01	P<0.05	P<0.01	P<0.01	NS	P<0.01
TOT4	P<0.01	P<0.01	P<0.01	P<0.01	NS	P<0.01
TOT5	P<0.01	NS	NS	P<0.05	NS	P<0.05
TOT6	NS	NS	NS	NS	NS	NS
STEMHA	P<0.01	NS	P<0.01	P<0.01	NS	P<0.01
CANCOV	P<0.01	NS	P<0.01	P<0.01	P<0.01	P<0.01
GRDCOV	P<0.01	P<0.01	P<0.01	P<0.01	NS	P<0.01
GRASS	P<0.01	P<0.01	P<0.01	NS	NS	NS
FORB	NS	P<0.05	NS	P<0.05	NS	P<0.05
LTR	P<0.01	P<0.05	P<0.01	P<0.01	NS	P<0.01
POPSHR	P<0.05	P<0.01	NS	NS	P<0.01	P<0.01
WILSHR	P<0.05	P<0.01	NS	NS	P<0.01	P<0.01
SHRDEN	P<0.01	P<0.01	P<0.01	P<0.01	P<0.01	P<0.01
CB1	P<0.01	NS	P<0.01	P<0.01	NS	P<0.01
CB2	P<0.01	P<0.05	P<0.01	P<0.01	NS	P<0.01
CB3	P<0.01	NS	P<0.01	NS	P<0.05	P<0.01
CB4	P<0.01	P<0.01	P<0.01	P<0.01	P<0.01	P<0.01
PQ	P<0.01	P<0.01	P<0.01	P<0.01	NS	NS
TRAGE	------	P<0.01	P<0.05	------	------	NS
SHRAGE	NS	P<0.01	P<0.01	P<0.01	P<0.01	NS

than individual shrub density. The east willow had a patchy distribution of shrubs with spaces between individual plants. In contrast, the west willow had uniform high density resulting from few breaks in the vegetation. The west willow had a greater inclusion of poplar shrubs and lower horizontal density at the 2.0-3.0m level. The shrubs in the east willow were significantly older than the west willow (19 vs. 12 years) accounting for taller shrubs and greater cover at 2.0-3.0m. Ground cover between the willow areas did not differ significantly.

Each of the measured vegetation variables was significantly correlated with at least 5 other variables (Table 11). The high degree of interrelationship between variable suggests that differences between areas were more complex than merely the sum of the contributions of individual variables.

Principle component analysis was employed to summarize the total variation in the vegetation data into an ecologically meaningful number of factors (Table 12). The first principle component is highly correlated, positively, with total stems/ha, the first four tree size-classes, canopy cover and litter, and negatively with shrub density, horizontal cover at the first three levels and ground cover. This component recognizes the major structural differences between the willow and poplar areas. The high percentage of variation explained by the first component (52.3%) suggests

TABLE 11. Statisitical significance of correlations between vegetation variables from the random vegetation survey at Beaverhill Lake, Alberta.

	TOT1	TOT2	TOT3	TOT4	TOT5	TOT6	STEMHA	CANCOV	GRDCOV	GRASS	FORB	LTR	POPSHR	WILSHR	SHRDEN	CB1	CB2	CB3	CB4	PQ
TOT1	------																			
TOT2	P<.01	------																		
TOT3	P<.01	P<.01	------																	
TOT4	P<.01	P<.01	P<.01	------																
TOT5	P<.05	P<.01	P<.01	P<.01	------															
TOT6	P<.05	P<.01	P<.01	P<.01	P<.01	------														
STHA	P<.01	P<.01	P<.01	P<.01	P<.01	P<.01	------													
CANCOV	P<.01	P<.01	P<.01	P<.01	P<.01	P<.05	P<.01	------												
GRDCOV	P<.01	P<.01	P<.01	P<.01	P<.01	P<.05	P<.01	P<.01	------											
GRASS	P<.05	P<.05	P<.01	P<.05	P<.01	NS	P<.05	NS	P<.01	------										
FORB	NS	NS	NS	NS	NS	NS	NS	NS	NS	P<.01	------									
LTR	P<.01	P<.01	P<.01	P<.01	P<.01	NS	P<.01	P<.01	P<.01	P<.01	NS	------								
POPSHR	P<.01	P<.05	NS	NS	NS	NS	P<.05	NS	NS	P<.05	P<.05	NS	------							
WILSHR	P<.01	P<.05	NS	NS	NS	NS	P<.05	NS	NS	NS	P<.05	NS	P<.01	------						
SHRDEN	P<.01	P<.01	P<.01	P<.01	P<.01	P<.01	P<.01	P<.01	P<.01	NS	NS	P<.01	NS	NS	------					
CB1	P<.01	P<.01	P<.01	P<.01	P<.01	P<.05	P<.01	P<.01	P<.01	P<.01	NS	P<.01	NS	NS	P<.01	------				
CB2	P<.01	P<.01	P<.01	P<.01	P<.01	P<.01	P<.01	P<.01	P<.01	P<.05	NS	P<.01	NS	NS	P<.01	P<.01	------			
CB3	P<.01	P<.01	P<.01	P<.01	P<.01	P<.01	P<.01	P<.01	P<.01	P<.05	NS	P<.01	NS	NS	P<.01	P<.01	P<.01	------		
CB4	P<.01	P<.01	P<.01	P<.01	P<.01	P<.05	P<.01	P<.01	P<.01	P<.05	NS	P<.05	NS	NS	P<.01	P<.01	P<.01	P<.01	------	
PQ	P<.05	P<.05	P<.01	P<.01	P<.01	NS	P<.01	NS	P<.01	NS	NS	P<.05	NS	NS	P<.01	P<.01	P<.01	P<.01	P<.01	------

TABLE 12. Correlations of the vegetation variables with the five rotated principle components extracted from the analysis of the random vegetation plots.

VARIABLE	COMPONENT				
	I	II	III	IV	V
STHA	**.93993**	.18107	.15317	-.00156	-.16553
TOT2	**.92681**	.15116	.17297	.05167	-.14742
TOT3	**.92124**	.15559	-.11015	-.07665	-.14732
TOT1	**.89935**	.07708	.26912	.01605	-.14128
CANCOV	**.85808**	.14374	.06802	.09260	-.06362
CB1	**-.83356**	-.23309	.07232	.13908	.34180
CB2	**-.76989**	-.36550	.01848	.01952	.39755
GRDCOV	**-.70928**	-.43528	.05994	.27708	-.13088
CB3	**-.69686**	-.39224	.02469	.04417	.51997
LTR	**.69556**	.48053	.00980	-.23507	.30244
TOT4	**.64713**	.46621	-.21494	-.00294	-.17393
SHRDEN	**-.62309**	-.28566	.31565	-.21319	.34944
TOT5	.26398	**.84482**	-.09937	-.15447	-.05502
TOT6	.15145	**.67337**	.15131	.13433	-.23521
POPSHR	.09817	.01803	**.94533**	.17914	-.07402
WILSHR	-.13604	-.05715	**-.92792**	-.17250	.02765
PQ	.34389	.24701	**-.45475**	.22545	-.28958
FORB	-.12451	-.09372	-.14782	**-.92556**	-.15233
GRASS	-.32672	-.18472	.15454	**.89523**	-.05050
CB4	-.44340	-.18199	-.09629	.19102	**.72846**
Variance Explained	52.3	13.1	8.1	5.5	4.8
Cummulative Variance	52.3	65.4	73.5	79.0	83.8

that the choice of vegetation variables was adequate to describe quantitatively what appeared to be a major pattern of variation in the study area vegetation structure, based on field observation.

The second principle component accounts for 13.1% of the variation and is highly correlated, positively, with the upper two tree size-classes. The third component accounts for 8.1% of the variation and is highly correlated, positively, with poplar shrubs and negatively with point quarter. Components 2 and 3 recognize the structural differences between west poplar and the other areas, and east poplar and the other areas respectively. The remaining two components account for a small amount of the variation and are ambiguous as to their ecological significance.

House Wrens occupied nestboxes in the west willow and poplar areas at similar densities, despite the wide disparity in vegetation structure. The data obtained from vegetation samples taken around each nestbox in the west willow and poplar areas were subjected to discriminant function analysis (DFA) in an attempt to separate sites used in all, some, or none of the years. The DFA failed to isolate any variables that were significant in discriminating between the groups. The lack of identification of discriminating variables indicates inadequate sampling of characters important to nest-site selection by wrens or, factors other than vegetation structure are more important in determining nest-site selection in this instance.

In contrast to the situation in the west areas, House Wrens demonstrated a strong preference for the willow habitat in the east areas. A DFA was employed to identify variables from the nestbox survey best able to discriminate between preferred and nonpreferred nesting sites. Only the data from the east willow area were used in the DFA. It would have been inappropriate to pool all of the data from the willow and poplar areas because any effect would be more due to the significant differences in structure between the two areas than to differences between individual sites (S. Barry pers. comm.). A step-wise DFA was performed on the vegetation data from east willow nestboxes that were used in all years compared to those that were never used.

The DFA produced a linear combination of shrub density and edge, plus a constant, to discriminate between groups. Nestboxes that were always used tended to be in more dense vegetation and on the edge of the grid. The group centroids differed significantly ($p<0.01$) and the function identified 85% of the cases correctly. The univariate group means for each variable and the statistical significance of the differences are presented in Table 13.

TABLE 13. Tests for significance between group means for nestboxes that were used by House Wrens in all years and nestboxes that were never used in the east willow grid.

VARIABLE	Occupied in All Years (N=12)	Never Occupied (N=9)	t-test
TOT1	2.25 (0.97)	3.78 (1.23)	t=0.94 NS
TOT2	2.42 (0.98)	6.11 (2.21)	t=1.69 NS
TOT3	1.42 (0.67)	4.11 (1.79)	t=0.28 NS
TOT4	0.33 (0.19)	4.11 (1.79)	t'=0.69 NS
TOT5	0.17 (0.11)	1.11 (0.45)	t=2.16*
TOT6	0.83 (0.08)	0.44 (0.18)	t=2.06 NS
STEMHA	170.8 (63.72)	477.8 (153.23)	t=1.92 NS
CANCOV	63.3 (3.91)	62.2 (4.72)	t=0.17 NS
GRDCOV	86.4 (2.75)	80.9 (1.85)	t=1.47 NS
GRASS	56.7 (5.65)	67.2 (3.34)	t=1.40 NS
FORB	30.8 (5.43)	16.7 (2.36)	t'=0.70 NS
LTR	11.7 (2.78)	16.1 (1.62)	t=1.20 NS
POPSHR	3.33 (2.25)	6.67 (2.20)	t=0.99 NS
WILSHR	96.67 (2.25)	94.33 (2.98)	t=0.65 NS
SHRDEN	77,308(7,754)	56,889(7.707)	t=1.74 NS
CB1	141.0 (5.14)	130.2 (8.46)	t=1.09 NS
CB2	291.5 (22.97)	250.1 (31.09)	t=1.04 NS
CB3	369.8 (29.91)	344.3 (39.48)	t=0.50 NS
CB4	280.8 (53.72)	364.1 (47.18)	t=1.07 NS
BOXD1	4.17 (1.53)	3.78 (1.59)	t=0.07 NS
BOXD2	8.50 (1.75)	6.67 (1.94)	t=0.66 NS
EDGE	0.92 (0.08)	0.22 (0.15)	t=4.17**

ARTHROPOD ABUNDANCE

There was an epidemic of western willow leaf beetles (*Pyrrhalta decora decora*) in the west willow grid in 1986. These insects emerged from hibernation as adults in late May and commenced feeding on the willow foliage. House Wrens were observed feeding extensively on this insect. The larvae appeared in early July and skeletonized the willow leaves by feeding on the undersurface (Furniss & Carolin 1980, Rose & Lindquist 1982). The wrens were not observed feeding on the larvae. Beetles caused heavy foliage damage resulting in most bushes appearing gray or brownish. Willow leaf beetles did not occur in epidemic proportions in 1987, however, the willow foliage did not entirely recover and many of the skeletonized leaves from 1986 were still present. This insect was not found in high numbers in any other study area.

All three years of the study coincided with an outbreak of forest tent caterpillars (*Malacosoma disstria*). The caterpillars were not observed to be eaten by the wrens, although the birds would remove them from the nest boxes. The moths, which began emerging in late June, were eaten in large numbers by the wrens. The east poplar grid was never heavily infested with forest tent caterpillars, while the other three grids had them in epidemic numbers. The exception being west willow in 1986 which was defoliated by the willow leaf beetle thus providing little food for the caterpillars.

Forest tent caterpillar adults were the most frequent prey item identified from faeces samples and collared nestlings (Tables 14 & 15). The next most abundant prey items were Araneida, larvae, Coleoptera, and Diptera. This list is not exhaustive of prey items taken by wrens since many of the fragments in the faeces were unidentifiable and small items may have been missed with the collaring technique.

The results of the sampling for invertebrate abundance are presented in appendix 2. The median number of invertebrates in each sampling period was significantly greater in the east willow area than all other areas (Table 16). West poplar had the second greatest number of invertebrates sample^{-1}and was significantly greater than west willow and east poplar. West willow and east poplar had the lowest counts sample^{-1}and did not differ significantly from each other.

The total invertebrate biomass collected on each sampling day is presented in figure 7. The total biomass from east willow was nearly double that of the next highest total from west poplar. Biomass estimates from east willow were sometimes more than 5 times greater than the next highest area estimate (i.e. sample period 5). West poplar and west willow were similar with both being almost twice as high as east poplar. Much of the biomass of west willow was contributed by Odonata (9,821 mg of 37,052 mg, 26.5%), a taxon that was

TABLE 14. Invertebrates identified from droppings of House Wrens at Beaverhill Lake, Alberta (N=61 droppings, 13 adults + 48 nestlings; 191 fragments identified).

Prey Item	# of Droppings Identified In	% of Droppings Identified In
Lepidoptera, M.disstria (ad)	43	70.5
Araneida	21	34.4
Diptera, Nematocera	11	18.0
Other Diptera	23	37.6
P. decora, Coleoptera	4	6.6
Other Coleoptera	15	24.6
Homoptera	17	27.9
Phalangida	14	23.0
Larvae (all)	14	23.0
Other Lepidoptera (ad)	14	23.0
Hymenoptera	8	13.1
Hemiptera	7	11.5
Neuroptera	2	3.3

TABLE 15. Invertebrate prey sampled from collared House Wren nestlings at Beaverhill Lake, Alberta (N=124).

Prey Item	Frequency	%
M.disstria (ad)	78	62.9
Araneida	12	9.6
Coleoptera	10	8.1
Larvae	8	6.4
Lepidoptera (ad)	6	4.8
Diptera	6	4.8
Phalangida	3	2.4
Neuroptera	2	1.6

FIG. 7 BIOMASS OF INVERTEBRATES SAMPLED IN 1987 AT BEAVERHILL LAKE, ALBERTA.

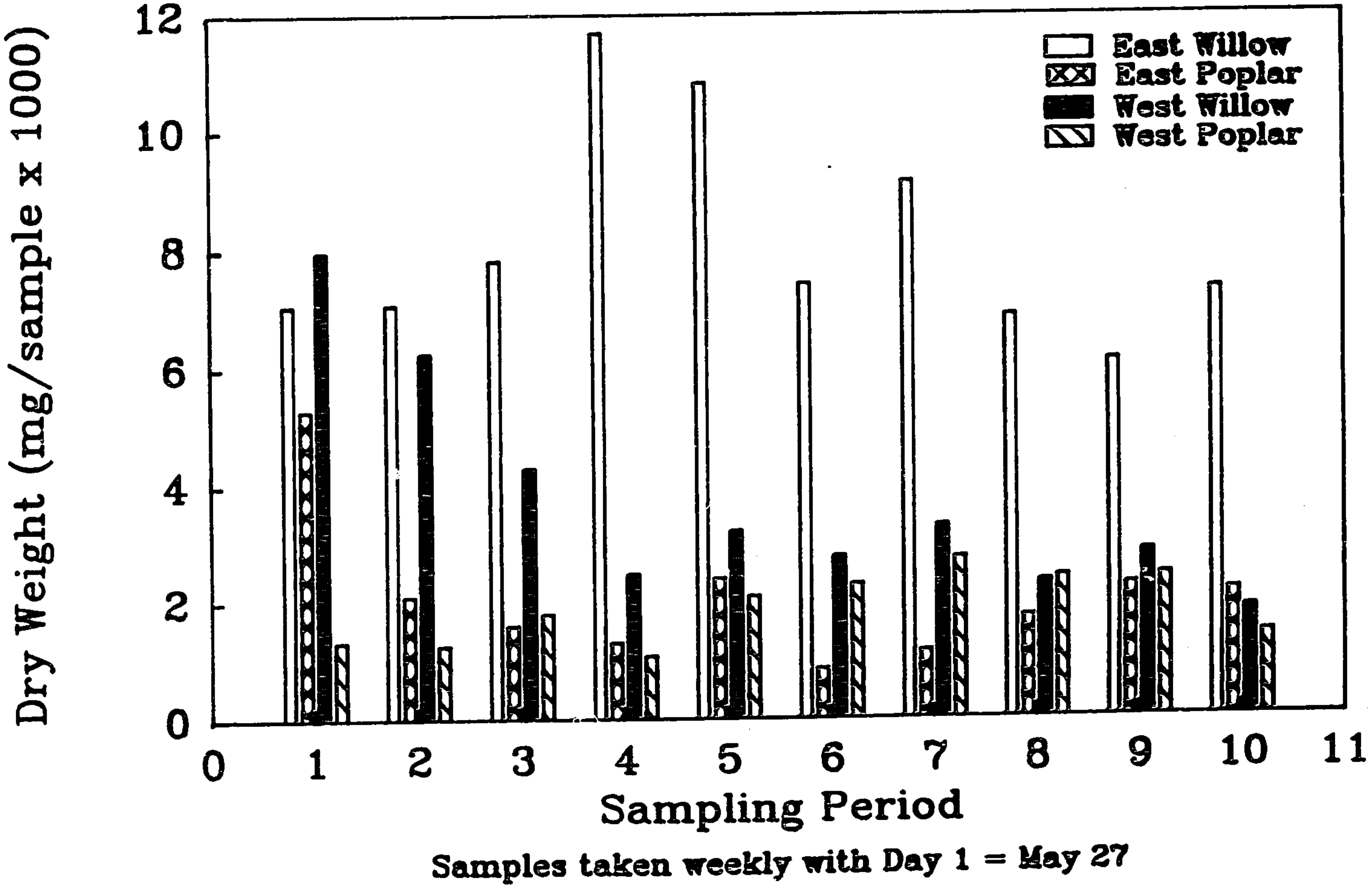
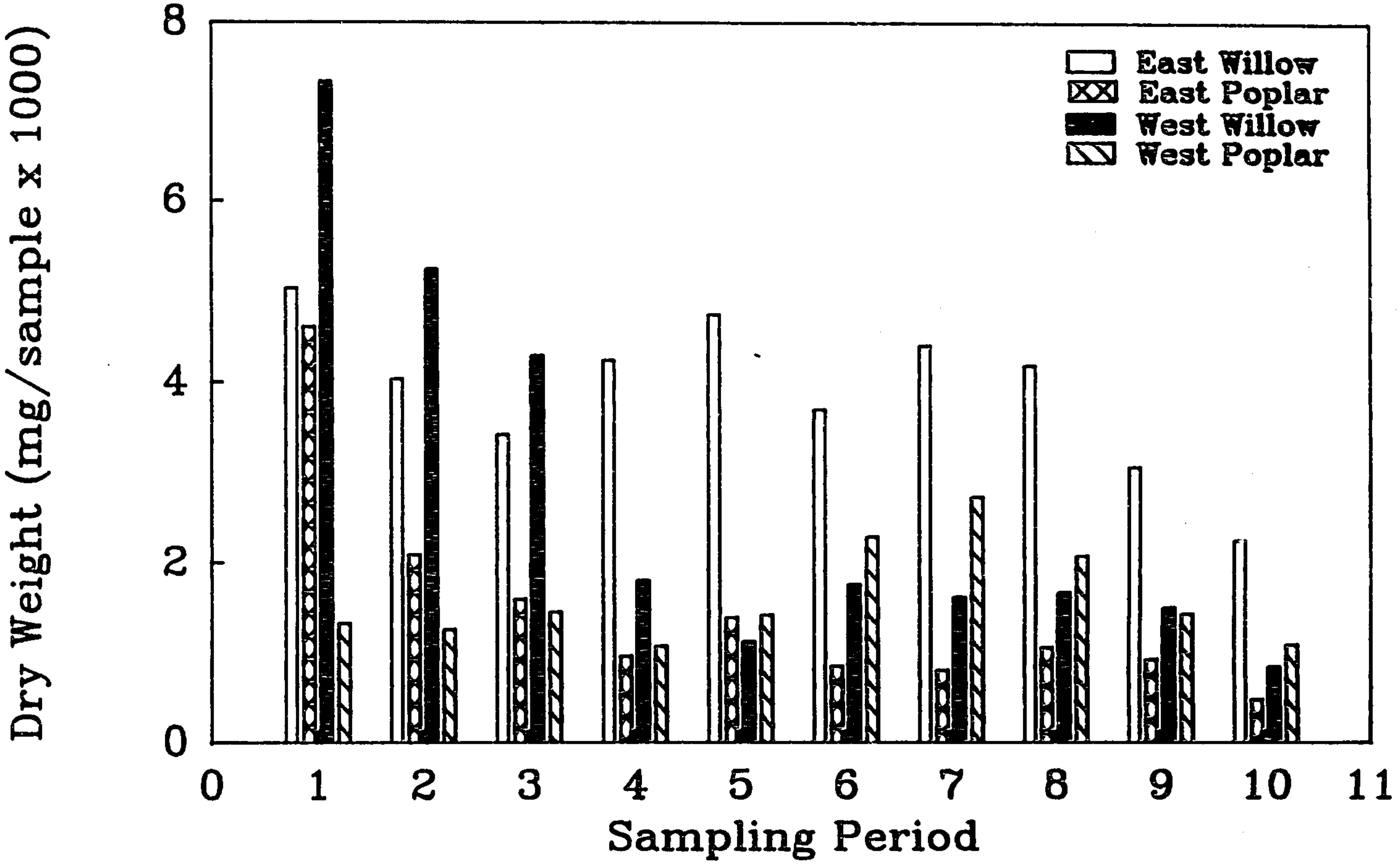


FIG.8 BIOMASS OF INVERTEBRATES SAMPLED IN 1987 AT BEAVERHILL LAKE, ALBERTA (ODONATA REMOVED).



Samples taken weekly with Day 1 = May 27

TABLE 16. Summary of tests for significant differences between the median number of arthropods sampled in each study area (Mann-Whitney U-Test).

AREA	East Willow	East Poplar	West Willow	West Poplar
		Median Number of Invertebrates Sample^{-1}		
	409	188	178	274
		Mann-Whitney U^{+}		
West Poplar	91.5**	80*	82**	----
West Willow	98**	57 NS	----	
East Poplar	97**	----		

$^{+}$ U-Statistic compared to a table of upper limits

* $P<0.05$

** $P<0.01$

not present in the diet sampling. Figure 8 presents the arthropod abundance with Odonata removed. In comparison to figure 7, figure 8 shows that the west poplar grid had more abundant invertebrates in weeks 5 - 7. This period is critical from a food availability perspective because most adults are feeding nestlings.

POLYGYNY

There were 13 confirmed cases of polygyny in 1986 and 1987. However, it was not possible to determine the status of 18 of 74 matings in 1986, and 50 of 90 matings in 1987. Therefore, 13 of 96 matings for which the mating status was known, were determined to be polygynous (15.7 % males polygynous, 27.1% females mated to polygynous males).

Young were successfully fledged from 21 of 26 (80.1%) of the nests with polygynous males (Table 17). Mortality of the nestlings in one instance (case 3) was due to starvation. Failure of nests in three of the cases was due to intraspecific nest-content destruction. In case 4 the nestlings of the primary female were killed by a House Wren, in case 7 the eggs of the primary female were broken by a House Wren, and in case 10 the eggs of the secondary female were broken by a House Wren (Table 17). The eggs in case 8 were abandoned by the secondary female for unknown reasons.

TABLE 17. Summary of known polygynous matings of House Wrens at Beaverhill Lake, Alberta.

Case	Area	Year	Distance Between	Date of 1st Egg 1^0	2^0	First Egg of 2^0 F Laid (B)*	(D)	(A)	# Young Fledged 1^0	2^0	Cause of Mortality
1	WP	1986	90M	8	29		A-1		8	7	
2	WP	1986	30M	7	29		A-2		7	7	
3	EP	1986	30M	7	9		B-4		7	0	starvation
4	EW	1986	30M	6	17		D-5		0	5	HOWR**
5	EW	1986	30M	5	16		D-4		7	5	
6	EW	1986	30M	8	30		A-2		7	5	
7	EW	1986	30M	16	33		D-10		0	5	HOWR
8	EW	1986	60M	6	26		A-2		7	0	UK aband.***
9	EW	1986	60M	8	30		A-6		6	6	
10	EW	1986	30M	5	25		A-1		7	0	HOWR
11	WP	1987	30M	22	43		A-3		5	6	
12	WP	1987	30M	10	24		D-8		6	6	
13	EW	1987	60M	37	52		D-10		5	3	

* B = days BEFORE the onset of incubation by the primary female
D = days after the onset of incubation by the primary female (DURING)
A = days AFTER incubation of primary female complete (i.e. hatch)

** HOWR - egg or nestling mortality inflicted by House Wren

*** UK aband. - abandonment for unknown reasons

In only 1 of the 13 incidences of polygyny was there an overlap in the nestling periods of the primary and secondary nests, and this resulted in starvation of the young. The initiation of egg-laying by the secondary female commenced during the incubation period of the primary female in 5 instances. Six of the secondary nests had the first egg laid shortly after the young of the primary nest had hatched.

The mating status for all nesting attempts was known in both years for West Poplar. In 1986, 2 of 8 males (25%) were polygynous and in 1987, 2 of 10 males (20%) were polygynous. No cases of polygyny were recorded in the west willow in 1986 when all males were marked. High nest failure in 1987 made it impossible to confirm the mating status of any nests in west willow in 1987. In the east willow 1986, the mating status of 29 nest attempts was known and 7 males (31.8%) were polygynous. Heavy losses due to predation made it impossible to adequately determine mating status in east willow in 1987. Only one case of polygyny was recorded in east poplar in both years and the mating status of 8 nests was known (14.3% males polygynous).

Table 18 presents a comparison between the success of monogamous, primary polygynous and secondary polygynous females. Primary polygynous females laid significantly larger clutches than monogamous females (Z=2.21, P<0.05) and primary polygynous females fledged significantly more young than

TABLE 18. Comparison of the reproductive success of monogamous, primary polygynous and secondary polygynous female House Wrens at Beaverhill Lake, Alberta in 1986 and 1987.*

Mating Status	Mean Clutch Size (SE)	Mean Number of Young Fledged (SE)
Monogamous N=43	6.44 (0.15)	5.51 (0.23)
Primary Polygynous N=13	7.15 (0.22)	5.61 (0.75)
Secondary Polygynous N=13	6.33 (0.31)	4.50 (0.67)

* Only those females for which the mating status was confirmed were included. Nesting attempts from the east willow grid in 1987 were not included.

secondary polygynous females (U=45, $P<0.05$). All other differences were statistically insignificant.

DISCUSSION

A. Availability of Suitable Nesting-Cavities

House Wrens responded to the provision of nestboxes by breeding at a much higher density than was observed in the surrounding natural environment. The response was consistent with prediction 1a and with previously reported results (Baldwin & Bowen 1928, Kendeigh 1941, Bent 1948). Furthermore, by nesting in a dense willow habitat, the wrens exploited an area not normally used for breeding (prediction 1b). The results suggest that the primary factor limiting the breeding density of House Wrens at Beaverhill Lake is the availability of suitable cavities for nesting, therefore, hypothesis 1 cannot be rejected.

The effect of nestboxes on the local population of wrens is one of increased breeding density. However, the impacts on the greater regional population are unknown. The question arises as to where the wrens that nested in the boxes came from. The increased breeding density may represent a compensatory displacement of birds from surrounding areas that would have bred elsewhere. Alternatively, the nestbox enriched habitat may have provided the opportunity for otherwise "surplus" birds to breed. If nest cavities are limiting, many of birds that are unable to locate and secure a site may not breed in a season (von Haartman 1957, 1971).

Adult House Wrens have been reported to exhibit high nest-area fidelity; 13.7% (11 of 85) of the female and 16.9% (11 of 65) of the male wrens (Baldwin & Bowen 1928), and 20.6% (251 of 1219) of the female and 38.1% (200 of 547) of the male wrens (Drilling & Thompson 1988) returned to breed near or at their previous years nest site at least once. The same studies report a very low return of nestlings (2.6% & 2.8% respectively). Low return to the natal site is characteristic of most passerines and is due to mortality and dispersal (Gauthereux 1982). The dispersal of first year birds is thought to reduce or prevent the incidence of inbreeding (Greenwood et al. 1978).

In the present study, the return of birds banded in 1986 to breed in 1987 was 3 of 46 males (6.5%), 0 of 66 females (0%) and 1 of 312 young (0.3%). Birds were not monitored in 1988 for the return of birds banded in 1987. The small sample size from only one year makes it impossible to draw any firm conclusions, but there appears to be a large loss of birds to mortality and or a lack of nest site fidelity. Further investigation is required to determine the nest site fidelity of House Wrens at Beaverhill Lake.

The high rate of dispersal of juvenile House Wrens may account for the rapid utilization of the nestbox enhanced areas in the first year of the study. Beaverhill Lake may also act as a slight barrier and/or an opportune foraging location for wrens on their spring migration. The local effect could be a funnelling of birds around the lake, increasing the probability of nestbox discovery and subsequent breeding by both adults and first year birds.

Suitable nesting cavities may be a primary factor limiting the number of breeding House Wrens, but it is not the sole factor. If nest sites were the only factor limiting the breeding population I would have expected to see every nestbox utilized. Other factors acting independently or in conjunction with each other must have limited the number of breeding wrens.

B. Vegetation Structure

Vegetation structure may be one of the factors limiting the breeding populations of House Wrens. Bent (1948) reported that House Wrens breed primarily in cavities concealed by dense vegetation. Cryptic nest sites may reduce the chances of predation (Garson 1980), and moderate microclimate (Kendeigh 1963). Dense vegetation may also provide an ample foraging substrate to which the wren is best adapted.

Concurrent to this study was a study of Tree Swallows (Tachycineta bicolor) wherein an abundance of nestboxes was made available along the grassy margins of the lake in close proximity to the west willow and poplar grids. No House Wrens used these sites with the exception of two boxes that were surrounded by willow shrub cover. The wrens chose instead to nest in the wooded areas where nestboxes had been placed. Tree Swallows initiated nesting before House Wrens and may have aggressively prevented wrens from breeding in the open area. However, wrens are known to displace Tree Swallows (Quinn & Holroyd 1989) and their absence in the open grassy area is more likely due to the lack of adequate vegetation cover.

There were significant differences in the vegetation measurements between the four areas (prediction 2b). In summary, both willow areas contained lower and more dense vegetation than both poplar areas. The willow areas differed in that the west willow was composed of uniformly dense shrubs with few breaks, while the east willow had a wider dispersion of shrubs resulting in open spaces between them. The poplar areas were similar, but the west poplar area contained significantly larger diameter, older trees and less shrubs than the east poplar area.

House Wrens initiated a greater proportion of nesting attempts in willow scrub areas than in open poplar forest. This apparent preference for dense vegetation structure is consistent with the review by Bent (1948), but inconsistent with Belles-isles and Picman (1986a). Belles-Isles and Picman reported a preference for sparsely vegetated sites by House Wrens. The investigators suggest that the preference is driven by an attempt to reduce predation by conspecifics.

They also suggest that wrens nesting in a more open environment have a greater chance of detecting and repelling would be nest attackers.

The present study supports the idea that the predation rate is higher in more dense vegetation since all cases of intraspecific nest-content destruction were recorded in the willow areas and all weasel predation was recorded in the east willow area. The preference for dense vegetation in spite of high predation rates suggests differences between the quality of the sparse vs. dense habitats in the two studies. It is difficult to make further comparisons between my and Belles-Isles and Picman's studies because the latter did not report quantitative differences between what they define as sparse, medium and dense vegetation.

The difference in results between the study by Belles-Isles and Picman and this study indicate that factors other than vegetation structure may be more important in determining where wrens will nest. Some other factor or combination of factors, used by House Wrens to judge suitability of breeding habitat, made the willow area more attractive to more pairs of wrens.

House wrens exhibited a strong preference for nesting in the east willow grid as compared to the east poplar grid. However, the wrens did not exhibit the same preference for dense willow in the west grids. There were no significant differences between the occupancy of the west willow and poplar grids despite the fact that they contain the most and least, respectively, densely vegetated sites measured. The failure of discriminant function analysis to statistically separate occupied vs. unoccupied nestboxes based on vegetation characteristics suggests that nest site selection may be independent of vegetation density in the west grids.

The difference in the occupancy of willow and poplar grids between the east and west areas may be due to an edge effect. The west willow and poplar grids are small in size and most of the boxes are along the edge of the grids. Nestboxes on the edge of a grid have no neighboring nestboxes on at least one side, thus reducing territorial interactions from at least one direction. The reduced intraspecific interaction may be very important given the destructive tendencies of wrens (Belles-Isles & Picman 1986b).

Kendeigh (1941) reported that the average territory of a House Wren had a diameter of 75 m. The west willow and poplar grids were bounded by areas of different vegetation composition. The west willow area was bounded by grassy fields on the north and east sides and poplar forest on the south and west sides. The west poplar area was surrounded by dense willow and poplar vegetation and small clearings. Wrens nesting on the margins of either grid could potentially exploit different vegetation types depending on which one had more or better quality food at any given time.

The preference for wrens to nest along the edge of a grid is further supported by the data from the east willow grid. Eleven of 12 (92%) nestboxes that were used in all years by House Wrens were located on the edge of the east willow grid. In contrast, 7 of 9 (78%) nestboxes that were never used by wrens were located away from the grid margins. The discriminant function analysis selected edge as the most important character in statistically separating occupied from unoccupied nestboxes.

C. Food Availability

The high use of nestboxes in both the west willow and poplar grids may also have been a response to insect outbreaks (western willow leaf beetle and forest tent caterpillar respectively). Several passerine species have been reported to respond to insect outbreaks through increased breeding density and extralimital nesting (Morris et al. 1958, Zach & Falls 1975, Morse 1978, Sealy 1979). House Wrens occupied 14 of 24 boxes in the west willow area during 1986 when the willow leaf beetles were present in epidemic numbers, and 9 of 24 boxes in the year following the outbreak. The west poplar area was heavily infested with forest tent caterpillars in all years. The wrens ate both the larvae and adults of the willow leaf beetle and the moths of the forest tent caterpillars.

The emergence of the forest tent caterpillar moths coincided with the nestling period of the wrens and the moths constituted a large portion of the nestling diet. Infestation by forest tent caterpillars was much less extreme in the east poplar area and may partly explain the difference in nestbox occupancy between the east and west poplar area.

Differences in the availability of other arthropod prey items might also explain differences in nestbox occupancy between the grids. Food availability is recognized as a major factor limiting breeding populations of many birds (see reviews in Newton 1980 & Martin 1987).

The sampling procedures used to provide an index of arthropod abundance resulted in the east willow area having the highest and the east poplar area having the lowest invertebrate abundance. This trend may be due partly to the sampling techniques. There was significantly more foliage in the space between 2 m and ground level in the willow areas as compared to the poplar areas resulting in more contact with the sweep net. The canopy foliage of the poplars was not sampled and may have contained invertebrates available to the wrens. However, wrens were rarely seen foraging in the upper canopy in the present study. Guinan (1985) reported that the height at which House Wrens foraged varied with individuals and time of season, but the area <4 m above ground was most often used.

Sweep nets are widely used to sample invertebrates from foliage, but probably underestimate the abundance of taxa that can avoid them or are not easily dislodged from the foliage (Southwood 1978). A major assumption of this study was that invertebrates sampled by sweep-netting provided a reasonable estimate of invertebrates actually available to foraging wrens. The presence of the majority of taxa and size classes sampled by sweep-netting in the collared nestling and faeces samples lends some support to the assumption. The assumption is further supported by detailed diet analysis of adult wrens as compared to sweep net samples by Guinan (1985).

The number of invertebrates in the west willow area in 1987 may have been affected by the outbreak of the willow leaf beetle in 1986. The willow shrubs were not well foliated in 1987 and the leaves were quickly skeletonized by a spring emergence of the willow leaf beetles. This, in turn, may have reduced the leaf surface area available to phytophagous insects and lowered the amount of available food for the wrens, especially in the latter part of the season. Low food availability may explain the high rate of abandonment in the west willow area in 1987 (5 of 9 attempts, 55%) and the incidence of starvation of one brood.

The first clutches were initiated in the east willow area in 1986 and 1987. Perrins (1970) proposed that the laying date in some species of birds is determined by the date at which a female is able to find enough food for egg production. Jones & Ward (1976) supported Perrin's hypothesis on the basis of two studies that quantified the protein reserves in the

Red-billed Quelea (_Quelea quelea_). The high arthropod abundance in the east willow area may have allowed females to attain physiological readiness to lay eggs sooner than in the other areas.

Alternatively, the nest sites with the highest food availability may have been chosen by females before lower quality sites resulting in eggs being laid earlier. Male House Wrens return to the breeding areas several days before the females (Bent 1948). The most dominant or experienced males may select and defend the highest quality territories and successfully attract a female early in the season. It is unknown whether female House Wrens select nest sites based on territory quality, some quality of the male, or a combination of the two. Regardless of the selection process, food is a critical factor in raising offspring and should figure prominently in the outcome.

D. Reproductive Success

Early season breeders may have increased fitness resulting from greater experience of their offspring before migration and winter (von Brommssen & Jansson 1980). An earlier start will also lead to a longer available breeding season and thus the potential for raising more than one brood or renesting in case of failure of the first nest.

The young from nests in the east willow had a significantly greater weight prior to fledging than did the young from nests in all other areas. This difference is associated with the area having the greatest measured invertebrate abundance. Greater fledging weight may be associated with a higher probability of survival during the first few weeks after fledging (Perrins 1965). The period immediately following fledging has been shown to be one of high susceptibility from predators and the ability to find food (Lack 1966). The other areas did not differ significantly in pre-fledging weights.

Clutch size did not differ significantly between any of the areas. Baltz & Thompson (1988) demonstrated that the clutch size of House Wrens is not limited by the wrens' ability to incubate extra eggs. The energy or nutrient availability in the period prior to clutch initiation must have been sufficient in all areas for wrens to be at or near their physiological limit of egg production (Martin 1987).

The number of young fledged from completed nest attempts also showed no significant difference between areas. The number of nests attempts that were successful in fledging young was greater in poplar areas than in the willow areas due to predation. The greater incidence of predation in the densely populated willow areas is consistent with hypothesis 3.

The west poplar area was as densely populated as the willow areas, but was not affected by the same high rate of predation. The lack of intraspecific nest-content destruction may be explained by ability of the wrens to defend their nests from conspecific attack because intruders can be seen more easily in the open forest (Belles-Isles & Picman 1986). Weasel predation may not have been a problem simply because of the absence of weasels.

Nestboxes were cleaned and repaired before the return of the House Wrens in the spring. When I checked the nestboxes in the east willow area before the 1987 and 1988 breeding seasons there was evidence that food had been eaten and cached by weasels. In 41 of the boxes in 1987 and 52 of the boxes in 1988, I discovered the remains of at least one of the following species: Peromyscus maniculatus, Sorex hoyi, S. arcticus. The same species were found cached in 4 of the west willow nestboxes in 1988. No evidence of caching was observed in the poplar areas. I assumed that Mustela erminea was responsible for the food caches because of previous reports in the literature (Banfield 1974) and because the species was seen caching killed birds in the boxes during the 1987 season.

Hypothesis 2, if nest sites are not limited, House Wrens will nest preferentially in areas that provide resources for the greatest reproductive success, cannot be rejected. In the east study area House Wrens nested at a higher density in the willow where food was more abundant, resulting in earlier nests and heavier young. Nests on the edge were probably preferred to those surrounded by other boxes to minimize territorial interaction and gain access to a larger foraging area outside of the grid. The high rate of predation by weasels is a factor that I do not believe the wrens are able to assess at the time of settlement.

House Wrens responded to insect outbreaks in the west grids by nesting at high densities in both areas. The west poplar area probably represents the optimal situation for House Wrens at Beaverhill Lake because of its abundance of food, low incidence of predation and availability of nestboxes along the edge of the grid.

E. Polygyny

Polygyny was confirmed in 13 of 96 matings for which the mating status was known. This may be an underestimate because of the difficulty in capturing and marking males to confirm mating status. Kendeigh (1941) reported 6% of House Wren matings to be polygynous. The greater incidence of polygyny at Beaverhill Lake may indicate higher quality habitat or may be a compensation for the lack of second broods.

House Wrens regularly produced two broods year^{-1} in the area studied by Kendeigh (Illinois). In the present study there was only one known case of a female producing a second clutch after successfully fledging her first brood. The breeding season may be too short to allow for the production of two broods.

The need for male parental care (Lack 1968) is thought to limit the incidence of polygyny in passerines. The parental care hypothesis is supported by the results of a polygynous mating in the east poplar area in 1986. This was the only known case of polygyny in which there was an overlap between the nestling periods of the primary and secondary broods. The result was the starvation of the young in the secondary nest. The male was seen feeding the young at both nests until the third day after the hatch of the secondary clutch, after which he was only seen feeding the primary brood. The secondary female was unable to satisfy the energy requirements of her brood without the assistance of the male.

The remaining 12 confirmed cases of polygyny had no overlap in the nestling periods of the primary and secondary nests. The secondary females initiated clutches during the time that the primary female was engaged in incubation. The incubation period of House Wrens in the study area was usually 13 days, and the nestling period 14 days. Therefore, if a male attracted a second female that initiated her clutch midway or further through the incubation period of the primary female, then the second clutch hatched near or after the time that the first brood fledged. In this way, the male was able to give full parental care to both broods during the nestling stage.

Female aggression is another factor that is thought to limit polygyny (Wittenberger & Tilson 1980). In the timing of events described above, the primary female may be unaware of the presence of a secondary female because she is spending most of her time incubating (male House Wrens do not assist in incubation). The secondary female may also be unaware of the primary female and enter into a polygynous mating unknowingly; the deception hypothesis (Alatalo and Lundberg 1984b).

Three of the cases of polygyny resulted in the eggs of one of the females being broken by a House Wren. It is possible that the eggs were broken by the other female mated to the polygynous male upon discovery another nest in the male's territory. Further experimentation is required to test the role of female aggression in limiting the incidence of polygyny in House Wrens. The other explanation for the loss of clutches to intraspecific predation may be that the males were unable to defend more than one nestbox effectively. That is, there was a need for male parental care outside of the nestling period.

Prediction 4a is supported because polygynous males were able to produce more young than monogamous males. The results obtained from known polygynous matings are insufficient to reject the polygyny threshold hypothesis. Polygynous matings occurred with little or no overlap in the nestling periods. The lack of nestling-overlap polygyny suggests that females are choosing to mate monogamously on lower quality territories rather than polygynously with little or no male parental care on superior territories. However, these females may also be waiting until a male is able to provide full care on the superior territory (i.e. no nestling overlap), or are prevented from mating polygynously by primary female aggression. More experiments are needed to identify the factors limiting polygyny in House Wrens.

Conclusion

The primary factor limiting the breeding population of House Wrens at Beaverhill Lake is the availability of suitable nesting-cavities. House Wrens responded to the provision of artificial nest sites by breeding at higher than natural densities. Furthermore, the wrens nested in a willow shrub habitat that could not otherwise be occupied because of the lack of cavities.

Nestboxes that were available in open areas, void of woody vegetation, were not occupied by House Wrens. This suggests that there is a requirement for some vegetative cover around the nestbox. This cover may be needed for concealment from predators, protection from weather, and/or may be a proximate factor used by the wrens to predict food abundance.

The results of this study suggest that once the threshold requirement for vegetative cover has been met, vegetation structure becomes a poor predictor of preferred nesting sites for House Wrens. House Wrens nested in the most and least dense vegetation (west willow and west poplar respectively) at the same density and with similar reproductive success (table 19). Statistical analyses indicate that nest site selection was made independent of vegetation structure.

Food abundance was well correlated with breeding density. I believe that food availability is the factor that limits the

TABLE 19. Summary of results from the study of House Wrens at Beaverhill Lake, Alberta.

	WEST POPLAR	WEST WILLOW	EAST POPLAR	EAST WILLOW
Vegetation Density	4th	1st	3rd	2nd
Breeding Density	high	high	lowest	high
Date of 1st Egg	3rd	2nd	4th	1st
Predation	none	light	none	high
Mean Clutch Size (1986)	6.75	7.71	7.25	6.92
Mean Clutch Size (1987)	7.12	6.75	7.00	7.00
Nestling Weight (Day 12)	10.23	10.14	10.29	11.24
Arthropod Abundance	2nd	3rd	4th	1st
% Polygynous Males	22%	0%	14%	32%

population of House Wrens faced with a surplus of suitable nest sites. Food availability also appears to be important in determining onset of egg-laying, fledging weight and incidence of polygyny.

Intraspecific interaction is probably the next critical factor in the hierarchy of factors regulating House Wren breeding populations. I predict that one could supply House Wrens with a surplus of nest sites and a superabundant food source, but there would be a limit as to how dense the birds would nest. Territorial aggression would limit the breeding density.

Predation is also regulator of House Wren populations. Large areas that are densely populated by breeding wrens are more likely to be discovered by predators than sparsely occupied areas. In the absence of predators, another factor such as disease, may provide a regulatory function.

House Wrens were polygynous in 27.1% of all matings for which the mating status was known. Polygyny occurred asynchronously with little or no overlap in the nestling stages of the primary and secondary nests. Female aggression is probably the factor that prevents males from being synchronously polygynous, although the need for full male parental care may also be a factor. Under natural conditions (no nestboxes) the availability of nesting-cavities may limit the incidence of polygyny in House Wrens.

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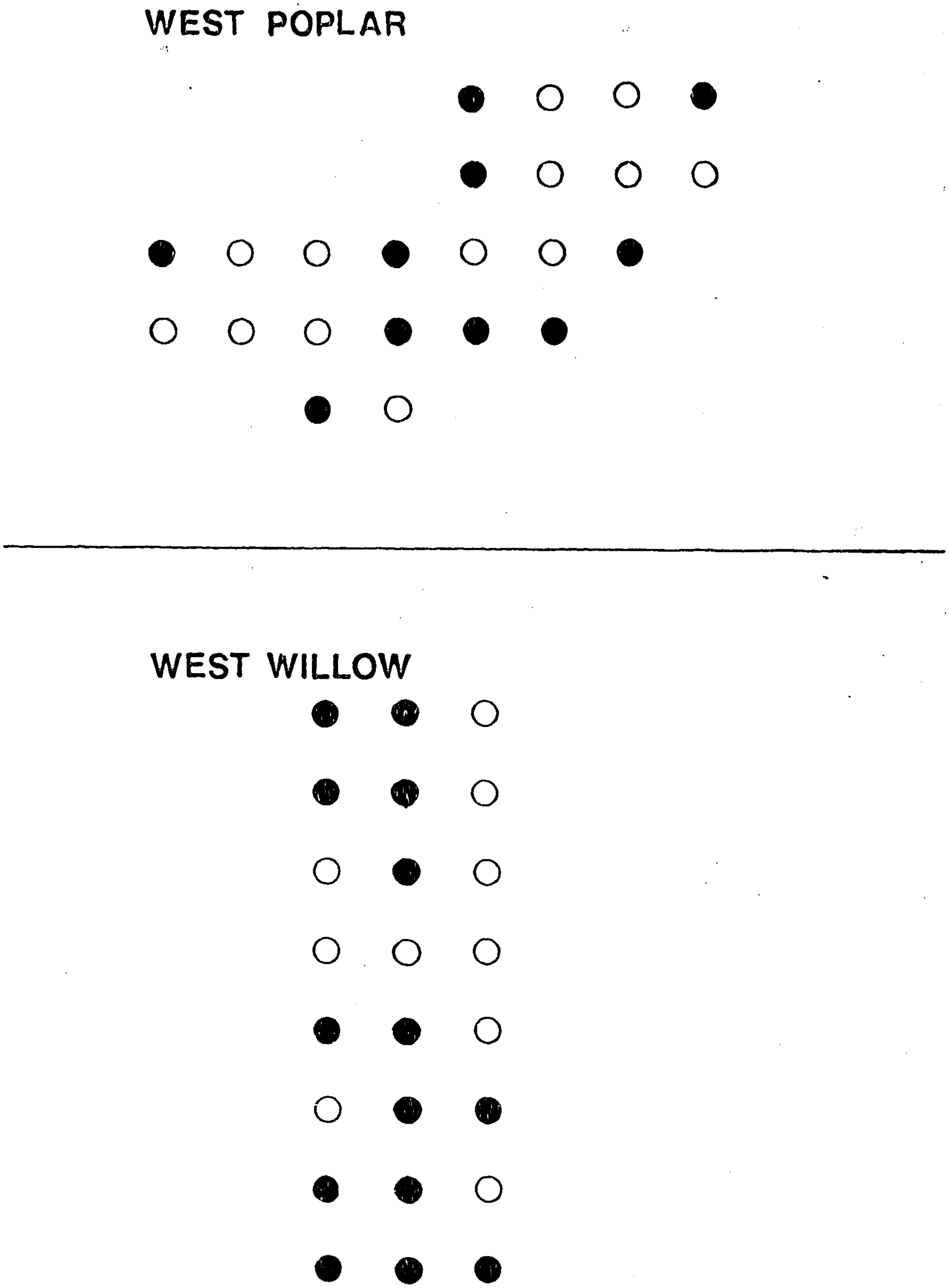
APPENDIX 1. Diagrams of the nestbox utilization in each of the four study areas in 1986, 1987, and 1988. The diagrams indicate all nest attempts by House Wrens with a solid black circle.

FIGURE A1-1. Nestbox utilization in the west willow and west poplar grids in 1986.



WEST POPLAR

WEST WILLOW

FIGURE A1-2. Nestbox utilization in the east willow and east poplar grids in 1986.

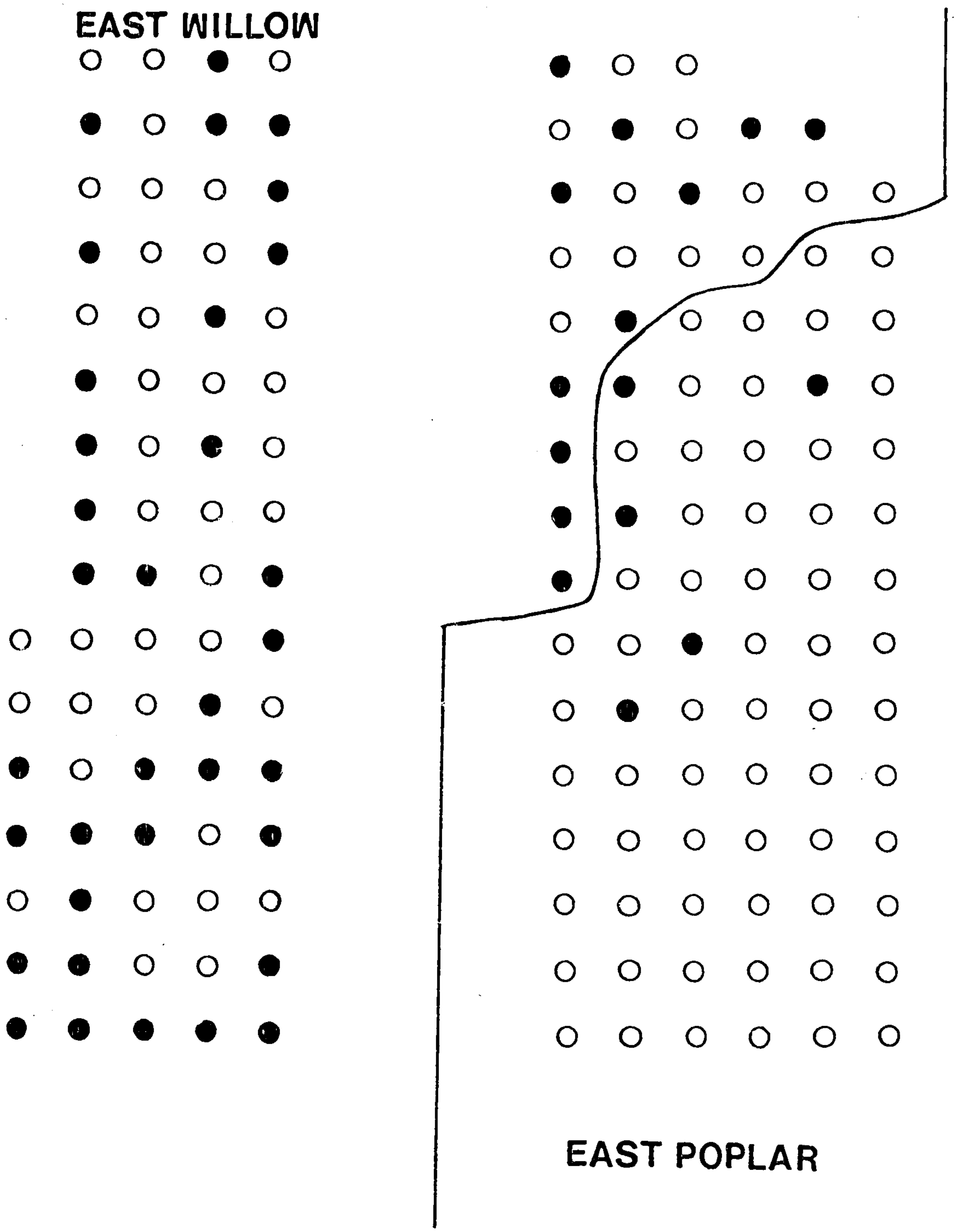


FIGURE A1-3. Nestbox utilization in the west willow and west poplar grids in 1987.

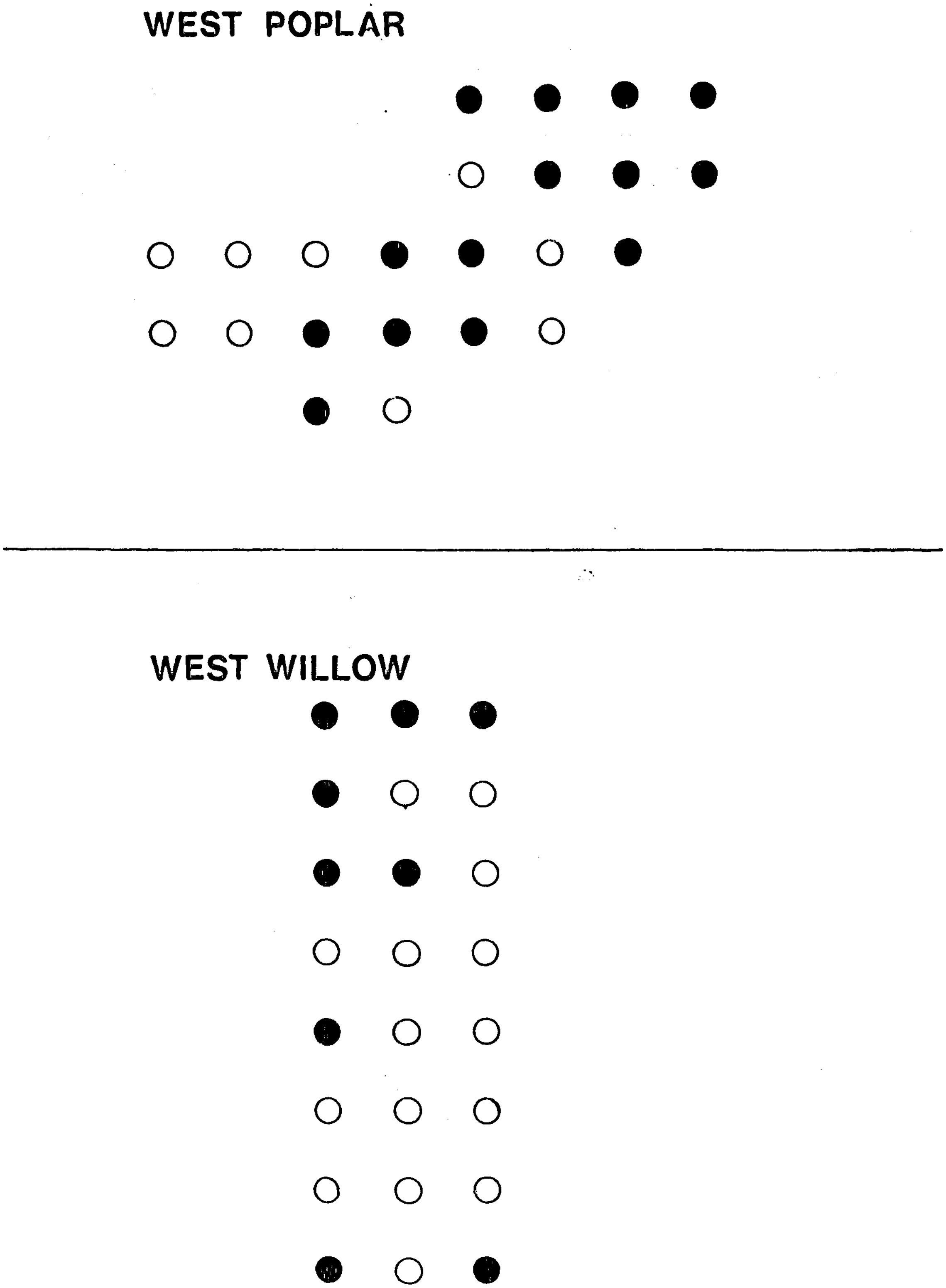


FIGURE A1-4. Nestbox utilization in the east willow and east poplar grids in 1987.

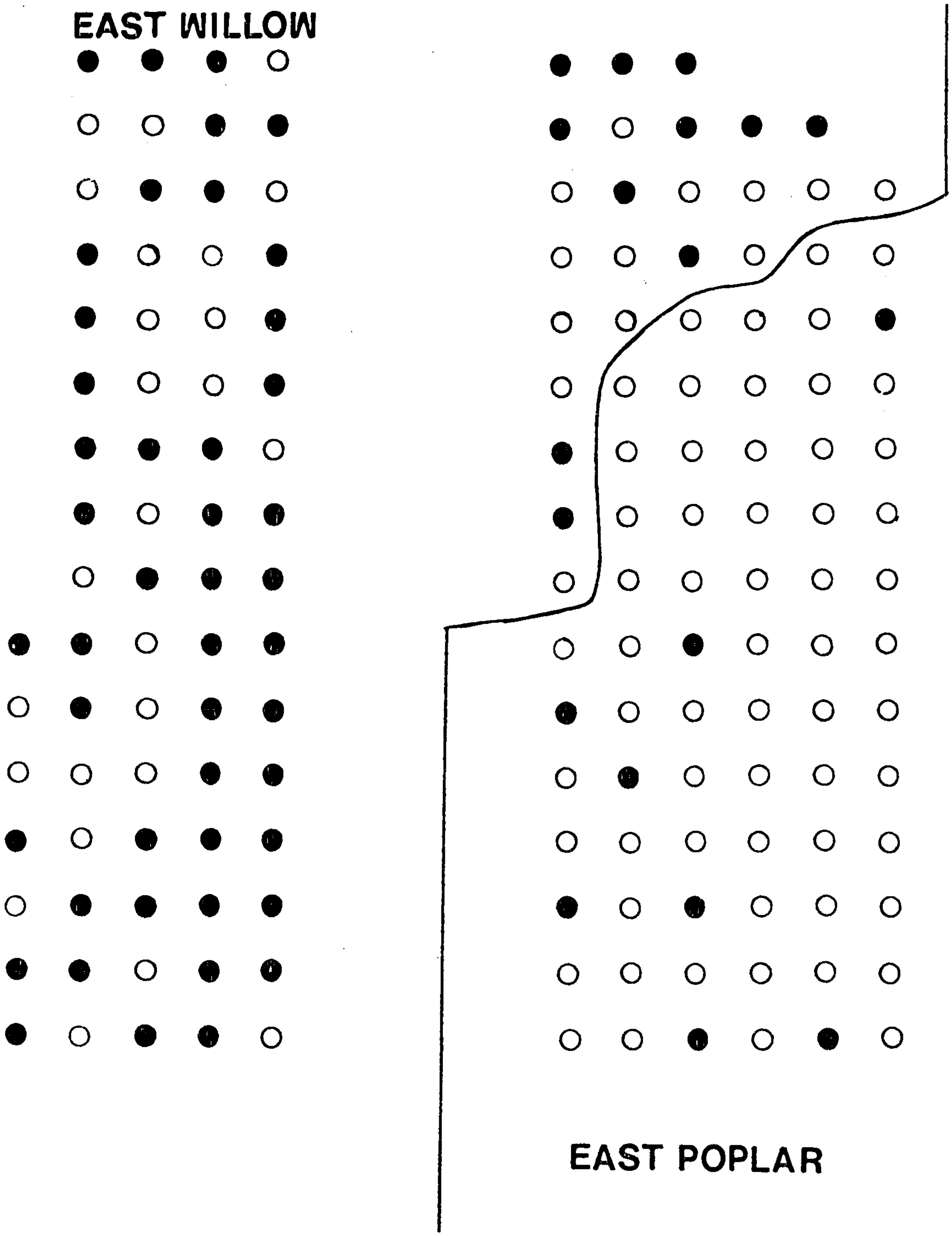


FIGURE A1-5. Nestbox utilization in the west willow and west poplar grids in 1988.

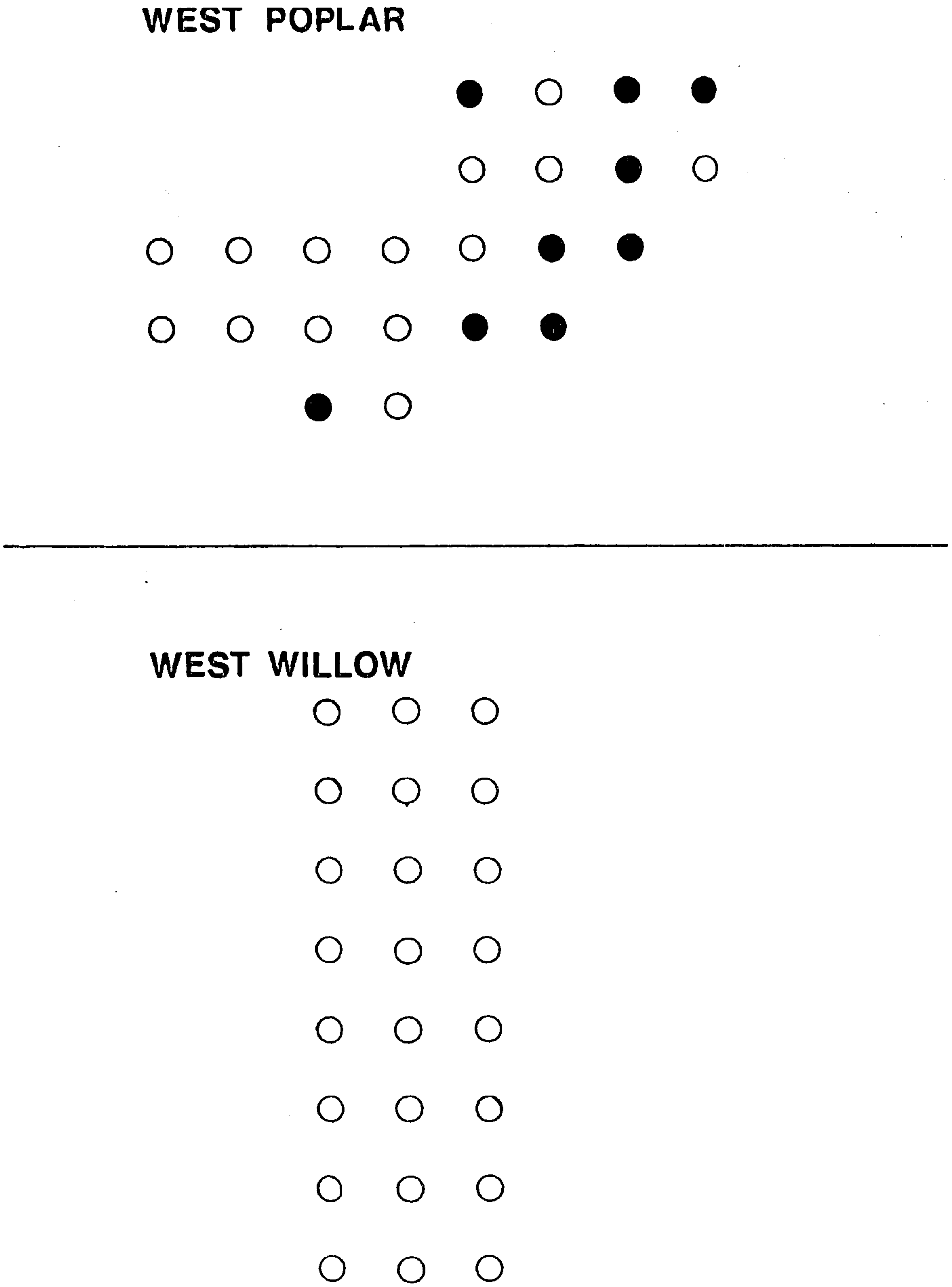
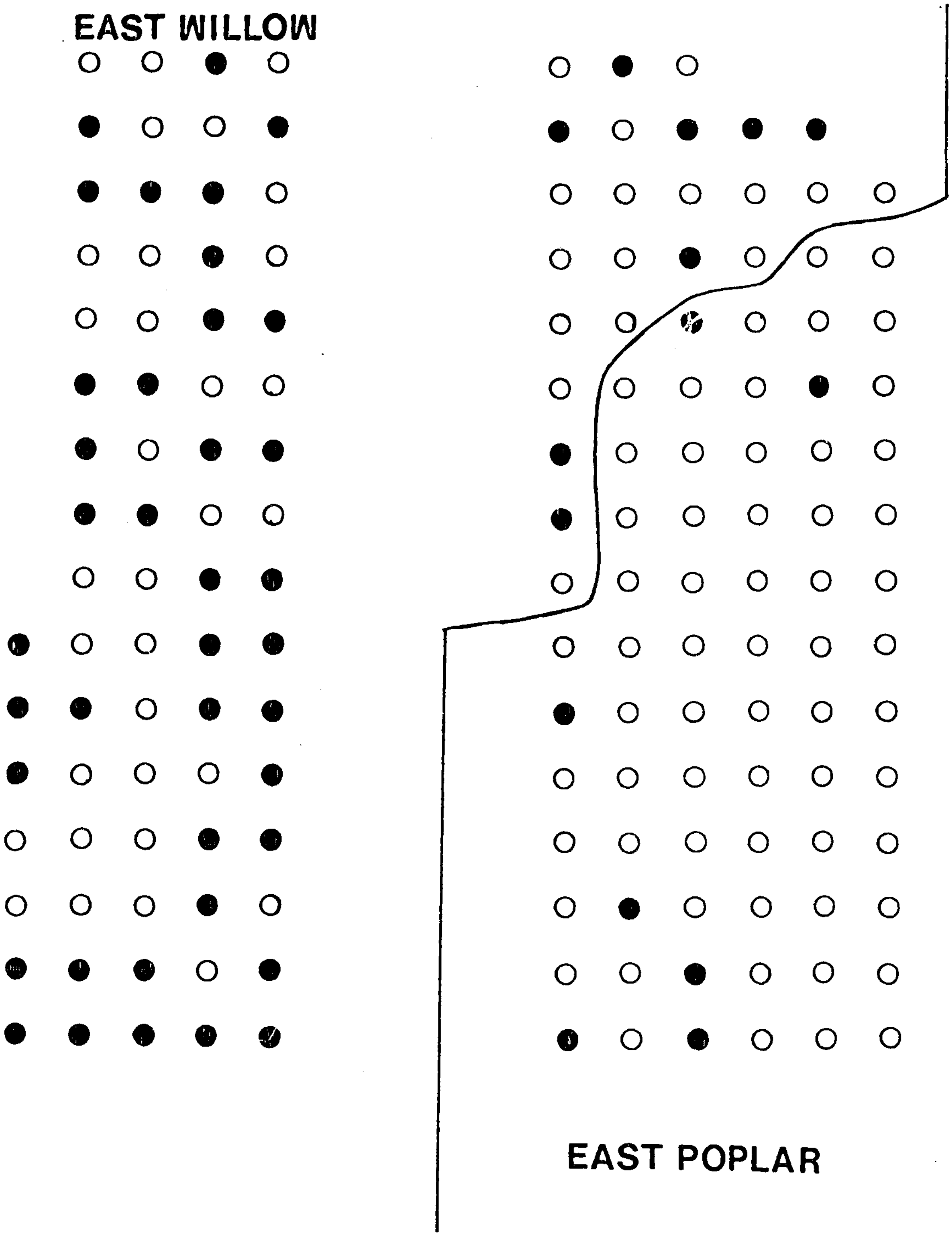


FIGURE A1-6. Nestbox utilization in the east willow and east poplar grids in 1988.



APPENDIX 2. Detailed results of the sampling for arthropod abundance in each of the four study areas in 1987. Each table lists the total number of invertebrates caught in each sampling period by Order and size-class and gives the estimated biomass for each size-class.

TABLE A2-1. Arthropod sampling summary for the west poplar area.

ORDER	LENGTH CLASS (MM)	SAMPLING DATE									
		MY27	JN04	JN10	JN18	JN24	JY02	JY08	JY15	JY23	JY29	ALL
ACARINA	0.0-3.0	2	3	1	0	1	1	1	0	0	0	9
	3.1-6.0	0	0	0	1	0	0	0	1	0	0	2
	6.1-9.0	0	0	0	0	0	0	0	0	0	0	0
	9.1-12.0	0	0	0	0	0	0	0	0	0	0	0
	12.1-15.0	0	0	0	0	0	0	0	0	0	0	0
	15.1-25.0	0	0	0	0	0	0	0	0	0	0	0
	25.1+	0	0	0	0	0	0	0	0	0	0	0
	TOTAL	2	3	1	1	1	1	1	1	0	0	11
PHALANGIDA	0.0-3.0	6	5	6	4	6	3	1	2	1	3	37
	3.1-6.0	0	2	2	1	2	8	4	1	4	6	30
	6.1-9.0	0	0	0	0	0	0	0	0	0	0	0
	9.1-12.0	0	0	0	0	0	0	0	0	0	0	0
	12.1-15.0	0	0	0	0	0	0	0	0	0	0	0
	15.1-25.0	0	0	0	0	0	0	0	0	0	0	0
	25.1+	0	0	0	0	0	0	0	0	0	0	0
	TOTAL	6	7	8	5	8	11	5	3	5	9	67
ARANEIDA	0.0-3.0	7	13	3	6	7	2	3	5	2	3	51
	3.1-6.0	4	6	11	7	9	9	2	4	8	3	63
	6.1-9.0	0	0	0	0	0	0	0	0	0	0	0
	9.1-12.0	0	0	0	0	0	0	0	0	0	0	0
	12.1-15.0	0	0	0	0	0	0	0	0	0	0	0
	15.1-25.0	0	0	0	0	0	0	0	0	0	0	0
	25.1+	0	0	0	0	0	0	0	0	0	0	0
	TOTAL	32	35	23	31	30	22	16	15	18	15	237
ODONATA	0.0-3.0	0	0	0	0	0	0	0	0	0	0	0
	3.1-6.0	0	0	0	0	0	0	0	0	0	0	0
	6.1-9.0	0	0	0	0	0	0	0	0	0	0	0
	9.1-12.0	0	0	0	0	0	0	0	0	0	0	0
	12.1-15.0	0	0	0	0	0	0	0	0	0	0	0
	15.1-25.0	0	0	0	0	0	0	0	0	0	0	0
	25.1+	0	0	1	0	2	0	0	1	3	1	8
ORTHOPTERA	0.0-3.0	2	1	0	1	0	0	0	0	0	0	4
	3.1-6.0	6	3	2	1	2	1	0	0	0	0	15
	6.1-9.0	1	4	3	2	1	1	0	1	2	1	16
	9.1-12.0	0	0	4	0	3	0	6	2	1	5	21
	12.1-15.0	0	0	0	0	0	0	0	0	0	0	0
	15.1-25.0	0	0	0	0	0	0	0	0	0	0	0
	25.1+	0	0	0	0	0	0	0	0	0	0	0
	TOTAL	9	8	9	4	6	2	6	3	3	6	56
HEMIPTERA	0.0-3.0	1	2	4	2	0	2	1	0	0	0	12
	3.1-6.0	4	3	1	2	2	2	2	1	3	3	23
	6.1-9.0	4	5	4	3	2	3	3	0	2	2	28
	9.1-12.0	0	0	0	0	0	0	0	0	0	0	0
	12.1-15.0	0	0	0	0	0	0	0	0	0	0	0
	15.1-25.0	0	0	0	0	0	0	0	0	0	0	0
	25.1+	0	0	0	0	0	0	0	0	0	0	0
	TOTAL	9	10	9	7	4	7	6	1	5	5	63

TABLE A2-1 continued.

HOMOPTERA	0.0-3.0	11	18	12	14	11	6	9	8	2	2	93
	3.1-6.0	18	26	16	11	11	9	3	7	4	6	111
	6.1-9.0	21	19	26	21	21	18	12	16	18	22	194
	9.1-12.0	0	0	0	0	0	0	0	0	0	0	0
	12.1-15.0	0	0	0	0	0	0	0	0	0	0	0
	15.1-25.0	0	0	0	0	0	0	0	0	0	0	0
	25.1+	0	0	0	0	0	0	0	0	0	0	0
	TOTAL	50	63	54	46	43	33	24	31	24	30	398
NEUROPTERA	0.0-3.0	0	0	0	0	0	0	0	0	0	0	0
	3.1-6.0	0	0	0	0	0	0	0	0	0	0	0
	6.1-9.0	0	0	0	0	0	0	0	0	0	0	0
	9.1-12.0	3	4	2	1	4	1	2	2	2	1	22
	12.1-15.0	0	0	0	0	0	0	0	0	0	0	0
	15.1-25.0	0	0	0	0	0	0	0	0	0	0	0
	25.1+	0	0	0	0	0	0	0	0	0	0	0
	TOTAL	3	4	2	1	4	1	2	2	2	1	22
COLEOPTERA	0.0-3.0	6	4	1	3	2	0	0	3	4	1	24
	3.1-6.0	5	6	5	3	4	2	1	3	1	3	33
	6.1-9.0	1	2	3	1	2	3	1	0	1	0	14
	9.1-12.0	0	0	2	1	0	0	0	0	1	0	4
	12.1-15.0	0	0	0	0	0	0	0	0	0	0	0
	15.1-25.0	0	0	0	0	0	0	0	0	0	0	0
	25.1+	0	0	0	0	0	0	0	0	0	0	0
	TOTAL	12	12	11	8	8	5	2	6	7	4	75
LEPIDOPTERA (adults)	0.0-3.0	1	0	2	0	3	1	2	1	0	0	10
	3.1-6.0	5	4	1	2	2	1	3	3	2	1	24
	6.1-9.0	0	1	1	0	0	3	4	1	2	1	11
	9.1-12.0	0	0	0	0	0	0	0	0	1	0	1
	12.1-15.0	0	0	1	1	0	0	2	3	0	0	7
	15.1-25.0	0	1	2	0	4	13	21	15	8	4	68
	25.1+	0	0	0	0	0	0	0	0	0	0	0
	TOTAL	6	6	7	3	9	18	32	23	11	6	121
NEMATOCERA	0.0-3.0	21	38	41	11	29	14	25	18	13	18	228
	3.1-6.0	52	80	61	26	19	22	30	34	52	21	397
	6.1-9.0	58	39	49	35	52	43	38	21	30	28	393
	9.1-12.0	6	3	4	2	5	4	2	0	1	0	27
	12.1-15.0	0	0	1	0	1	0	0	0	0	0	2
	15.1-25.0	0	0	0	0	0	0	0	0	0	0	0
	25.1+	0	0	0	0	0	0	0	0	0	0	0
	TOTAL	137	160	156	74	106	83	95	73	96	67	1047
OTHER DIPTERA	0.0-3.0	3	1	2	6	9	7	4	4	2	8	46
	3.1-6.0	11	18	6	16	9	21	8	27	21	19	156
	6.1-9.0	39	31	17	41	28	37	19	24	8	12	256
	9.1-12.0	8	4	12	7	2	14	12	10	8	9	86
	12.1-15.0	0	2	1	0	1	0	2	2	0	0	8
	15.1-25.0	0	0	0	0	0	0	0	0	0	0	0
	25.1+	0	0	0	0	0	0	0	0	0	0	0
	TOTAL	61	56	38	70	49	79	45	67	39	48	552
HYMENOPTERA	0.0-3.0	1	0	0	0	4	1	0	1	0	0	7
	3.1-6.0	4	5	0	6	9	11	2	4	8	10	59
	6.1-9.0	3	2	1	0	2	9	8	2	1	0	28
	9.1-12.0	0	2	0	1	0	0	1	0	0	0	4
	12.1-15.0	0	0	0	0	0	0	0	0	0	0	0
	15.1-25.0	0	0	0	0	0	0	0	0	0	0	0
	25.1+	0	0	0	0	0	0	0	0	0	0	0

TOTAL	8	9	1	7	15	21	11	7	9	0	98

TABLE A2-1. continued

LARVAE	0.0-3.0	1	0	2	0	1	1	0	2	0	0	7
	3.1-6.0	1	0	1	2	0	0	3	4	2	1	14
	6.1-9.0	4	1	2	0	3	0	2	1	1	2	16
	9.1-12.0	0	2	5	6	1	2	3	0	2	4	25
	12.1-15.0	1	6	2	0	1	4	3	2	1	2	22
	15.1-25.0	3	1	0	2	1	0	0	2	1	0	10
	25.1+	18	12	10	9	7	6	2	1	0	1	66
	TOTAL	28	22	22	19	14	13	13	12	7	10	160
OTHER ADULTS	0.0-3.0	1	0	0	1	1	0	0	2	0	1	6
	3.1-6.0	0	0	0	1	0	0	0	2	0	0	3
	6.1-9.0	0	1	0	1	0	0	0	1	1	2	6
	9.1-12.0	0	0	0	0	1	2	0	0	0	0	3
	12.1-15.0	0	0	0	2	0	0	1	0	0	0	3
	15.1-25.0	1	0	0	0	0	1	0	0	0	0	2
	25.1+	0	0	0	0	0	0	0	0	0	0	0
	TOTAL	2	1	0	5	2	3	1	5	1	3	23
ALL TAXA	0.0-3.0	62	85	72	48	73	36	46	45	24	36	534
	3.1-6.0	126	163	103	88	74	88	64	89	103	78	990
	6.1-9.0	131	110	115	111	117	126	87	70	71	71	1025
	9.1-12.0	17	13	24	12	15	21	23	14	14	15	193
	12.1-15.0	0	2	3	3	2	0	5	5	0	0	42
	15.1-25.0	1	1	2	0	4	14	21	15	8	4	80
	25.1+	0	0	1	0	2	0	0	1	3	1	74
	TOTAL	337	374	320	262	287	285	246	239	223	205	2938
BIOMASS (mg)	0.0-3.0	5.5	7.5	6.4	4.2	6.4	3.2	4.1	4.0	2.1	3.2	47.1
	3.1-6.0	197.7	255.8	161.6	138.1	116.1	138.1	100.4	139.7	161.6	122.4	1554
	6.1-9.0	783.8	658.2	688.1	664.2	700.1	753.9	520.6	418.8	424.8	424.8	6133
	9.1-12.0	245.6	187.8	346.8	173.4	216.7	303.4	332.3	202.3	202.3	216.7	2788
	12.1-15.0	0	55.8	83.7	83.7	55.8	0	139.6	139.6	0	0	1172
	15.1-25.0	0	0	338.7	0	677.3	0	0	338.7	1016	338.7	25060
	TOTAL	1311	1243	1782	1064	2085	2293	2738	2415	2432	1418	43008

TABLE A2-2. Arthropod sampling summary for the west willow area.

ORDER	LENGTH CLASS (MM)	SAMPLING DATE MY27	JN04	JN10	JN18	JN24	JY02	JY08	JY15	JY23	JY29	ALL
ACARINA	0.0-3.0	7	6	1	3	4	2	3	2	0	1	29
	3.1-6.0	0	2	0	0	0	1	0	0	0	0	3
	6.1-9.0	0	0	0	0	0	0	0	0	0	0	0
	9.1-12.0	0	0	0	0	0	0	0	0	0	0	0
	12.1-15.0	0	0	0	0	0	0	0	0	0	0	0
	15.1-25.0	0	0	0	0	0	0	0	0	0	0	0
	25.1+	0	0	0	0	0	0	0	0	0	0	0
	TOTAL	7	8	1	3	4	3	3	2	0	1	32
PHALANGIDA	0.0-3.0	3	1	0	0	3	1	0	2	1	0	11
	3.1-6.0	2	0	0	1	0	2	0	2	0	2	9
	6.1-9.0	0	0	0	0	0	0	0	0	0	0	0
	9.1-12.0	0	0	0	0	0	0	0	0	0	0	0
	12.1-15.0	0	0	0	0	0	0	0	0	0	0	0
	15.1-25.0	0	0	0	0	0	0	0	0	0	0	0
	25.1+	0	0	0	0	0	0	0	0	0	0	0
	TOTAL	5	1	0	1	3	3	0	4	1	2	20
ARANEIDA	0.0-3.0	9	8	6	7	7	5	3	2	2	3	52
	3.1-6.0	9	11	12	8	5	6	3	5	6	2	67
	6.1-9.0	9	8	8	7	6	5	8	4	6	4	65
	9.1-12.0	3	2	4	1	0	0	2	2	2	1	17
	12.1-15.0	0	0	4	0	0	1	0	0	0	0	5
	15.1-25.0	0	0	0	0	0	0	0	0	0	0	0
	25.1+	0	0	0	0	0	0	0	0	0	0	0
	TOTAL	30	29	34	23	18	17	16	13	16	10	206
ODONATA	0.0-3.0	0	0	0	0	0	0	0	0	0	0	0
	3.1-6.0	0	0	0	0	0	0	0	0	0	0	0
	6.1-9.0	0	0	0	0	0	0	0	0	0	0	0
	9.1-12.0	0	0	0	0	0	0	0	0	0	0	0
	12.1-15.0	0	0	0	0	0	0	0	0	0	0	0
	15.1-25.0	0	0	0	0	0	0	0	0	0	0	0
	25.1+	1	3	0	2	6	3	5	2	4	3	29
	TOTAL	1	3	0	2	6	3	5	2	4	3	29
ORTHOPTERA	0.0-3.0	2	1	0	2	1	0	0	0	0	0	6
	3.1-6.0	1	3	1	0	0	2	0	0	1	3	11
	6.1-9.0	0	1	0	2	0	0	0	1	0	4	9
	9.1-12.0	0	0	0	0	0	0	0	0	0	0	0
	12.1-15.0	0	0	0	0	0	0	0	0	0	0	0
	15.1-25.0	0	0	0	0	0	0	0	0	0	0	0
	25.1+	0	0	0	0	0	0	0	0	0	0	0
	TOTAL	3	5	1	4	1	2	0	1	2	7	26
HEMIPTERA	0.0.3.0	3	3	1	0	1	2	0	0	2	1	13
	3.1-6.0	8	9	6	4	2	2	3	0	2	4	40
	6.1-9.0	4	3	2	0	0	3	2	2	1	1	18
	9.1-12.0	0	0	0	1	2	0	1	0	1	0	5
	12.1-15.0	0	0	0	0	0	0	0	0	0	0	0
	15.1-25.0	0	0	0	0	0	0	0	0	0	0	0
	25.1+	0	0	0	0	0	0	0	0	0	0	0
	TOTAL	15	15	9	5	5	7	6	2	6	6	76

TABLE A2-2. continued

HOMOPTERA	0.0-3.0	4	6	3	2	2	1	11	5	3	3	40
	3.1-6.0	2	3	1	0	0	2	4	5	2	0	19
	6.1-9.0	12	27	31	21	12	18	16	17	11	12	186
	9.1-12.0	0	0	0	0	0	0	0	0	0	0	0
	12.1-15.0	0	0	0	0	0	0	0	0	0	0	0
	15.1-25.0	0	0	0	0	0	0	0	0	0	0	0
	25.1+	0	0	0	0	0	0	0	0	0	0	0
	TOTAL	27	36	35	23	14	21	31	27	16	15	245
NEUROPTERA	0.0-3.0	0	0	0	0	0	0	0	0	0	0	0
	3.1-6.0	0	0	0	0	0	0	0	0	0	0	0
	6.1-9.0	0	0	0	0	0	0	0	0	0	0	0
	9.1-12.0	0	0	0	1	0	0	1	0	0	0	2
	12.1-15.0	0	0	0	0	0	0	0	0	0	0	0
	15.1-25.0	0	0	0	0	0	0	0	0	0	0	0
	25.1+	0	0	0	0	0	0	0	0	0	0	0
	TOTAL	0	0	0	1	0	0	1	0	0	0	2
COLEOPTERA	0.0-3.0	2	1	4	2	7	11	4	3	1	2	37
	3.1-6.0	14	17	19	4	8	6	6	2	11	6	93
	6.1-9.0	1	0	3	2	1	0	0	0	2	2	11
	9.1-12.0	2	1	0	0	2	0	1	0	1	0	7
	12.1-15.0	0	0	0	0	0	3	0	1	0	1	5
	15.1-25.0	0	1	0	0	0	0	1	0	0	0	2
	25.1+	0	0	0	0	0	0	0	0	0	0	0
	TOTAL	19	20	26	8	18	20	12	6	15	11	155
LEPIDOPTERA	0.0-3.0	0	0	2	1	0	2	0	0	1	0	6
	3.1-6.0	0	0	0	0	1	1	0	1	0	0	3
	6.1-9.0	2	1	0	1	0	0	2	0	3	0	9
	9.1-12.0	0	0	0	0	0	0	0	0	0	0	0
	12.1-15.0	0	1	0	2	0	0	1	0	1	0	5
	15.1-25.0	2	3	4	1	5	9	11	8	6	4	53
	25.1+	0	0	0	0	0	0	0	0	0	0	0
	TOTAL	4	5	6	5	6	12	14	9	11	4	76
NEMATOCERA	0.0-3.0	51	16	37	24	21	11	16	19	12	31	238
	3.1-6.0	62	37	25	19	24	20	33	18	41	12	291
	6.1-9.0	44	21	19	22	11	12	24	13	21	25	212
	9.1-12.0	0	1	1	0	0	1	1	2	3	0	10
	12.1-15.0	0	0	1	0	0	0	2	0	0	0	3
	15.1-25.0	0	0	0	0	0	0	0	0	0	0	0
	25.1+	0	0	0	0	0	0	0	0	0	0	0
	TOTAL	157	75	83	65	56	44	76	52	77	69	754
OTHER DIPTERA	0.0-3.0	3	4	2	1	0	6	4	2	1	10	33
	3.1-6.0	8	3	14	2	3	6	9	12	4	5	66
	6.1-9.0	15	37	21	8	14	9	5	17	15	6	147
	9.1-12.0	0	0	3	1	4	2	3	4	1	0	18
	12.1-15.0	0	1	0	0	2	1	0	0	1	0	5
	15.1-25.0	0	0	0	0	0	0	0	0	0	0	0
	25.1+	0	0	0	0	0	0	0	0	0	0	0
	TOTAL	26	45	40	12	23	24	21	35	22	21	269
HYMENOPTERA	0.0-3.0	1	1	0	0	2	1	0	1	3	0	9
	3.1-6.0	1	0	0	3	2	0	1	2	2	1	12
	6.1-9.0	0	1	10	1	0	8	0	2	2	1	25
	9.1-12.0	0	1	2	0	1	0	0	0	0	0	4
	12.1-15.0	0	0	0	0	0	0	0	0	0	0	0
	15.1-25.0	0	0	0	0	0	0	0	0	0	0	0
	25.1+	0	0	0	0	0	0	0	0	0	0	0

	TOTAL	2	3	12	4	5	9	1	5	7	2	50

TABLE A2-2. continued

LARVAE	0.0-3.0	0	0	0	1	0	0	0	2	0	0	3
	3.1-6.0	2	1	3	6	9	2	4	1	0	1	29
	6.1-9.0	0	1	0	0	2	0	0	1	0	0	4
	9.1-12.0	0	0	2	0	0	0	1	0	0	0	3
	12.1-15.0	0	2	1	0	3	1	0	2	1	0	10
	15.1-25.0	12	8	3	5	2	1	0	1	0	1	33
	25.1+	16	10	8	2	0	1	0	1	1	0	39
	TOTAL	30	22	17	14	16	5	5	8	2	2	121
OTHER ADULTS	0.0-3.0	0	1	0	0	1	0	0	1	0	0	3
	3.1-6.0	0	0	0	2	0	0	0	0	2	1	5
	6.1-9.0	0	0	0	0	0	0	0	0	0	0	0
	9.1-12.0	1	0	0	0	0	1	0	0	0	0	2
	12.1-15.0	0	0	0	0	0	0	0	0	0	0	0
	15.1-25.0	0	0	0	1	0	0	0	0	0	0	1
	25.1+	0	0	0	0	0	0	0	0	0	0	0
	TOTAL	1	1	0	3	1	1	0	1	2	1	11
ALL TAXA	0.0-3.0	85	48	56	43	49	42	41	39	26	51	480
	3.1-6.0	109	86	81	49	54	50	63	48	71	37	648
	6.1-9.0	96	100	94	64	46	55	57	57	62	55	686
	9.1-12.0	6	5	12	4	9	4	10	8	8	2	68
	12.1-15.0	0	4	6	2	5	6	3	3	3	1	33
	15.1-25.0	14	12	7	7	7	10	12	9	6	5	89
	25.1+	17	13	8	4	6	4	5	3	5	3	68
	TOTAL	327	268	264	173	176	171	191	167	181	154	2072
BIOMASS	0.0-3.0	7.5	4.2	4.9	3.8	4.3	3.7	3.6	3.4	2.3	4.5	42.4
	3.1-6.0	171	135	127	76.9	84.7	78.5	98.9	75.3	111	58.1	1016
	6.1-9.0	574	598	562	382	275	329	341	341	371	329	4104
	9.1-12.0	86.7	72.2	173	57.8	130	57.8	144	116	116	28.9	982
	12.1-15.0	0	111	167	55.8	140	167	83.7	83.7	83.7	27.9	921
	15.1-25.0	1094	937	547	547	547	781	938	703	469	391	6956
	25.1+	5757	4402	2709	1354	2032	1355	1693	1016	1693	1016	23028
	TOTAL	7691	6261	4292	2479	3213	2772	3303	2339	2846	1855	37052

TABLE A2-3. Arthropod sampling summary for the east poplar area.

ORDER	LENGTH CLASS (MM)	SAMPLING DATE MY27	JN04	JN10	JN18	JN24	JY02	JY08	JY15	JY23	JY29	ALL
ACARINA	0.0-3.0	6	4	0	0	0	2	1	0	1	1	15
	3.1-6.0	0	1	2	0	0	0	0	0	0	0	3
	6.1-9.0	0	0	0	0	0	0	0	0	0	0	0
	9.1-12.0	0	0	0	0	0	0	0	0	0	0	0
	12.1-15.0	0	0	0	0	0	0	0	0	0	0	0
	15.1-25.0	0	0	0	0	0	0	0	0	0	0	0
	25.1+	0	0	0	0	0	0	0	0	0	0	0
	TOTAL	6	5	2	0	0	2	1	0	1	1	18
PHALANGIDA	0.0-3.0	5	2	2	1	0	2	1	0	0	2	15
	3.1-6.0	4	4	1	3	0	3	0	1	2	1	19
	6.1-9.0	0	0	0	0	0	0	0	0	0	0	0
	9.1-12.0	0	0	0	0	0	0	0	0	0	0	0
	12.1-15.0	0	0	0	0	0	0	0	0	0	0	0
	15.1-25.0	0	0	0	0	0	0	0	0	0	0	0
	25.1+	0	0	0	0	0	0	0	0	0	0	0
	TOTAL	9	6	3	4	0	5	1	1	2	3	34
ARANEIDA	0.0-3.0	9	4	6	4	1	0	2	3	2	2	33
	3.1-6.0	11	8	12	13	11	9	2	4	8	3	81
	6.1-9.0	5	2	1	0	4	2	1	1	3	0	19
	9.1-12.0	3	0	0	1	2	0	1	1	2	0	10
	12.1-15.0	0	0	0	0	1	0	0	1	0	0	2
	15.1-25.0	0	0	0	0	0	0	0	0	0	0	0
	25.1+	0	0	0	0	0	0	0	0	0	0	0
	TOTAL	28	14	19	18	19	11	6	10	15	5	145
ODONATA	0.0-3.0	0	0	0	0	0	0	0	0	0	0	0
	3.1-6.0	0	0	0	0	0	0	0	0	0	0	0
	6.1-9.0	0	0	0	0	0	0	0	0	0	0	0
	9.1-12.0	0	0	0	0	0	0	0	0	0	0	0
	12.1-15.0	0	0	0	0	0	0	0	0	0	0	0
	15.1-25.0	0	0	0	0	0	0	0	0	0	0	0
	25.1+	2	0	0	1	3	0	1	2	4	5	18
	TOTAL	2	0	0	1	3	0	1	2	4	5	18
ORTHOPTERA	0.0-3.0	0	0	1	0	0	0	2	0	0	0	3
	3.1-6.0	2	0	0	1	0	0	0	3	0	0	6
	6.1-9.0	0	0	2	1	1	2	0	1	0	0	7
	9.1-12.0	0	0	0	1	1	0	2	0	0	3	7
	12.1-15.0	0	0	0	0	0	0	0	0	0	0	0
	15.1-25.0	0	0	0	0	0	0	0	0	0	0	0
	25.1+	0	0	0	0	0	0	0	0	0	0	0
	TOTAL	2	0	3	3	2	2	4	4	0	3	23
HEMIPTERA	0.0-3.0	11	13	11	10	5	6	2	2	1	2	63
	3.1-6.0	3	4	4	2	6	1	4	5	4	2	35
	6.1-9.0	0	4	4	1	5	0	2	2	1	0	19
	9.1-12.0	0	0	0	0	1	0	1	0	0	0	2
	12.1-15.0	0	0	0	0	0	0	0	0	0	0	0
	15.1-25.0	0	0	0	0	0	0	0	0	0	0	0
	25.1+	0	0	0	0	0	0	0	0	0	0	0
	TOTAL	14	21	19	13	17	7	9	9	6	4	119

TABLE A2-3. continued.

HOMOPTERA	0.0-3.0	3	4	9	2	11	6	4	7	0	2	48
	3.1-6.0	31	8	16	22	9	3	2	6	9	23	129
	6.1-9.0	25	27	30	25	14	21	16	12	12	8	190
	9.1-12.0	0	0	0	0	0	0	0	0	0	0	0
	12.1-15.0	0	0	0	0	0	0	0	0	0	0	0
	15.1-25.0	0	0	0	0	0	0	0	0	0	0	0
	25.1+	0	0	0	0	0	0	0	0	0	0	0
	TOTAL	59	39	55	49	34	30	22	25	21	33	367
NEUROPTERA	0.0-3.0	0	0	0	0	0	0	0	0	0	0	0
	3.1-6.0	0	0	0	0	0	0	0	0	0	0	0
	6.1-9.0	0	0	0	0	0	0	0	0	0	0	0
	9.1-12.0	2	1	1	3	1	0	2	0	0	2	12
	12.1-15.0	0	0	0	0	0	0	0	0	0	0	0
	15.1-25.0	0	0	0	0	0	0	0	0	0	0	0
	25.1+	0	0	0	0	0	0	0	0	0	0	0
	TOTAL	2	1	1	3	1	0	2	0	0	2	12
COLEOPTERA	0.0-3.0	1	3	1	0	2	1	0	0	0	3	11
	3.1-6.0	4	0	3	1	2	2	0	2	0	1	15
	6.1-9.0	1	4	2	0	0	2	0	1	1	1	12
	9.1-12.0	0	0	0	0	1	0	1	0	0	0	2
	12.1-15.0	0	0	0	0	0	0	0	0	0	0	0
	15.1-25.0	0	0	0	0	0	0	0	0	0	0	0
	25.1+	0	0	0	0	0	0	0	0	0	0	0
	TOTAL	6	7	6	1	5	5	1	3	1	5	40
LEPIDOPTERA	0.0-3.0	0	0	0	1	0	0	0	0	0	0	1
	3.1-6.0	2	0	0	0	1	0	1	1	0	0	5
	6.1-9.0	0	2	0	1	0	0	0	0	0	0	3
	9.1-12.0	0	0	1	0	0	0	0	0	2	1	4
	12.1-15.0	4	6	4	2	1	0	1	2	1	0	21
	15.1-25.0	1	0	0	0	2	4	3	6	2	1	19
	25.1+	0	0	0	0	0	0	0	0	0	0	0
	TOTAL	7	8	5	4	4	4	5	9	5	2	53
NEMATOCERA	0.0-3.0	37	28	47	31	28	35	19	21	15	22	283
	3.1-6.0	21	18	17	12	8	19	14	9	9	11	138
	6.1-9.0	37	28	36	41	21	16	14	15	22	6	236
	9.1-12.0	0	2	1	0	0	1	2	0	0	1	7
	12.1-15.0	0	0	0	0	0	0	0	0	0	0	0
	15.1-25.0	0	0	0	0	0	0	0	0	0	0	0
	25.1+	0	0	0	0	0	0	0	0	0	0	0
	TOTAL	95	76	101	84	57	71	49	45	46	40	664
OTHER DIPTERA	0.0-3.0	19	21	1	3	4	9	7	6	8	4	82
	3.1-6.0	31	12	19	20	9	14	7	4	9	1	126
	6.1-9.0	19	22	18	31	20	19	14	11	15	16	185
	9.1-12.0	1	2	3	0	1	2	0	3	1	0	13
	12.1-15.0	0	0	0	0	0	0	0	0	0	0	0
	15.1-25.0	0	0	0	0	0	0	0	0	0	0	0
	25.1+	0	0	0	0	0	0	0	0	0	0	0
	TOTAL	70	57	41	54	34	44	28	24	33	21	406
HYMENOPTERA	0.0-3.0	0	1	0	0	2	0	1	0	0	0	4
	3.1-6.0	9	2	1	3	4	2	1	2	0	1	25
	6.1-9.0	1	2	0	1	0	0	1	1	0	0	6
	9.1-12.0	1	0	0	0	1	0	0	0	0	0	2
	12.1-15.0	0	0	0	0	0	0	0	0	0	0	0
	15.1-25.0	0	0	0	0	0	0	0	0	0	0	0
	25.1+	0	0	0	0	0	0	0	0	0	0	0
	TOTAL	11	5	1	4	7	2	3	3	0	1	37

TABLE A2-3. continued.

LARVAE	0.0-3.0	0	1	0	2	0	0	0	1	0	0	4
	3.1-6.0	0	0	0	0	1	0	2	0	0	0	3
	6.1-9.0	2	0	0	0	1	0	1	0	0	0	4
	9.1-12.0	3	4	0	1	0	2	0	0	0	0	10
	12.1-15.0	1	0	1	0	0	0	2	1	2	1	8
	15.1-25.0	10	6	0	1	3	0	0	1	2	0	23
	25.1+	8	2	2	0	1	0	0	0	0	0	13
	TOTAL	24	13	3	4	6	2	5	3	4	1	65
OTHER ADULTS	0.0-3.0	6	0	2	1	0	1	2	0	1	0	13
	3.1-6.0	0	0	0	1	0	0	1	0	0	0	2
	6.1-9.0	0	1	0	0	0	0	0	1	0	1	3
	9.1-12.0	1	0	0	0	0	0	0	0	0	0	1
	12.1-15.0	0	0	0	0	0	0	0	0	2	0	2
	15.1-25.0	0	0	0	0	0	0	0	0	0	0	0
	25.1+	0	0	0	0	0	0	0	0	0	0	0
	TOTAL	7	1	2	2	0	1	3	1	3	1	21
ALL TAXA	0.0-3.0	97	81	80	55	53	62	41	40	28	38	575
	3.1-6.0	118	57	75	78	51	53	34	37	41	43	587
	6.1-9.0	90	92	93	101	66	62	49	45	54	32	684
	9.1-12.0	11	9	6	6	8	5	9	4	5	7	70
	12.1-15.0	5	6	5	2	2	0	3	4	5	1	33
	15.1-25.0	11	6	0	1	5	4	3	7	4	1	42
	25.1+	10	2	2	1	4	0	1	2	4	5	31
	TOTAL	342	253	261	244	189	186	140	139	141	127	2022
BIOMASS (MG)	0.0-3.0	8.6	7.1	7.0	4.8	4.7	5.5	3.6	3.5	2.5	3.4	50.7
	3.1-6.0	185	89.4	117	122	80.0	83.1	53.4	58.1	64.3	67.5	921
	6.1-9.0	538	550	556	604	394	371	293	269	323	191	4093
	9.1-12.0	158	130	86.7	86.7	115	72.2	130	57.8	72.2	101	1011
	12.1-15.0	139	167	140	55.8	55.8	0	83.7	112	140	27.9	921
	15.1-25.0	860	469	0	78.2	391	313	234	547	313	78.2	3283
	25.1+	3387	677	677	339	1355	0	339	677	1355	1693	10498
	TOTAL	5277	2090	1585	1291	2396	844	1137	1725	2269	2162	20778

TABLE A2-4. Arthropod sampling summary for the east willow area.

ORDER	LENGTH CLASS (MM)	SAMPLING DATE										
		MY27	JN04	JN10	JN18	JN24	JY02	JY08	JY15	JY23	JY29	ALL
ACARINA	0.0-3.0	6	7	4	3	0	1	2	0	1	2	26
	3.1-6.0	1	0	2	0	1	1	0	0	0	1	6
	6.1-9.0	0	0	0	0	0	0	0	0	0	0	0
	9.1-12.0	0	0	0	0	0	0	0	0	0	0	0
	12.1-15.0	0	0	0	0	0	0	0	0	0	0	0
	15.1-25.0	0	0	0	0	0	0	0	0	0	0	0
	25.1+	0	0	0	0	0	0	0	0	0	0	0
	TOTAL	7	7	6	3	1	2	2	0	1	3	32
PHALANGIDA	0.0-3.0	1	0	2	0	0	0	3	1	0	1	8
	3.1-6.0	0	0	0	0	1	0	0	0	0	2	3
	6.1-9.0	0	0	0	0	0	0	0	0	0	0	0
	9.1-12.0	0	0	0	0	0	0	0	0	0	0	0
	12.1-15.0	0	0	0	0	0	0	0	0	0	0	0
	15.1-25.0	0	0	0	0	0	0	0	0	0	0	0
	25.1+	0	0	0	0	0	0	0	0	0	0	0
	TOTAL	1	0	2	0	1	0	3	1	0	3	11
ARNEIDA	0.0-3.0	2	4	9	3	6	2	1	8	3	3	41
	3.1-6.0	26	20	21	21	16	9	14	10	12	2	151
	6.1-9.0	11	9	6	7	6	3	4	4	5	1	56
	9.1-12.0	0	1	0	2	0	1	0	0	0	0	4
	12.1-15.0	0	0	0	0	0	0	0	0	0	0	0
	15.1-25.0	0	0	0	0	0	0	0	0	0	0	0
	25.1+	0	0	0	0	0	0	0	0	0	0	0
	TOTAL	39	34	36	33	28	15	19	22	20	6	252
ODONATA	0.0-3.0	0	0	0	0	0	0	0	0	0	0	0
	3.1-6.0	0	0	0	0	0	0	0	0	0	0	0
	6.1-9.0	0	0	0	0	0	0	0	0	0	0	0
	9.1-12.0	0	0	0	0	0	0	0	0	0	0	0
	12.1-15.0	0	0	0	0	0	0	0	0	0	0	0
	15.1-25.0	0	0	0	0	0	0	0	0	0	0	0
	25.1+	6	9	13	22	18	11	14	8	9	15	125
	TOTAL	6	9	13	22	18	11	14	8	9	15	125
ORTHOPTERA	0.0-3.0	0	2	0	0	0	0	0	0	0	0	2
	3.1-6.0	0	0	1	0	0	3	1	0	0	2	7
	6.1-9.0	0	0	0	0	0	0	2	0	0	1	3
	9.1-12.0	0	0	0	0	0	0	0	0	0	0	0
	12.1-15.0	0	0	0	0	0	0	0	0	0	0	0
	15.1-25.0	0	0	0	0	0	0	0	0	0	0	0
	25.1+	0	0	0	0	0	0	0	0	0	0	0
	TOTAL	0	2	1	0	0	3	3	0	0	3	12
HEMIPTERA	0.0-3.0	4	6	3	9	2	2	0	1	3	1	31
	3.1-6.0	11	6	5	4	4	4	3	4	2	2	45
	6.1-9.0	1	3	7	13	10	8	9	9	7	2	69
	9.1-12.0	0	0	2	0	1	1	0	0	2	1	7
	12.1-15.0	0	0	0	0	0	0	0	0	0	0	0
	15.1-25.0	0	0	0	0	0	0	0	0	0	0	0
	25.1+	0	0	0	0	0	0	0	0	0	0	0
	TOTAL	16	15	17	26	17	15	12	14	14	6	152

TABLE A2-4. continued.

HOMOPTERA	0.0-3.0	8	27	19	16	9	10	12	15	14	13	143
	3.1-6.0	14	8	6	19	32	18	20	20	8	12	157
	6.1-9.0	31	40	26	25	16	18	22	21	27	189	245
	9.0-12.0	0	0	0	0	0	0	0	0	0	0	0
	12.1-15.0	0	0	0	0	0	0	0	0	0	0	0
	15.1-25.0	0	0	0	0	0	0	0	0	0	0	0
	25.1+	0	0	0	0	0	0	0	0	0	0	0
	TOTAL	53	75	51	60	57	46	54	56	49	44	545
NEUROPTERA	0.0-3.0	0	0	0	0	0	0	0	0	0	0	0
	3.1-6.0	0	0	0	0	0	0	0	0	0	0	0
	6.1-9.0	0	0	0	0	0	0	0	0	0	0	0
	9.1-12.0	0	0	2	0	1	0	0	0	0	0	3
	12.1-15.0	0	0	0	0	0	0	0	0	0	0	0
	15.1-25.0	0	0	0	0	0	0	0	0	0	0	0
	25.1+	0	0	0	0	0	0	0	0	0	0	0
	TOTAL	0	0	2	0	1	0	0	0	0	0	3
COLEOPTERA	0.0-3.0	12	19	18	14	16	8	5	6	4	12	114
	3.1-6.0	16	21	14	12	16	3	16	10	6	9	123
	6.1-9.0	6	2	2	6	4	2	4	3	3	7	39
	9.1-12.0	0	0	1	0	0	0	0	2	2	0	5
	12.1-15.0	1	0	0	0	1	0	2	0	0	1	5
	15.1-25.0	0	0	0	0	0	0	0	0	0	0	0
	25.1+	0	0	0	0	0	0	0	0	0	0	0
	TOTAL	35	42	35	32	37	13	27	21	15	29	286
LEPIDOPTRA (ADULTS)	0.0-3.0	0	0	1	0	3	2	1	0	1	1	9
	3.1-6.0	2	6	3	4	2	1	0	2	5	1	26
	6.1-9.0	1	0	0	1	0	2	0	0	3	2	9
	9.1-12.0	0	4	0	1	2	0	0	1	1	0	9
	12.1-15.0	2	1	0	0	1	0	2	2	1	0	9
	15.1-25.0	2	0	1	0	4	9	14	22	16	7	75
	25.1+	0	2	1	0	0	0	0	0	0	0	3
	TOTAL	7	13	6	6	12	14	17	27	27	11	140
NEMATOCERA	0.0-3.0	17	21	17	36	25	14	21	9	15	16	191
	3.1-6.0	64	43	31	21	18	27	18	13	28	37	300
	6.1-9.0	21	48	73	62	41	18	37	28	33	21	382
	9.1-12.0	6	2	1	1	2	1	0	1	0	3	17
	12.1-15.0	0	0	0	0	1	0	0	0	1	0	2
	15.1-25.0	0	0	0	0	0	0	0	0	0	0	0
	25.1+	0	0	0	0	0	0	0	0	0	0	0
	TOTAL	108	114	122	120	87	60	76	51	77	77	892
OTHER DIPTERA	0.0-3.0	4	3	19	20	8	16	4	5	9	13	101
	3.1-6.0	26	31	14	38	22	18	14	30	11	20	224
	6.1-9.0	256	18	29	33	44	41	56	21	33	18	549
	9.1-12.0	13	12	9	22	31	27	18	11	18	31	192
	12.1-15.0	0	0	0	0	1	3	1	0	0	0	5
	15.1-25.0	0	0	0	0	0	0	0	0	0	0	0
	25.1+	0	0	0	0	0	0	0	0	0	0	0
	TOTAL	299	64	71	113	106	105	93	67	71	82	1071
HYMENOPTERA	0.0-3.0	0	0	0	1	2	4	0	2	0	1	10
	3.1-6.0	3	2	19	2	11	8	9	21	0	4	79
	6.1-9.0	1	2	0	4	9	3	2	1	8	8	38
	9.1-12.0	2	1	0	0	8	1	0	1	1	2	16
	12.1-15.0	0	0	0	0	0	0	0	0	0	0	0
	15.1-25.0	0	0	0	0	0	0	0	0	0	0	0
	25.1+	0	0	0	0	0	0	0	0	0	0	0
	TOTAL	6	5	19	7	30	16	11	25	9	15	143

TABLE A2-4. continued.

LARVAE	0.0-3.0	2	1	0	2	0	9	3	1	2	1	21
	3.1-6.0	4	3	5	0	2	3	2	1	6	2	28
	6.1-9.0	10	14	8	13	12	9	22	7	6	1	102
	9.1-12.0	8	6	4	2	3	7	9	16	4	3	62
	12.1-15.0	4	7	9	11	15	17	16	12	2	4	97
	15.1-25.0	16	21	8	4	13	9	6	2	1	3	83
	25.1+	2	0	1	6	3	1	2	2	1	0	18
	TOTAL	46	52	35	38	48	55	60	41	22	14	411
OTHER ADULTS	0.0-3.0	2	3	0	1	4	1	2	1	0	0	14
	3.1-6.0	1	0	2	0	0	0	0	2	0	0	5
	6.1-9.0	3	0	0	0	0	0	0	0	0	1	4
	9.1-12.0	1	1	5	0	4	1	0	0	1	2	15
	12.1-15.0	0	2	0	0	2	2	0	1	0	0	7
	15.1-25.0	0	0	0	0	0	0	1	0	0	1	2
	25.1+	0	0	1	0	0	0	0	0	0	0	1
	TOTAL	7	6	8	1	10	4	3	4	1	4	48
ALL TAXA	0.0-3.0	58	93	92	105	75	69	54	49	52	64	711
	3.1-6.0	168	140	123	121	125	95	97	113	78	94	1154
	6.1-9.0	341	136	151	164	142	104	158	94	125	81	1496
	9.1-12.0	30	27	24	28	52	39	27	32	29	42	330
	12.1-15.0	7	10	9	11	21	22	21	15	4	5	125
	15.1-25.0	18	21	9	4	17	18	21	24	17	11	160
	25.1+	8	11	16	28	21	12	16	10	10	15	147
	TOTAL	630	438	424	461	453	359	394	337	315	312	4123
BIOMASS (MG)	0.0-3.0	14.8	12.3	10.8	10.7	11.0	8.4	8.6	10.0	6.9	8.3	102
	3.1-6.0	264	220	193	189	196	149	152	177	122	148	1811
	6.1-9.0	2040	813	904	981	850	622	945	562	748	485	8951
	9.1-12.0	433	390	347	405	751	563	390	462	419	607	4768
	12.1-15.0	195	279	251	307	586	614	586	418	112	139	3489
	15.1-25.0	1407	1641	703	313	1328	1406	1641	1875	1328	859	12506
	25.1+	2709	3752	5418	9482	7111	4064	5418	3386	3386	5080	49782
	TOTAL	7064	7081	7827	11688	10835	7428	9142	6893	6123	7326	81409