BREEDING DISTRIBUTION, HABITAT SELECTION AND FACTORS AFFECTING

COLONIALITY IN EARED GREBES IN BRITISH COLUMBIA

By

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ABSTRACT

In this study, I first describe distribution and abundance of breeding Eared Grebes (*Podiceps nigricollis*) in British Columbia. Second, I characterize and examine the relationships between nesting habitat and nest site selection on breeding group size. Finally, I examine effects of colony size, nesting chronology and nesting synchrony on reproductive success at Eared Grebe colonies.

I surveyed 421 wetlands in 1985 and 1986 and located 47 lakes used by nesting Eared Grebes. Those 47 lakes accomodated from a low estimate of 1761 to a high estimate of 4474 pairs. Breeding abundance, calculated from adult, nest and young counts, ranged from single pairs to more than 590 pairs per lake. Breeding took place in shallow lakes of various sizes, subject to extensive variations in water levels. Breeding abundance was positively correlated with lake area. Fewer breeding pairs utilized nesting areas close to shore (in shallower water) than nesting areas far from shore (in deeper waters). Nesting areas close to shore were found in smaller lakes and were used less often in consecutive years than nesting areas far from shore, presumably because of lower habitat predictability. An experiment with unattended artificial nests showed that nest predation was higher far from shore than close to shore. Nesting areas close to shore were used by small groups. These maximized concealment by being located in denser vegetation. Nesting areas far from shore were used by larger groups and were

located in more open areas.

On both years, adults arrived at nesting lakes in April and May, started laying on 27 May and departed from nesting areas in late July and early August. Nesting was significantly earlier and reproductive success per pair was significantly higher in 1985 than in 1986. A stepwise multiple regression examined effects of colony size, synchrony and chronology on nesting success. Only nesting chronology accounted for differences in nesting success. Late nesters were not birds attempting to renest. Instead, there appeared to be qualitative differences across colonies that were related to ages of breeders.

Eared Grebe colonies are likely not formed from passive aggregation at limiting resources and there are likely no foraging benefits from colonial nesting. Nesting colonies could increase detection and mobbing of predators, but no evidence supported this. Anti-predator benefits of coloniality might have been masked by differences in breeding chronology and synchrony, or were missed because of low sample size.

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and new insights on old problems. I also thank a 16th century philosopher (Don Marquis) for an obscure quote appropriate to advanced studies. He wrote: "If you make people believe they think, they will love you; if you make them think, they will curse you."

CHAPTER 1: GENERAL INTRODUCTION

Eared Grebes (*Podiceps nigricollis*) breed colonially throughout the Northern Hemisphere (Palmer 1962; Cramp and Simmons 1977) and in Northern Africa (Cramp and Simmons 1977). Small populations are also found in South Africa (Liversidge and McLachlan 1957; Broekhuisen 1963) and in South America (Jehl 1988). The North American breeding range centers on the Northern Great Plains and the Great Basin (Palmer 1962; Jehl 1988), with British Columbia at the northwestern limit of the range. Although the breeding distribution is relatively well established in North America, no quantitative studies have yet focused on regional breeding populations.

In British Columbia, known breeding colonies are concentrated over small isolated areas (Munro 1941; 1942; McAllister 1956; 1958; Campbell and Garrioch 1978; Campbell *et al.* 1979; Campbell *et al.* in press) in or near areas of extensive agricultural, industrial or recreational use. The Canadian Wildlife Service (Pacific and Yukon Region) ranked Eared Grebes amongst the top 15 species least studied in a priority migratory bird species list (Boyd 1982). Effective management and protection of the species depends upon detailed knowledge of distribution, abundance and breeding biology, which are all currently lacking for British Columbia and the rest of North America.

Breeding biology of Eared Grebes presents interesting theoretical problems. Although Eared Grebes are considered colonial

nesters, breeding groups range from 1 to 2600 pairs (Palmer 1962).
Colonial and solitary nesters can be found in the same general area,
allowing the study of cost and benefits of colonial nesting.
Further, water levels on nesting grounds fluctuate widely within and
between years (Cramp and Simmons 1977), affecting food and nesting
habitat availability. The constraints (if any) that habitat
variability places on colonial nesting are unknown.

This study combines 1) management concerns and 2) theoretical
considerations. The management objective of this study is to
characterize breeding biology, distribution and abundance of Eared
Grebes in B.C. Known breeding areas are subject to habitat threats
(see below), whose potential impacts on breeding populations cannot
be assessed due to lack of information on distribution and biology
of the species. The theoretical objective is to characterize
coloniality in Eared Grebes. Each objective will be considered
separately.

1- Management concerns

Eared Grebes are not only colonial nesters but also highly
gregarious in winter and on various staging points during migration.
Concentrations of over 20,000 have been observed on Malheur Refuge,
Oregon during spring migration (Palmer 1962). Each fall, some

750,000 birds concentrate on Mono Lake, California for their wing moult (Cooper *et al.* 1984; Storer and Jehl 1985; Winkler and Cooper 1986; Jehl 1988). Over half a million individuals winter on the Salton Sea in California (Palmer 1962). Gregariousness on breeding and wintering grounds raises the possibility of localized incidents affecting large portions of populations (Jehl and Bond 1983).

In British Columbia, lakes chosen for nesting are shallow, highly productive water bodies providing nest cover and abundant aquatic invertebrate food (Campbell *et al.* in press). Major factors affecting or threatening nesting habitat in B.C. are:

A- Natural variations in water levels

Seasonal water level fluctuations may flood, destroy or expose whole Eared Grebe colonies to predation (Munro 1941, Cramp and Simmons 1977).

B- Man-caused alterations of breeding habitat

i) - Impact of oil exploration

Drilling sites have sometimes been located on Eared Grebe breeding lakes (e.g. Boundary Lake). Oil exploration also involves construction of access roads, increased accessibility to nesting areas and sulphur gas releases at drilling sites. No information is

available on the frequency and impact of those disturbances.

ii) – Agricultural practices

Ranching and farming practices affect wetlands in several ways. Most commonly, wetlands are drained to create sedge meadows, pasture areas or arable land, resulting in loss of foraging and/or nesting areas. Water can also be used to irrigate fields, which can result in decreased water levels and could leave nests stranded on dry ground.

iii) – Water level controls

Organizations such as Ducks Unlimited preserve wetlands by acquiring water rights and by controlling water levels. Water controls can have positive or negative effects on plant and invertebrate populations, depending on timing and water volumes affected (Kadlec 1962; Meeks 1969), and hence may affect Eared Grebes. Ducks Unlimited is considering acquiring water rights for different nesting lakes in the Central and Southern Interior regions (e.g. Little White, Elkhorn and McMurray Lakes); these are currently used by a total of roughly 1000 nesting pairs.

iv) – Composition of the vertebrate community

Eared Grebes feed on aquatic and land insects and their larvae (Munro 1941; Palmer 1962). Eared Grebes do not nest on lakes where fish are present (pers. obs.). Introduction of fish for

recreational purposes might greatly affect invertebrate availability, as fish will compete with grebes for preys (Wetzel 1975; Eriksson 1979; Anderson 1981a; Eadie and Keast 1982; Des Granges and Brodeur 1985).

Apart from having their breeding habitat threatened, Eared Grebes are also susceptible to disturbance by humans and other animals (Campbell *et al.* 1979) during laying and incubation. Disturbances at those times causes them to leave their nests, and unattended nests are subject to predation (Riske 1975). Recreational development along shores, increased industrial, agricultural or recreational activities close to breeding areas may disturb incubating birds, and could eventually reduce reproductive success or cause colony abandonment.

2- Theoretical considerations

Bird colonies are places where a number of individuals or pairs nest at a more or less centralized location which they recurrently depart to forage (Wittenberger 1985; Kharitonov and Siegel-Causey 1988). Passive aggregation at limiting resources and benefits derived from the presence of conspecifics can both lead to the formation of bird colonies. First, colonies can form when individuals are independently attracted to specific locations such as safe nesting sites. This is thought to be the case with species

such as seabirds (Lack 1968; Nelson 1970; Ashmole 1971). However, because colonies are usually more compact than scarcity of nests alone dictates [Coulson (1971); Birkhead (1976) in Wittenberger and Hunt 1985], there must also be other benefits to nesting at high densities.

Benefits and cost associated with colonial nesting have been detailed in various reviews (see Ward and Zahavi 1973; Wittenberger and Hunt 1985; Kharitonov and Siegel-Causey 1988). Costs of living in colonies include increased competition for mates, food and space, increased risk of depredation and diseases, and increased risk of transmission of ectoparasites (Alexander 1974; Wittenberger and Hunt 1985). Intraspecific nest parasitism and infanticide can also occur (Hoogland and Sherman 1976). Benefits result from either increased food access, social facilitation, or lower predation risks (Wittenberger and Hunt 1985; Kharitonov and Siegel-Causey 1988).

The key hypothesis I test in this thesis is that Eared Grebe colonies are an anti-predator adaptation. If colony size offers major anti-predator advantages (to decrease predation on eggs), reproductive success (number of young fledged per pair) should increase with colony size (see Hoogland and Sherman 1976, Andersson and Wiklund 1978; Wiklund and Andersson 1980; Wiklund 1982). Other studies, however, have failed to demonstrate a relationship between colony size and breeding success (e.g. Snapp 1976; Hoogland and

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Sherman 1976; Brown and Brown 1987; Shields and Crook 1987).

Different mechanisms can also act to decrease predation at nesting colonies. Breeding chronology is known to affect reproductive success (see reviews in Burger 1979; Wittenberger and Hunt 1985), with early nesters usually enjoying higher reproductive success. Higher within-colony breeding synchrony was related to increased breeding success in Bank Swallows (*Riparia riparia*) (Emlen and Demong 1975; Parsons 1976), but other studies have not found any correlation between synchrony and colony size (see Burger 1979). Synchronized breeding could be advantageous by 1) decreasing the number of days during which active nests are exposed to predators; 2) providing more food than predators can consume (predator swamping effect); 3) helping social-feeding birds get information on the location of food sources from other foraging individuals; 4) increasing capture success by cooperative hunting; or 5) using the group to decrease chances of an individual being preyed upon (selfish herd effect) (from Wittenberger 1985).

Although group size, synchrony within colony and breeding chronology have all been related to breeding success, effects of each factor have usually been investigated separately. Because group size, synchrony and breeding chronology can be correlated to one another (Burger 1979), those 3 variables deserve to be studied simultaneously to understand the relationships between them.

Studies of coloniality have commonly quantified costs and benefits associated with colonial nesting for colonies of different sizes (see above reviews). Most widely-studied species (e.g. gulls, terns, swallows and herons) have in common: 1) nest sites that are stable and predictable across years; 2) parents that fly to and from foraging grounds and 3) foraging areas with no obvious physical or geographical boundaries. Eared Grebes differ from the above species in all these points. First, nesting habitat is unpredictable and fluctuates widely within and across years (Cramp and Simmons 1977). Fluctuations in water levels probably affect nest site availability, food abundance and possibly philopatry and dispersal. Secondly, adults rarely fly during the breeding season. Nesting and rearing of young takes place in a limited and well-defined area (the breeding lake), which provides both nest sites and foods used during the breeding season (Cramp and Simmons 1977).

Eared Grebes provide an ideal system for studying how physical resources affect habitat selection and colonial nesting. They also provide an opportunity to study if and how colonial nesting can be adaptive in unpredictable or highly variable aquatic environments. I expected attachment to nest sites and colonies to be minimal in spatially and temporally fluctuating environments. Nesting requirements should also be flexible, to allow for variability in nesting conditions.

My thesis is organized as follows. I examine first distribution, abundance and habitat selection of breeding Eared Grebes in British Columbia. Secondly, I characterize breeding habitat and nest site selection. Thirdly, I determine 1) if there are net reproductive benefits to nesting in colonies and 2) how group size, breeding chronology and breeding synchrony contribute to variations in breeding success across colonies. My study of coloniality focuses on current cost (in terms of predation) and benefits (breeding success) of colonial nesting; I then interpret my results from an evolutionary perspective.

Chapter 2 covers distribution, abundance and breeding biology of Eared Grebes in British Columbia. Chapter 3 characterizes breeding habitat (morphology of breeding lakes, water chemistry and seasonal variability in water levels), and relates habitat characteristics to breeding group size. The anti-predator value of nest site location is also covered. Chapter 4 uses a multivariate approach to study the effects of group size, breeding chronology and breeding synchrony on breeding success. Chapter 5 is a general discussion.

CHAPTER 2: DISTRIBUTION AND ABUNDANCE OF

EARED GREBES IN BRITISH COLUMBIA

Introduction

Eared Grebes are considered abundant breeders in some areas of British Columbia (Munro 1941; 1942; Campbell *et al.* in press), with breeding concentrations ranging from isolated pairs to about 2500 pairs per lake (e.g. Cecil Lake) (Munro 1941; Campbell *et al.* in press).

Information on past breeding distribution in British Columbia was obtained from McTaggart-Cowan (1939); Munro (1941; 1942); Guiguet (1954); Palmer (1962); Campbell and Garrioch (1978); Campbell *et al.* (1979; in press) and the British Columbia Nest Record Scheme. For various reasons, those records are of little use in assessing current distribution or past abundance. First, breeding groups often shift location between years because of ecological instability of nesting habitat (Cramp and Simmons 1977). Because past surveys were spread over a 50-year period, with only a few lakes surveyed on any given year, we cannot tell whether abundance and distribution records are additive or reflect changes in breeding distribution. More seriously, there is little information on how data were collected. The precision of breeding abundance estimates depends on the number, timing, and quality of surveys. Information derived from multiple surveys conducted on a single year is likely to be more accurate than incidental observations. Timing of surveys is also critical, as surveys of

adults conducted during incubation are likely to miss incubating birds. Information on survey type and intensity is critical, as it is the only way to separate anecdotal observations from exhaustive surveys. Finally, information is needed on how breeding abundance was estimated, because the estimates can vary depending on different ways of calculation (see below).

Breeding abundance can be estimated by counting adults, nests, or young; each method has biases and limitations (Cooperidder et al. 1986). Adult counts can be biased by the presence of non-breeders, by the absence of incubating adults, and by birds foraging underwater at the time of the observations. Adult movements between breeding areas are rare (Palmer 1962), so counts conducted on different lakes likely represent different birds. Quality of nest counts depends on survey timing and degree of nesting synchrony (Bull 1981). Nest counts will underestimate true nest numbers if breeding is not fully synchronized. Each pair of Eared Grebes can also build more than one platform (Palmer 1962), in which case platform counts overestimate true nest number. Chick counts present 2 problems; how to count chicks, and how to relate chick counts to number of breeders. Chick visibility varies with age and chick foraging behaviour (Palmer 1962, Cramp and Simmons 1976). If information is available on age-specific chick survival, chick counts can be transformed into number of breeding pairs. However, such transformations are limiting in that they assume that chick

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survival is similar across lakes, which is likely not to be the
case. Population estimates should be accompanied by both an error
term and a description of calculation methods. So far, this has not
been the case.

This chapter will: 1) summarize past breeding distribution of
Eared Grebes in British Columbia, and 2) assess current distribution
and abundance. Extensive information on past and current breeding
distribution in British Columbia has been given by Breault *et al.*
(1988), so only general conclusions will be presented here. Note
that number of breeding pairs per lake is not the same as colony
size, because some lakes support more than 1 colony (pers. obs.).
This chapter will solely discuss overall breeding abundance.
Coloniality will be treated in Chapter 4.

Methods

1- Surveys on abundance of breeders

Historic records on distribution and number of pairs of Eared
Grebes nesting in British Columbia were obtained from: 1) the B.C.
Nest Records Scheme (housed at the Royal British Columbia Museum),
2) graduate theses, 3) published literature, 4) Canadian Wildlife
Service surveys, 5) Ducks Unlimited surveys and 6) British Columbia

Ministry of Environment surveys. Also, a survey form was distributed in 1986 along with the newsletters of the B.C. Federation of Naturalists and the Williams Lake Naturalist Club to solicit further information on past and present breeding records. No new information was collected from the newsletters.

Breeding records were grouped into four geographical areas including suitable nesting habitat: Central Interior, Southern Interior, Okanagan/Kamloops and Peace River regions (see Fig. 1 for area locations). New surveys were conducted in those areas from May to August in 1985 and 1986 (see Fig. 2 for area surveyed in 1985 and/or 1986) and covered 421 lakes (36 lakes for which there were historical breeding records and 385 new lakes) (see Table I for surveying effort per area). Lakes not previously surveyed were selected from 1:50,000 topographic maps based on the following criteria: a) being accessible by road, b) being located in open habitat (prairie or parkland), c) having part of their shoreline devoid of forest and d) showing signs of marshy areas or emergent vegetation. Those criteria were selected because all known breeding lakes in British Columbia met conditions b), c) and d). Condition a) was added to increase the number of lakes that could be surveyed per unit of time.

The following information was recorded for most lakes: number of adults, number and age of chicks and number of nests and eggs

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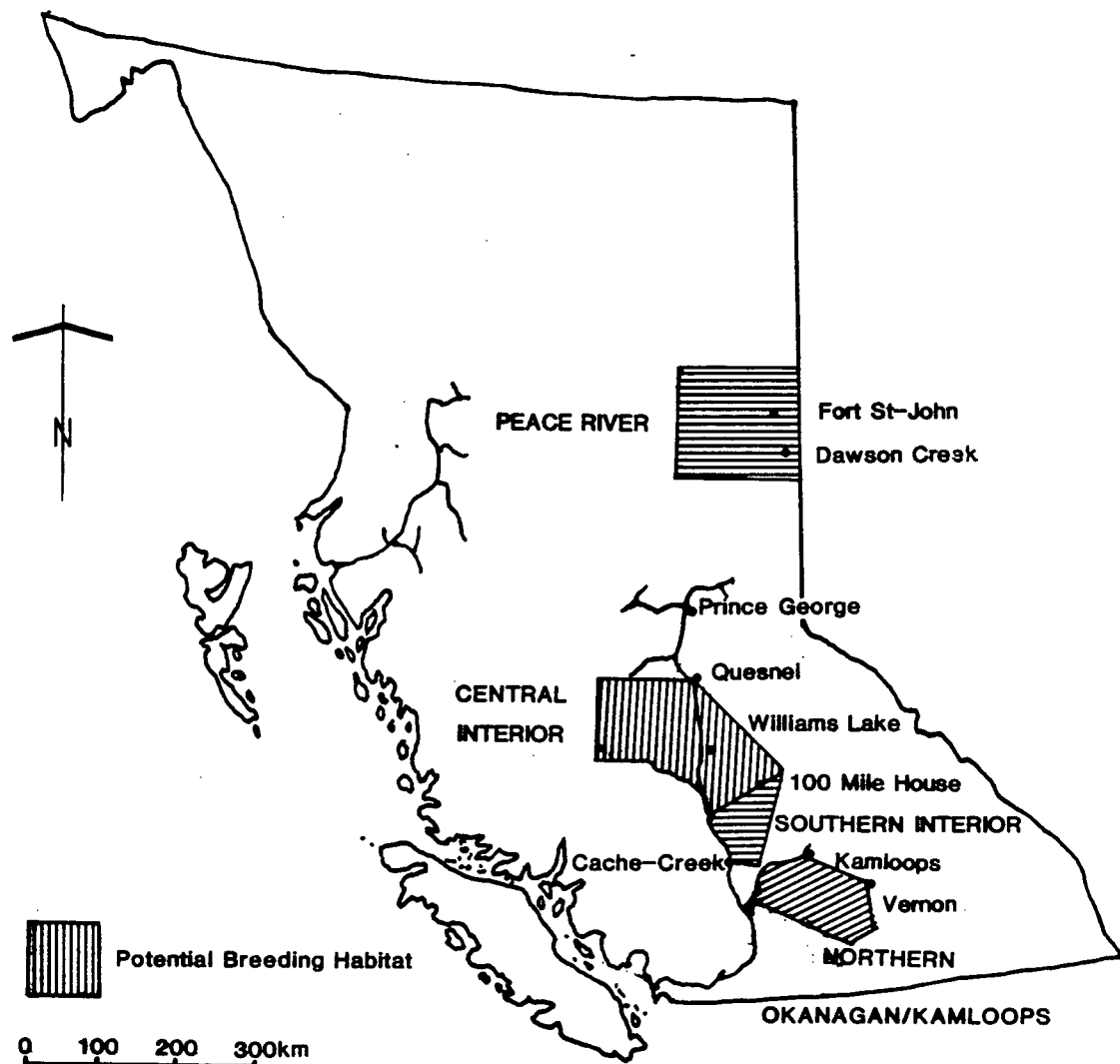
Figure 1: Zones with potential breeding habitat for Eared Grebes in British Columbia.
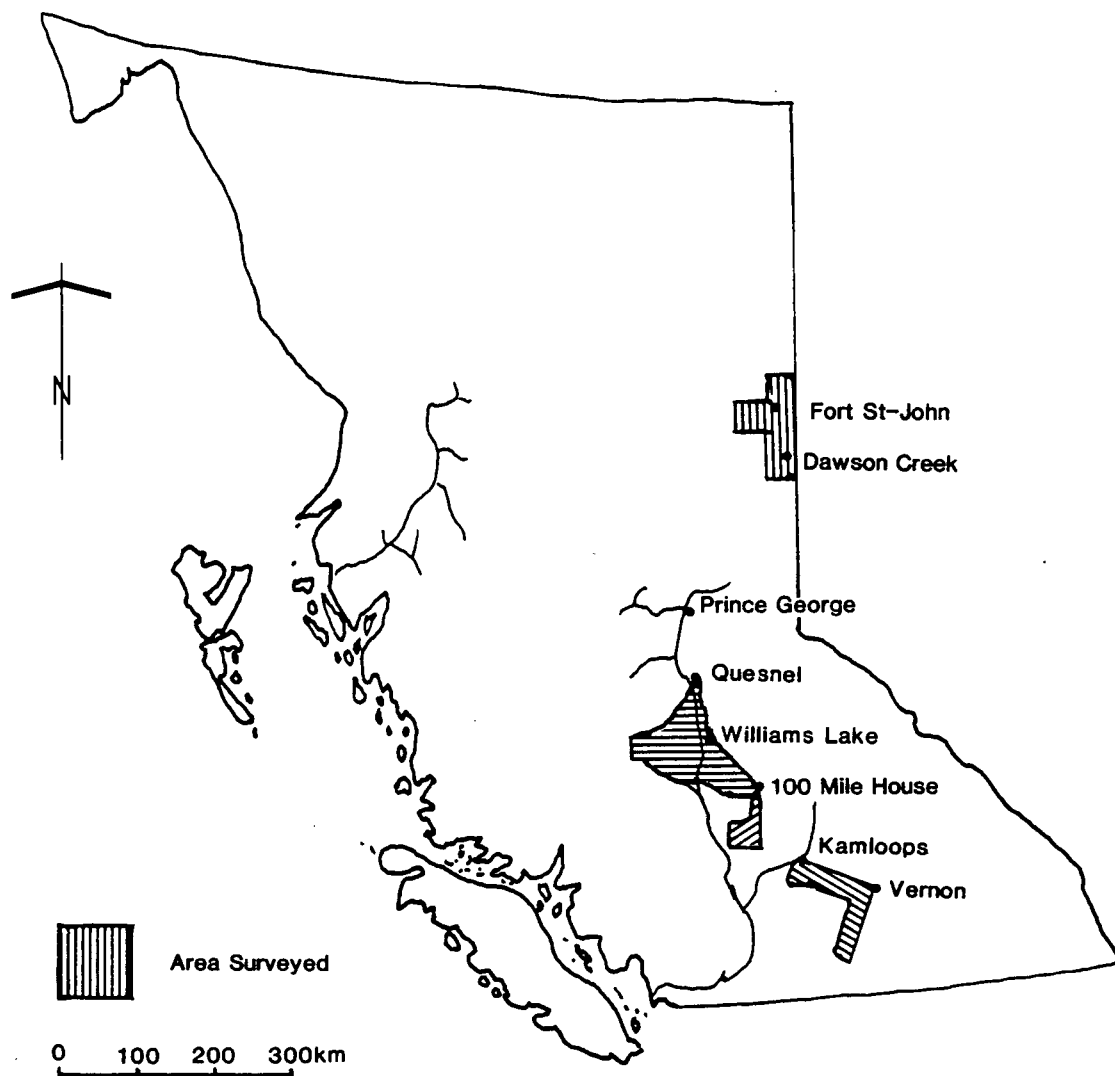
Figure 2: Areas surveyed in 1985 and 1986 to locate Eared Grebe breeding lakes.

Table I. Surveying effort at Eared Grebe breeding lakes in British Columbia in 1985 and 1986.

Region	LAKES IDENTIFIED FROM HISTORIC RECORDS				OTHER LAKES		TOTAL[1]
	n	locatable[2]	visited	active	active	visited	active (n)
Northern Okanagan /Kamloops	17	8	3	2	4	66	6 (69)
Southern Interior	5	4	3	3	4	34	7 (37)
Peace River	12	11	10	8	2	25	10 (35)
Central Interior	28	25	20	7	17	260	24 (280)
TOTAL	62	48	36	20	27	385	47 (421)

[1] n = number of lakes visited

[2] Lakes accessible or lakes which could be located on topographic maps.

observed. Not all types of counts were conducted on each lake. Type and frequency of counts varied with lake location and accessibility.

Only lakes with confirmed breeding records (nests with eggs, eggshells or presence of unfledged chicks) were used to study

breeding distribution. Empty nesting platforms or presence of adults alone or fledged chicks was not considered evidence of breeding attempts. Breeding abundance was studied regionally.

A) Counts of adults and chicks

Adults and chicks were counted from vantage points on the shore with binoculars and/or a spotting scope. Counts were repeated at least twice on lakes <26 ha and the maximum count was recorded. On larger lakes, adults were counted only once, but slowly enough to take into account diving and resurfacing birds. Age and number of chicks were recorded on audio tapes. Aging was done according to Gollop and Marshall's system of plumage development in waterfowl (Gollop and Marshall 1954; Bellrose 1978). No efforts were made to flush birds from emergent vegetation so counts represent minimum values. When chicks fed actively, several counts were conducted consecutively and the highest count was used. Breeding adults are not known to move between lakes (Palmer 1962), so there is little chance of repeated counting and overestimating adult numbers.

B- Counts of nests

Nests were counted while wading through emergent vegetation on each lake. Active nests (with eggs or signs of hatching such as presence of vascularized membranes and small pieces of shell) were distinguished from empty platforms. In areas of high nest density, counted nests were identified with small pieces of rope (2-3cm long)

to avoid double counting. The number of eggs in each nest was recorded for each visit.

2- Estimating abundance of breeders

Depending on the number and timing of surveys, up to 3 estimates of the number of breeding pairs per lake were derived from:

A) Adult counts

An estimate was obtained by dividing the maximum number of adults seen during the April-August period by 2.

B) Nest counts

The highest recorded number of active nests during each breeding season was used as the minimum number of breeding pairs per lake (because nesting is not necessarily synchronized). Empty platforms (before laying, after hatching or after predation at nest) were recorded separately but treated as active nests. Platform counts were used only for lakes where no or incomplete active nest counts were available. All platforms from previous years were presumed to have been destroyed by ice, wind and wave action unless they were located in abnormally sheltered area (e.g. McMurray Lake).

C) Chick counts

This estimate was obtained by dividing the observed number of

chicks of a given age by the mean number of chicks per pair surviving to that age. The period from hatching to fledging was divided into 3 periods, based on chick visibility and behaviour. The first period covered from hatching to 2 weeks of age. Chicks are poorly visible at that age and spend most of their time under the folded wings of their parents (Cramp and Simmons 1976). The second period was from 2 weeks to 1 month old. Chicks of that age are not found under their parent's wings, but they are still fed by them. From 1 month of age to fledging, chicks are rarely accompanied by parents and are easily detectable when not diving for food. The equation used to estimate breeding abundance from chick counts is presented in Appendix 1.

D) Overall estimate of breeding pair abundance

When available, maximum nest counts (complete or incomplete) were used as an overall estimate of the abundance of breeding pairs. When nest counts were not available or when estimates based on incomplete nest counts were lower than estimates based on chick counts, I used estimates based on chick counts.

Estimates of the number of breeding pairs per lake thus took the form of single values or ranges. Single values were obtained from multiple nest surveys, or when the estimate based on adult counts was identical to the estimate derived from nest counts. In all other cases, abundance is presented as a range consisting of

both minimum and maximum estimates as calculated by the above methods. Estimates from both 1985 and 1986 were used to derive the range.

Regional estimates of breeding abundance were derived by adding minimum and minimum estimates from each lake. For cases where only 1 or a few surveys were conducted late in the year (e.g. surveys in the Peace River region in 1985), a subjective correction factor was used. The correction factor was based on comparisons with lakes used by known numbers of breeding pairs also surveyed late in the summer. Size of regional populations was obtained by separately adding lowest and highest estimates of breeding populations for all lakes.

Errors inherent to each method and the fact that minimum and maximum estimates were usually derived from different methods (minimum counts from nests, maximum counts from adult surveys) are likely responsible for the wide range between maximum and minimum estimates. Adult counts are biased downwards by missing incubating or feeding adults and upwards by including non-breeders. Nest counts are also biased downwards, because egg-laying is rarely fully synchronized and nests are lost to predators, and upwards by the presence of empty platforms. Multiple surveys could compensate for those biases, but this was rarely possible. Biases associated with chick counts mostly depend on how chick counts are adjusted to

number of breeders. If age-specific survival rates of chicks are high, chick counts will underestimate true population size. Conversely, if age-specific survival rates are low, numbers of breeding pairs will be overestimated. Precision of chick counts increases with chick age and size (because chicks cease to be transported under their parents' wings), but plumage characteristics on which aging is based are affected by preferential feeding by the parents.

The number of breeding pairs per lake and the distribution of the population across lakes was investigated in 1985 and 1986. Breeding lakes were arbitrarily grouped into 5 categories based on the number of breeding pairs using a lake: 1-25, 26-50, 51-75, 76-100 and 101+ breeding pairs per lake. Breeding abundance was defined as the highest estimate from adult, chick and nest counts when multiple surveys were available or as the mean of the range for each lake.

3- Statistics

Statistical analyses presented in this thesis were done with SYSTAT (Wilkinson 1989). Normality of data sets was ascertained with a Lilliefors test. Most measurements shown in the thesis are accompanied by their standard error (S.E.).

Results

1- Breeding distribution and abundance

Surveys conducted on 421 lakes in 1985 and 1986 identified 47
·lakes used by breeding Eared Grebes in 4 regions of B.C. (Table I).
Eared Grebes were known to breed on 20 of those 47 lakes prior to
1985. The other 27 breeding lakes were identified in a survey of
385 lakes not previously surveyed. Sixteen of the 36 lakes (44.4%)
that I surveyed where breeding had taken place prior to 1985 were
not used for breeding in 1985 and 1986. The most recent estimates
of breeding abundance for those lakes indicate that all 16 lakes
were each last used by 35 pairs or less. Overall, I located from
1761 to 4474 breeding pairs on those lakes. The number of breeding
lakes and breeding pairs in each region was as follows (see Breault
et al. 1988 for more details).

A) Northern Okanagan/Kamloops

Prior to 1985, 17 breeding lakes had been identified in the
area. The 1985 and 1986 surveys covered 3 of those lakes and
identified 4 new breeding lakes. Overall, only Stump Lake was used
by a large number (70-100) of breeding pairs.

Assuming that lakes with historical records that were not
surveyed in 1985 and 1986 are still used by the same number of

breeders, estimated breeding population in the area ranges from 109 to 280 pairs (Appendix 2), or 6.2 to 6.3% of the provincial population.

B) Peace River Region

At one time, this region included the 2 lakes with the largest number of breeding pairs in British Columbia: Cecil Lake, with more than 1000 pairs in 1978 and 1981 and Boundary Lake, with 600 to 800 pairs in 1978 (British Columbia Nest Record Scheme). Overall, 12 lakes in the region supported breeders prior to 1985. All but 2 lakes were visited in 1985 and 1986, with 8 out of the remaining 10 lakes used by breeding pairs. The number of pairs nesting on Boudreau and Cecil lakes in 1985 and 1986 was less than previously reported. This could be due in part to late surveying in both years or it may reflect actual decreases in numbers. Further surveys are needed to confirm the possible decline.

The Peace River region accounted for 342 to 1775 breeding pairs (Appendix 3), or 19.4 to 39.7 % of the estimated provincial population. Breeders were concentrated on 3 lakes: Cecil, Boundary and Boudreau Lakes.

C) Southern Interior

Historically, 5 breeding lakes were known in the area. Three of them were revisited in 1985 and 1986, and few changes were observed

in breeding numbers. Prior to the 1985-86 surveys, only Meadow Lake was known to be used by more than 50 breeding pairs, and my surveys indicated that breeding population there remained the same or possibly increased, even though non-breeders were also observed throughout the breeding season. Nesting habitat is limited to the northeast shore of the lake, and this area was completely searched for nests. Adult surveys conducted at the time of the nest searches accounted for more than the number of pairs predicted from nest counts. Large groups of adults were observed away from the shore, which is contrary to usual breeding behaviour. Those birds were classified as non-breeders.

Four new breeding lakes were located in 1985 and 1986. Little White Lake was used by approximately 500 pairs in 1986. However, a higher population was suspected, because 1) the estimate was derived from a chick count conducted on 18 July 1988, and chick counts are certainly underestimates on larger lakes because of problems with visibility, feeding behaviour, high chick density, etc.; 2) no nest searches were conducted on the lake, thus any incubating birds would have been missed; 3) counting young on that lake took twice as long as on another lake of similar size used by 440 pairs with chicks of the same age, suggesting the presence of more young; and 4) a 1986 survey conducted by Ducks Unlimited during peak breeding time (June) reported 1600 adults on the lake.

Overall, the Southern Interior accommodated from 676 to 940 breeding pairs (Appendix 4), or roughly 38.4 to 21.0% of the estimated provincial population.   Breeding birds were mostly concentrated on Little White Lake and Meadow Lake.

D) Central Interior

More than half the historically-known breeding lakes in the province were located in this region.   The largest populations were found on Westwick Lake (419 nests and 50 platforms in 1978), Rock Lake (160 nests in 1978) and Sorenson Lake (50+ pairs in 1949).

Surveys conducted in 1985 and 1986 covered 20 of the 28 lakes used in the past.   Changes in breeding abundance were observed on some lakes.   For example, Eared Grebes still bred on Westwick and Rock Lakes in 1985 and 1986, but the numbers were down compared to 1978.   My surveys also found lower numbers of Eared Grebes on Sorenson Lake, probably because of active drainage of the lake for irrigation purposes.

Seventeen new breeding lakes were identified in the region during this study, the most notable being McMurray Lake (2 bodies of water connected by a narrow channel of open water), used by more than 400 pairs both in 1985 and 1986.   Elkhorn Lake was used by roughly 260 pairs in 1985, whereas Lake 8432 North was used by between 80 and 100 pairs in 1986.   No other lakes were used by more

than 40 pairs.

The Central Interior accounted for 634 to 1479 breeding pairs (Appendix 5), or 36.0 to 33.1 % of the estimated breeding population in B.C.

2- Number of breeding pairs

Breeding abundance per lake ranged from single pairs to more than 590 pairs in 1985 and 1986 (Appendices 2, 3, 4 and 5). Higher estimates of breeding abundance are available from historic records, the highest being for Cecil Lake (Peace River Region), with an estimated 2500 nests in 1962.

More lakes were used by few (<25 pairs) breeders than by many (>100 pairs) breeders (Fig. 3). However, lakes used by many breeders accounted for more than 60% of the surveyed population in both years. Lakes used by less than 51 pairs accounted for roughly 14% (1986) to 23% (1985) of all estimated breeding pairs.
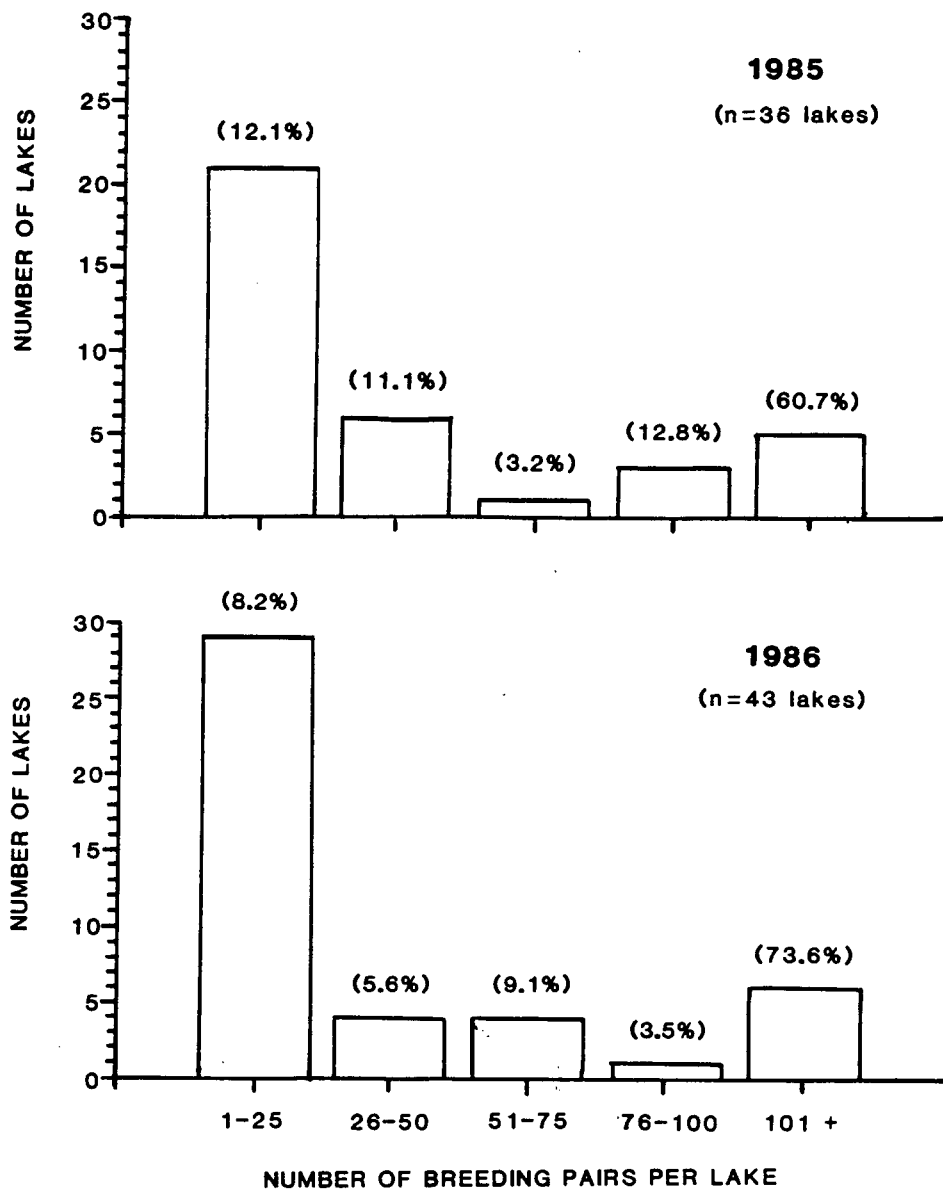
Figure 3. Number of breeding pairs per lake and distribution of the breeding population (%) across lakes.

Discussion

1- Distribution and abundance in B.C.

In British Columbia, the 4 areas where Eared Grebes nest include the most productive wetlands for waterfowl in the province (Waterfowl production areas in British Columbia, Canadian Land Use survey map, Environment Canada). The known Eared Grebe population nesting on the 47 lakes I surveyed in those 4 areas was estimated at between 1761 and 4474 breeding pairs in 1985 and 1986. The provincial population is undoubtedly much higher, as only a portion of the suitable breeding habitat was surveyed. Areas showing the highest potential for undiscovered breeding lakes are the Southern and Central Interior, which include many wetlands, few of which have been surveyed.

Old breeding records were useful in the study of distribution of breeding Eared Grebes, but methodological limitations kept them from providing reliable information on past abundance. Past records do, however, illustrate continuity of use of breeding areas. Breeding densities varied widely in amplitude on certain lakes, and a large number of breeding areas were not consistently used across years. For example, the number of breeding pairs on Westwick Lake went from 0 in 1931 to 228 pairs in 1941 (Munro 1942). Variability in distribution and abundance appears to be inherent to the species

(Palmer 1962, Cramp and Simmons 1977).

Breeding abundance varied widely both seasonally and across lakes. Even though few lakes were used by more than 100 nesting pairs, these accounted for more than 60% of the known provincial population. Those lakes should be protected because of their significance. Groups of less than 50 pairs accounted for 15 to 22% of the overall number of pairs surveyed, but the occurrence of nesting by small groups is likely higher than reported here. Lakes used by few breeders are less known to biologists and naturalists than large breeding concentrations. Detection also increases with group size, favoring localization of large breeding groups. Ecological correlates of group size will be investigated in Chapter 3.

One aim of this study was to provide a data base against which future changes in distribution and abundance could be measured. The information I collected achieves that purpose. There is no strong evidence that abundance has declined. Breeding lakes previously supporting large numbers of pairs were found to be still active, even though breeding abundance sometimes varied. Differences in abundance between my surveys and old records could be accounted for by differences in surveying techniques such as survey timing. Surveys conducted during peak breeding time in the Peace River region could determine whether the apparent decline there is real.

Methods used to determine breeding abundance are highly relevant to the understanding of breeding biology, as quantitative data on habitat use are a prerequisite to good studies of habitat selection (Woolhead 1987). From the 3 techniques available to estimate breeding abundance, repeated nest counts are least biased, provided that nesting is synchronized. Nest counts, however, are time-consuming and disturb incubating birds. Non-systematic nest counts are of limited value to assess breeding abundance, but can be useful in distribution studies. Adult surveys are the easiest to conduct. They provide precise estimates if multiple surveys are available, especially if they are conducted right before the onset of laying (early June in central British Columbia). After that time, they underestimate true breeding numbers because incubating adults, non-breeders and adults that have failed will be missed. There are so many problems with chick counts that they should not be used to assess breeding abundance.

Extensive information on techniques used to survey colonial waterbirds can be found in Cooperidder *et al.* (1986). Assessment of the number of breeding grebes has been studied in Great Crested Grebes (*Podiceps cristatus*) in Europe. This facultatively-colonial species nest in emergent vegetation (Cramp and Simmons 1976). Counting nests is not easy, as nests are located in dense rushes or

reeds (Cramp and Simmons 1976). Leys and de Wilde (1971) therefore concluded that chick counts in July and August were the best method to count Great Crested Grebes. Woolhead (1987) pointed out that chick counts are biased by nest failures and predation on chicks, and suggested using adult counts prior to nesting. Other studies also identified the start of the breeding season as the optimum period to estimate the number of breeding pairs from adult counts (Green 1985; Nilsson 1981; Woolhead 1987). I recommend the use of nest counts to determine breeding abundance. If nest counts are not possible, abundance of Eared Grebes would be best determined from multiple adult surveys conducted prior to nesting.

Summary

I determined breeding distribution and abundance from historical records and field surveys. Historical nesting records were found for 62 lakes in B.C. I surveyed 36 of those lakes and another 385 lakes in 1985 and 1986. I found 47 lakes used by breeding Eared Grebes. The breeding population of the 47 lakes was estimated at 1761 to 4474 pairs, with breeding abundance per lake ranging from single pairs to more than 590 pairs in 1985 and 1986..

CHAPTER 3: HABITAT CHARACTERISTICS, NEST SITE SELECTION AND BREEDING GROUP SIZE IN EARED GREBES

Introduction:

Different ecological factors affect breeding distribution and habitat use: 1) inter- and intraspecific competition, 2) resource distribution (e.g.food), and 3) predation (Buckley and Buckley 1980). This chapter will focus on resource ·distribution and predation. My approach is to quantify Eared Grebe breeding habitat at the lake and nest site levels, and then consider ecological factors associated with group size and nest site selection.

1- Breeding habitat

Eared Grebes breed worldwide in "highly productive" wetlands (Cramp and Simmons 1977). In North America, overall breeding distribution (Palmer 1962) coincides with presence of shallow productive wetlands. Breeding pairs are found in sheltered, shallow and reedy portions of medium-size or larger wetlands (Palmer 1962). Although general breeding habitat descriptions are available from observations in Washington State (Yocom *et al.* 1958), British Columbia (Munro 1941; 1942; Guiguet 1954; Campbell *et al.in* press), and from general accounts (e.g. Bent 1919; Cramp and Simmons 1977), detailed information on breeding habitat is only available for isolated lakes in B.C. (e.g. McTaggart-Cowan 1939; McAllister 1956; 1958; Munro 1941; 1942; Forbes 1985) and North Dakota (Faaborg, 1976). Only Faaborg (1976) has so far studied habitat selection

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quantitatively, and he found that Eared Grebes nest on large semi-permanent open ponds. Because of seasonal and annual fluctuations in water levels, breeding habitat is known to be somewhat unpredictable (Cramp and Simmons 1977), but habitat predictability and its effects on habitat selection have not been studied.

2- Ecological correlates of breeding group size

The taxonomic distribution and ecological correlates of avian coloniality have been documented by Crook (1964, 1965) and Lack (1968). Ecological factors related to breeding group size include size of breeding habitat, distribution and use of essential resources such as food (Crook 1972; Cody 1971; Horn 1968) and vulnerability to predation (Hamilton 1971). Studies of island biogeography have shown that larger land bird populations are found on bigger or more productive islands (see Simberloff 1974; Pielou 1979; Anderson 1981b; Bengston and Bloch 1983).

Eared Grebes breed in groups of extremely variable size (from 1 pair to more than 590 pairs in B.C.) (see Chapter 1), and breeding lake size is also highly variable (Munro 1941; 1942; Palmer 1962; Faaborg 1976; Cramp and Simmons 1982). Their diet consists of tiny insects or insect larvae (Palmer 1976), whose abundance and distribution is correlated to water chemistry (Lancaster 1985). I

will examine the extent to which breeding group size in Eared Grebes is related to habitat productivity (e.g. food and cover).

I estimated habitat productivity from water chemistry analyses. Animal zooplankton standing crop is positively and linearly correlated to Dissolved Solid Content (DSC), which affects nutrient availability and growth rate in aquatic systems (Northcote and Larkin 1956; Wetzel 1975; Topping 1985), and DSC can be quickly evaluated from water conductivity (Northcote and Larkin 1956). I use water conductivity as an index of wetland productivity (see Lancaster 1985 for more details).

3- Nest site selection

Different types of nest sites are used by Eared Grebes. Nests are either anchored to bulrush (*Scirpus spp.*), cattail (*Typha spp.*) (Palmer 1976), or are exposed and free-floating (Bent 1919; Munro 1941). Cattail and bulrush stands are usually limited to shorelines, while exposed nests can be seen at quite a distance from shore (pers. obs.). Using vegetation to anchor nests might be beneficial, as bulrush and cattail could decrease nest visibility and detection by predators. Being close to shore would, however, increase nest accessibility, and large breeding groups could quickly lose benefits from nest concealment. Use of both types of nest sites might indicate trade-offs between nest-concealment, distance

from shore (affecting nest accessibility to predators), group size, and nest predation rates.

4- Anti-predator value of nest sites

One of the most important aspects of nest site selection in birds is safety from predators (Buckley and Buckley 1980). Predation on bird nests can have a major influence on young production (Lack 1968; Ricklefs 1969). Predation rates are affected by habitat type (Burger 1973), nest substrate and nest height (Ricklefs 1969), habitat location (Loiselle and Hoppes 1983) and nest position within a colony (Patterson 1965; Coulson 1968, Dexheimer and Southern 1974).

Two primary defenses can be used against nest predation: 1) locate nests in sites inaccessible to predators or 2) conceal nests from predators (Wittenberger and Hunt 1985). Use of inaccessible nest sites is most obvious with marine seabirds nesting on small islands or rocks devoid of predators (Lack 1968) and with cavity-nesting birds (Sonerud 1985). These sites are, however, limited in number. Concealment is effective only if body size is small and breeding density is low. Experiments have suggested that concealment is most effective when nests are widely dispersed and uncommon (Tinbergen *et al.* 1967, Croze 1970). Beyond a certain

group size, concealment becomes less effective, as nesting activities betray colony and nest site location.

I designed an experiment to test for trade-offs between nest concealment, nest accessibility and predation on eggs. Artificial platforms were used to represent different nesting conditions: nests were concealed or exposed, close to or far from shore and with eggs exposed or concealed. My predictions were that 1) nest predation should be lower on concealed platforms and on nests close to shore; and 2) exposed platforms close to shore should suffer the heaviest predation because of increased detection and accessibility to predators.

Eared Grebes normally cover their eggs before leaving the nest, but not always so (Broekhuisen 1963). I repeatedly observed uncovered Eared Grebe eggs during visits to nesting areas. McAllister (1956) suggested 2 non-exclusive functions of egg cover: keep eggs warm while untended or/and conceal eggs from predators. Artificial platforms were used to determine whether predation rates differed between covered and uncovered eggs.

The chapter is divided in 4 sections: 1) a description of physical and chemical characteristics of breeding lakes; 2) a study of relationships between physical and chemical characteristics and

number of breeding pairs per lake; 3) a description of nest site selection; and 4) a study of the anti-predator value of nest sites.

Methods

1- Lake characterization:

The following variables were studied on lakes used by breeding Eared Grebes: lake morphology (area, mean and maximum depth), water chemistry (pH, conductivity, salinity and hardness), and water level fluctuations within and across years.

Lake area was determined for 28 lakes by tracing lake contours on 1:50,000 topographic maps with an IBM-PC graphics tablet, then calculating area by program. Information on mean and maximum depths was obtained for 17 and 15 lakes from either Ducks Unlimited surveys, Boyd and Savard (1987), or from field surveys. Water depth at nest was estimated from water height on chest waders or measured with a meter stick in 1986.

Water samples were collected on 27 lakes in June 1986 (methods in Boyd and Savard 1987). Samples were frozen at the field camp and analyzed in early August. Conductivity, salinity and hardness were

measured on a S-C-T Meter (Yellow Springs Instruments Ltd.). PH was measured on DUAL-TINT pH test paper (graduation 0.3).

Water level fluctuations were studied on 11 lakes in 1985 and 1986 in the Riske-Creek, B.C. area. Submerged permanent stakes were set as far away as possible from Eared Grebe nesting areas. Readings were taken weekly from May to July with a 30cm ruler positioned at the end of the stake. Stakes were submerged under at least 15cm of water, to keep them from being destroyed by ice in the winter. Two extra lakes were measured in 1985.

2- Ecological correlates of breeding abundance:

Data on lake area, pH, conductivity, salinity and hardness were collected for 27 lakes. Number of breeding pairs using those lakes, hardness and conductivity were log-transformed to normalize the data. A stepwise multiple regression analysis was conducted on normalized data to relate number of breeding pairs per lake to the above characteristics. Alpha values for entering variables were set at 0.15, on the basis of Monte Carlo studies of stepwise regression (Bendel and Afifi 1977, in Wilkinson 1989).

3- Nest site selection:

Nest sites were located on 29 lakes where multiple nest surveys were made (see Chapter 1 for survey methods). Breeding areas were mapped and classified as either close to shore (within 5m from the shore) or far from shore (more than 5m from shore).

Physical (lake area; maximum, minimum and mean lake depths; seasonal and annual water level fluctuations) and chemical (pH, conductivity, salinity, hardness) characteristics of wetlands were compared for lakes with nesting areas close to and far from shore with paired t-tests. Data on nest site selection were standardized and tested for normality. Log transformations produced normally-distributed values for number of breeding pairs, lake area, and hardness. Statistical transformations did not normalize the distribution of pH data, so pH was analyzed with non-parametric statistics. Because some of the information utilized was obtained from other studies, sample sizes varied from analysis to analysis.

I used 15 lakes with nesting areas close to shore and 10 lakes with nesting areas far from shore to determine the effect of nest site location on lake use on consecutive years. I only used lakes for which multiple adult surveys and nest searches were available for both 1985 and 1986. Those lakes were classified as either used by breeders (presence of nesting platforms) or not used by breeders

(absence of adults or absence of nesting platforms) on each year. I compared the ratio of lakes unused/total number of lakes surveyed on consecutive years for nests located close to and far from shore.

4- Anti-predator value of nest site:

Artificial platforms were used to relate nest predation in small breeding groups (3 nests) to: 1) distance from the shore (close *vs.* far), 2) nest concealment (exposed *vs.* partially-concealed platforms) and 3) egg concealment (exposed *vs.* concealed eggs). I built platforms representing each combination of factors except the following: concealed nests close to shore with exposed eggs and exposed nests close to shore with exposed eggs. Each combination of factors (involving 3 nests each) was replicated twice on each of 8 different lakes in the Riske-Creek area, for a total of 288 artificial platforms. All lakes were in a 4 km^2 area and unused by Eared Grebes, but adjacent to lakes used by breeding grebes. My experiment assumed that experimental lakes were subject to similar predator pressure as neighbouring lakes used by Eared Grebes.

Artificial nests were built from decomposing bulrush placed on square wooden platforms (roughly 400-625cm^2) set between 1 June and 15 June 1986. Platforms were attached to three poles to keep them from swaying and to provide support for potential predators. The platforms were estimated to be as stable as natural nests. Each

nest was provisioned with 3 Japanese Quail (*Coturnix japonica*) eggs.
The eggs I used were pale creamy-buff, with fine over-all speckling
and sparser irregular spotting and blotching buffish-brown or dark
brown (Harrison 1978). Quail eggs are markedly smaller and likely
more cryptic than Eared Grebes eggs. Quail eggs were available in
large quantities, and have been used successfully in other studies
of nest predation (e.g. Schaeff and Picman 1988, Picman and Belles-
Isles 1988). Nests close to shore were set within 2 m from shore in
water 0.5m deep, whereas nests away from shore were set within 2 to
3 m from shore, in water 1.3m deep. Nests were concealed by
drilling 6cm-diameter holes on 3 sides of each wooden platform, and
inserting dead and fresh bulrush stems collected in the area into
the holes until all holes were filled. Eggs were covered with palm-
sized patties of decaying vegetation and mud, equivalent in size,
texture and coloration to that used by Eared Grebes.

Egg losses were measured after 4 and 8 days. Predator type was
identified from egg remains (Rearden 1951; Green 1987). Avian
predators produce triangular punctures on the egg side and push the
eggshell inwards. Mammalian predators make a small hole out of one
end or break eggshells into small pieces, but the edges of some
shells may show fine tooth marks. The area beneath each platform
was searched for eggshell fragments or for eggs that had fallen off.
Eggs that disappeared from the platforms were presumed to be preyed
upon unless they were found on the lake bottom. Platform solidity

and amount of vegetation left on the platform were also noted, and that information was used to assess whether egg losses could have been caused by wave action. Cases where wave action was thought to be the cause of egg attrition were removed from analyses.

I conducted univariate analyses of variance between egg losses and 1) distance from shore, 2) nest concealment and 3) egg cover. Because the number of eggs left in each nest after 4 and 8 days (ranging from 0 if all eggs were preyed upon to 3 if no eggs were preyed upon) did not follow a normal distribution, I used a Kruskal-Wallis analysis of variance to analyze the data.

Results

1- Physical characteristics of breeding lakes:

Morphological data was collected on 23 lakes (see Table II). All breeding lakes were quite shallow, with maximum lake depth ranging from 1.0 to 3.4m. Lake depth averaged 1.0m (+0.1) (n=17), while maximum depths averaged 1.8m (+0.2) (n=15). Water depth at nest sites averaged 0.9m (+0.1) (n=19). Mean water levels decreased by 5.6cm (+0.3) (n=12) between 15 May and 31 July 1985 and 15.9cm (+0.7) for the same period in 1986. Decreases in water level were significantly different between years (paired t-test, t=15.1, df=9,

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Table II. Lake morphology at selected Eared Grebe breeding lakes.

| LAKE | WATER DEPTH | | | FLUCTUATIONS IN WATER LEVELS | | |
	MEAN (m)	MAX (m)	AT NEST (m)	1985 (cm)	1986 (cm)	1985-1986 (cm)
6	1.4	2.5	0.8	-4.5	-11.0	-16.7
11	0.9	1.9	0.8	-4.5	–	-10.3
12	0.8	1.5	1.0	-5.5	-18.8	8.2
16	1.0	1.0	1.0	-4.7	-16.6	-16.7
24	1.3	2.1	0.5	-4.8	-16.8	–
26	0.8	1.5	0.8	-5.1	-15.0	-14.3
28	0.7	2.5	0.5	–	-14.7	–
55	0.6	1.0	0.5	-6.6	-18.9	-17.9
42	1.0	2.0	0.8	-6.0	–	-8.1
53	1.9	3.4	0.6	-5.7	-13.7	-8.1
50	0.8	1.2	1.0	-5.7	-16.2	-8.9
McMRY	1.5	2.2	1.4	-8.6	-17.1	-11.5
WESTW	1.0	–	1.5	-5.9	-15.8	-11.8
NL1	1.0	–	1.0	–	–	–
NL2	–	–	1.0	–	–	–
NL3	–	–	1.2	–	–	–
NL4	0.6	1.2	–	–	–	–
NL5	–	–	0.5	–	–	–
NL6	1.1	2.0	–	–	–	–
NL7	–	1.0	–	–	–	–
NL8	–	–	1.0	–	–	–
NL9	0.7	–	–	–	–	–
NL10	–	–	1.0	–	–	–
MEAN	1.0	1.8	0.9	-5.6	-15.9	-10.6
SE	0.1	0.2	0.1	0.3	0.7	2.2
(n)	(17)	(15)	(19)	(12)	(11)	(11)

p<0.01), with water levels on 15 May 1986 averaging 10.56cm ($\pm$2.16) less than on the same date in 1985.

Water chemistry analyses were performed on samples originating from 27 lakes (Table III). All lakes were alkaline, with pH averaging 8.3 ($\pm$0.1). Conductivity averaged 2518.4 ($\pm$437.4) umhs/sec, while salinity averaged 1.7 ($\pm$0.3) ppt. Hardness readings averaged 380.6 ($\pm$74.8). Many-fold variations in magnitude were observed for all water chemistry variables.

Breeding lakes ranged in size from 0.7ha to 716.3ha, the average being 103.6ha ($\pm$35.5). Breeding abundance per lake ranged from 1 to 440 pairs.

Eight lakes in the Riske-Creek area were sampled on both 3 June and 10 July 1986 to determine seasonal variations in water chemistry (see Table IV for data). A Wilcoxon Signed Ranks Test showed no significant differences between June and July readings, although all readings were on average higher in July than in June (see Table IV). Evaporation was likely responsible for higher readings in late summer.

Table III. Water chemistry characteristics and lake area of Eared
   Grebe breeding lakes in B.C.

LAKE	NO. BREEDING PAIRS	PH	CONDUCTIVITY (umhs/sec)	SALINITY (ppt)	HARDNESS (ppm)	AREA (ha)
COYOTE	6	8.5	4050.0	2.9	307.8	16.0
McMURRAY	440	8.8	7200.0	3.5	153.9	162.0
8432	21	8.6	800.0	1.0	547.2	19.5
UPPERDRY	28	7.9	148.0	0.0	119.7	27.1
JAMIESON	8	7.6	320.0	0.3	256.5	17.9
3-DRY	2	8.2	165.0	0.0	102.6	10.0
55	4	8.5	2050.0	1.7	649.8	1.3
12	20	8.8	990.0	0.8	102.6	3.0
11	35	8.6	3730.0	3.0	290.7	7.0
GREEN-B	6	8.6	8000.0	6.5	340.2	4.0
McQUEEN	25	7.3	450.0	0.2	256.5	152.3
BOUNDARY	175	6.2	260.0	0.0	171.0	460.0
GREEN-A	3	8.5	2750.0	2.0	615.6	39.3
BOUDREAU	100	8.2	180.0	0.0	119.7	453.8
CECIL	400	8.5	328.0	0.0	171.0	716.3
4403	36	8.2	1820.0	1.3	837.9	73.4
LITLWHIT	400	8.5	5100.0	4.0	171.0	166.7
SLOANESL	3	7.4	165.0	0.0	85.5	10.0
42	17	8.5	1750.0	1.0	546.3	4.8
24	2	8.6	5500.0	3.5	1915.2	3.4
6	85	8.5	3220.0	2.0	153.9	27.2
53	4	8.4	1270.0	0.8	307.8	3.3
16	28	8.5	5800.0	3.7	153.9	11.6
26	7	8.5	3300.0	2.2	889.2	2.7
28	1	8.5	3200.0	2.0	222.3	5.1
50	5	8.2	1950.0	1.2	649.8	.7
MEADOW	37	8.5	3500.0	2.3	102.6	496.6
ELKHORN	200	-	-	-	-	90.8
WESTWICK	220	-	-	-	-	40.6
MEAN=	79.9	8.3	2518.4	1.7	380.6	103.6
SE =	24.1	0.1	437.4	0.3	74.8	34.5
(n) =	(29)	(27)	(27)	(27)	(27)	(29)

Table IV. Water chemistry readings on 3 June and 10 July 1986.

LAKE	CONDUCTIVITY (umhs/sec)		SALINITY (ppt)		PH		HARDNESS (ppm)	
	3 June	10 July	3 June	10 July	3 June	10 July	3 June	10 July
24	3200	5500	2.1	3.5	8.2	8.6	410.4	1915.2
50	1600	1950	1	1.2	8.1	8.2	427.5	649.8
26	2550	3300	1.8	2.2	8.2	8.5	666.9	889.2
6	2420	3220	1.6	2	8.5	8.5	119.7	153.9
42	1370	1750	0.8	1	8.3	8.5	239.4	546.3
40	1530	1480	1	1	8.2	8.6	393.3	410.4
28	3430	3200	2.2	2	8.5	8.5	102.6	223.3
55	1650	2050	1	1.7	8.2	8.5	530.1	649.8
MEAN	2218.8	2806.3	1.44	1.83	8.28	8.49	361.24	679.74
SE	282.9	463.0	.20	.29	.05	.04	69.42	195.81

2- Effects of abiotic factors on breeding density

The stepwise multiple regression identified only lake area as a predictor of the number of breeding pairs, with larger lakes supporting significantly larger breeding populations than smaller ones ($r^2 = 0.60$, t=6.36, p<0.01). Lake productivity (as estimated by water conductivity) did not significantly affect number of breeding pairs.

3- Nest site selection

Twenty-nine lakes were used to characterize nest-site location.
Three lakes had nesting areas both close and far from shore and were
not included in the following analyses. Of the remaining 26, 10
lakes had nesting areas close to shore, and 16 had nesting areas far
from shore. Physical and chemical characteristics of lakes with
nesting areas close to and far from shore are presented in Table V.

The number of breeding pairs was significantly lower when nests
were close to shore than when nests were far from shore ($t=-5.50$,
$p<0.01$) (Fig. 4a). Lake area ($t=-5.53$, $p<0.01$), hardness ($t=-2.57$,
$p=0.02$) and water depth at nest ($t=-4.79$, $p<0.01$) also differed on
lakes where nests were close and far from shore (see Fig. 4b, c and
d). Nesting areas close to shore were found in smaller lakes with
higher hardness readings, and nesting areas were located in
shallower water. Other than size, there were no significant
differences in lake morphology (mean and maximum depth) between
lakes with nesting areas close to and far from shore, and both types
of lakes exhibited similar seasonal and annual fluctuations in water
levels.

Lakes with nesting areas close to shore were used less
consistently (10 out of 15) than lakes with nesting areas far from
shore (10 of 10).

Table V. Habitat characteristics (+se) of breeding lakes with Eared Grebe nests located close to and far from shore.

	NEST SITE LOCATION	
VARIABLE	CLOSE TO SHORE	FAR FROM SHORE
No. Breeding pairs	6.9 + 3.2 (n=10)	138.0 + 38.2 *(n=16)
Lake area (ha)	5.3 + 3.8 (n=10)	182.4 + 55.5 *(n=16)
Water chemistry:		
- PH	8.5 + 0.1 (n=10)	8.1 + 0.2 (n=14)
- Conductivity (umhos/sec)	2796.5 + 479.6 (n=10)	2651.9 + 756.5 (n=14)
- Salinity (ppt)	1.9 + 0.3 (n=10)	1.8 + 0.5 (n=14)
- Hardness (ppm) (log scale)	6.1 +0.1 (n=10)	5.3 +.2*(n=14)
Lake depth:		
- Average (m)	1.00 + 0.17 (n=7)	1.03 + 0.11 (n=8)
- Maximum (m)	1.94 + 0.31 (n=7)	1.64 + 0.27 (n=6)
- At nest (m)	0.6 + 0.1 (n=9)	1.1 + 0.1 *(n=9)
Fluctuations in water level (cm):		
- May/July 1985	5.4 + 0.3 (n=6)	5.9 + 0.9 (n=4)
- May/July 1986	15.9 + 0.8 (n=6)	15.1+ 1.4 (n=4)
- May 1985/May 1986	11.9 + 1.8 (n=6)	14.2 + 1.5 (n=4)
No. of lakes used in consecutive years	10 (n=15)	10 (n=10)

*p<0.05, determined by t-test analysis
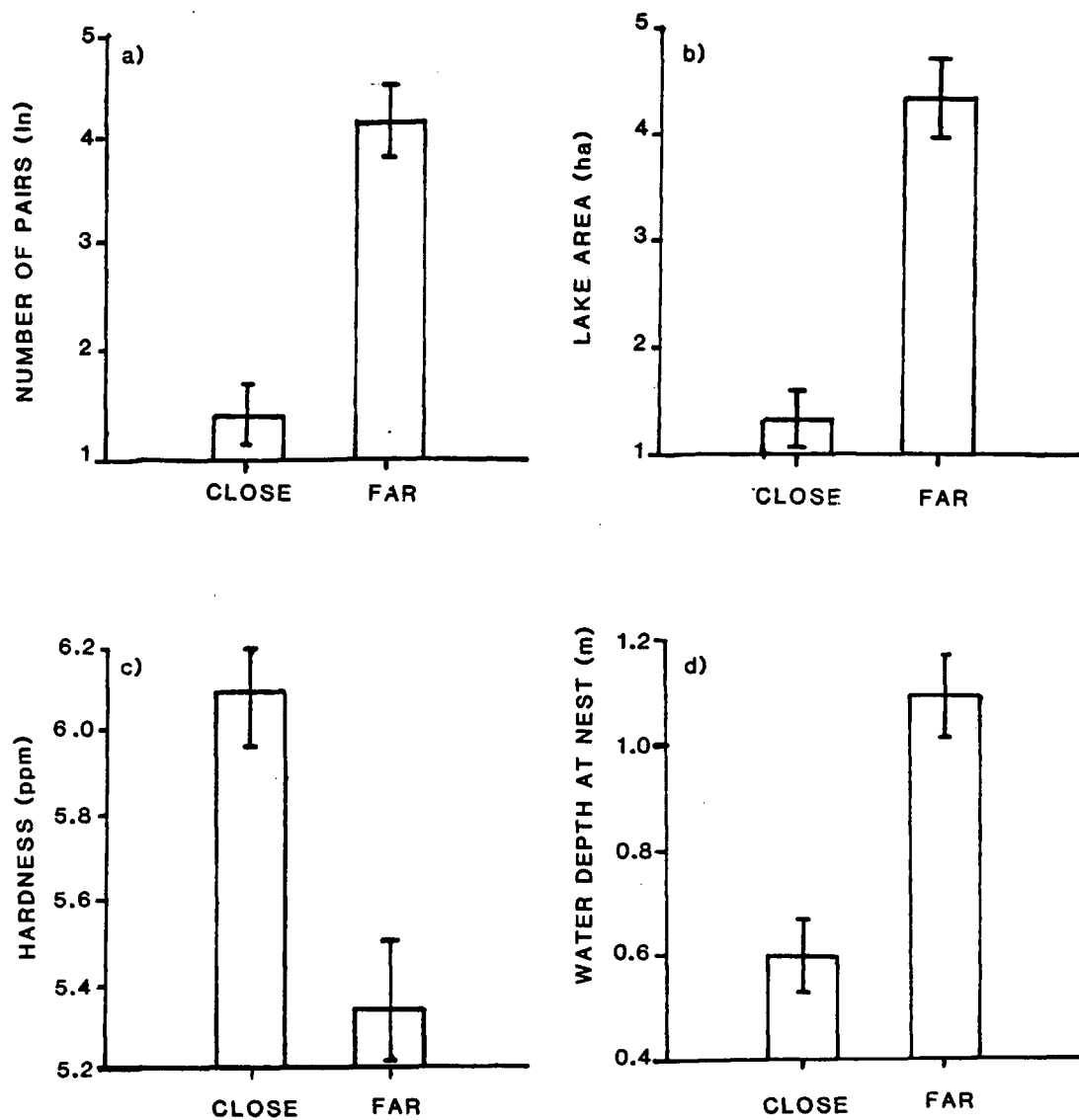
Figure 4. Number of breeding pairs (a), b) lake area, c) hardness and d) water depth at nest (+SE) for lakes where nesting areas are located close and far from shore.

On nests with covered eggs, predation caused more losses (x^2=11.67, p<0.01, n=190 nests) far from shore than close to shore (Fig. 5a). The effects of egg cover and nest concealment were only measured on nests far from shore. For those nests, covered eggs suffered less predation (x^2=21.22, p<0.01, n=192 nests) than exposed eggs (Fig 5b), but concealed nests did not have significantly lower egg predation rates than exposed nests (x^2=0.27, p=0.60, n=190 nests) (Fig. 5c).

Similar results were obtained for egg predation after 8 days. On nests with covered eggs, predation was higher away from shore (x^2=9.54, p<0.01, n=181 nests) than close to shore (Fig. 6a). On nests far from shore, nests with exposed eggs suffered higher predation (x^2=27.15, p<0.01, n=173) than nests with covered eggs (Fig. 6b), while there were no significant differences in rates of egg loss between concealed and non-concealed nests (x^2=0.89, p=0.34, n=173 nests) (Fig. 6c).

The type of predation observed on quail eggs was similar to that observed on eggs of grebes and other waterbirds nesting in the Riske-Creek area (pers. obs.). Many eggs showed roughly triangular-shaped punctures on the side of the eggs, indicating avian predation (Rearden 1951). American Coots were observed puncturing some eggs.
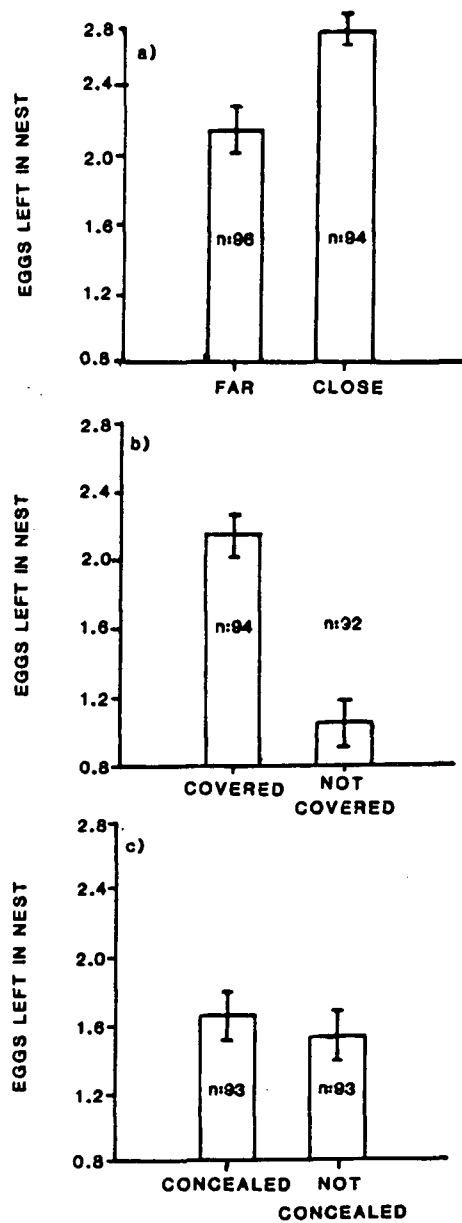
Figure 5. Comparison of the number of eggs left in artificial platforms (±SE) after 4 days in relation to a) nest location for nests with covered eggs, b) egg cover for nests far from shore and c) nest concealment for nests far from shore.
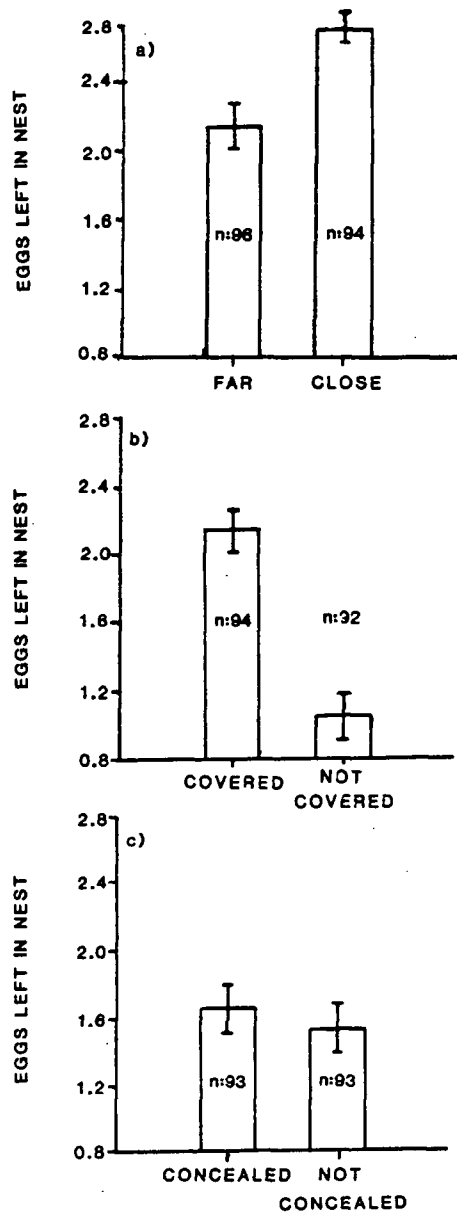
Figure 6. Comparison of the number of eggs left in artificial platforms (+SE) after 8 days in relation to a) nest location for nests with covered eggs, b) egg cover for nests far from shore and c) nest concealment for nests far from shore.

Muskrats (*Ondatra zibethicus*) were repeatedly observed eating bulrush on Eared Grebe nests, which sometimes resulted in crushed grebe eggs.

Discussion

1- Breeding habitat

General descriptions of Eared Grebe breeding habitat indicate that they nest in small productive lakes in Europe (Cramp and Simmons 1977) and mostly in medium-sized or larger lakes in North America (Palmer 1962). Previous descriptions for British Columbia show that Eared Grebes nest in marshy habitat on lakes of moderate size (Munro 1941). Habitat characteristics were not quantified in these studies.

In North Dakota, Eared Grebes prefer shallow large ponds (>19.4ha) with abundant emergent vegetation over small ponds (Faaborg 1976). I found that Eared Grebes in British Columbia also nest in shallow, productive lakes with emergent cover. However, breeding lake size varied widely. Twelve out of 27 breeding lakes were small (<10 ha). Nesting on small lakes is likely more common than previously suspected for the following reasons. First, larger lakes contain larger breeding populations and are thus more known

and easily detected than smaller lakes. Breeding records may also be biased in favor of larger lakes or concentrations of birds. Furthermore, larger lakes are used more continuously than smaller lakes.

2- Correlates of breeding group size

a) habitat size

Habitat size affects habitat selection in various ways. First, larger lakes may provide more diverse habitats than smaller lakes, and thus support more individuals (Faaborg 1976). Although I did not study this, I believe that increased habitat diversity is not important for the number of breeding pairs, because: 1) breeding pairs used similar nesting habitats on wetlands of different sizes, and 2) foraging success did not differ significantly across lakes (unpubl. data).

A second hypothesis is that larger lakes provide larger amounts of resources (food or nest sites) than smaller lakes, and that breeding abundance is resource-limited. Nest site availability is not likely limiting breeding abundance, as most breeding lakes are bordered with extensive bulrush stands. I used water conductivity as an index of food abundance and I compared adult foraging rates and foraging success on different lakes. Wetland productivity was not significantly related to breeding density, but this is not

conclusive, as productivity was not adjusted for lake size. Also, there is a hyperbolic relationship between water conductivity and wetland productivity (Northcote and Larkin 1956).

b) Habitat predictability

Extensive seasonal and annual variations in water levels were observed on all breeding lakes. On a 1m-deep lake, I found 25% decreases in water levels over a 12-month period including a "typical" summer and a low snowpack winter. Fluctuations in water levels are related to variations in water chemistry, plant growth and invertebrate food abundance (see Lancaster 1985). For Eared Grebes, this may translate into variations in food abundance and nest site availability.

Winter snow pack and summer weather have a major influence on water levels. Because both are unpredictable, distribution and quality of breeding habitat are also unpredictable. Temporary losses of nesting habitat because of fluctuations in water levels have been recognized by Palmer (1962) and Cramp and Simmons (1977). My study quantified those losses and found that 20% of the wetlands surveyed on consecutive years were not used by breeders on both years. This finding has important implications for the species management.

Larger breeding groups were found in more predictable hatitat. Nests close to shore in shallow water were used by fewer pairs than nests far from shore in deeper water. Decreases in water level would most severely affect nests located in shallower water in areas close to shore, as I observed. However, species nesting in unpredictable environments should not be highly philopatric, because prior reproductive success cannot be used to predict future prospects (Shields *et al.* 1988). Lower philopatry could result in smaller group sizes in lakes with nests located in shallower water.

Even though I cannot discard the hypothesis that low philopatry explains small breeding group sizes when nests are close to shore, I suspect that breeding group size is better explained by trade-offs between nest concealment and predation (see below).

3- Nest site location

Nest close and far from shore were found at different locations on otherwise similar lakes. Nests close to shore were found on smaller lakes, used by fewer breeders and had nests located in shallower water than lakes with nesting areas far from shore. The relationship between lake size and nest location was probably because emergent vegetation was only found close to shore on small lakes (pers. obs.). All lake sizes considered, birds nested far from shore when vegetation was available both close to and far from

shore in all but 3 cases. Those 3 cases, however, are interesting and show that lake size cannot fully account for nest location.

4- Antipredator value of nest sites

The experiment I conducted showed that, for nests with covered eggs, predation rates inherent to nest site location were lower close to shore than far from shore. On nests far from shore, covered eggs were less preyed upon than exposed eggs, while nest concealment did not appear to affect predation rates.

If predation is lowest close to shore, why are most birds nesting far from shore? I hypothesized that predation close to shore was by both mammalian and avian predators, while predation away from shore was solely by avian predators. If both predator types occur as frequently and have the same impact on nesting birds, predation would be minimized by nesting far from shore, where nests are only exposed to avian predators. I found the opposite, i.e. predation is lower close to shore than away from shore. This indicates either: 1) an effective parental defense of the nest against avian predators but not against mammalian predators (I did not measure nest attendance and nest defense) or 2) frequency of occurrence and impact of predators are different close to and far from shore.

In my study area, Somerville (1985) repeatedly observed corvids preying upon eggs. Mammalian predators such as Mink (*Mustela vison*) consume eggs and adults (Arnold and Fritzell 1987), and their impact is likely greater than avian predators preying solely upon eggs. A Mink killed 51 out of 200 Eared Grebes breeding close to shore on Westwick Lake, B.C. in 1986, while a second breeding group of the same size nesting near the center of the same lake was left untouched (Breault and Cheng 1988). The colony nesting close to shore was subsequently abandoned. I also observed coyotes (*Canis Latrans*) searching emergent vegetation close to shore. Those observations suggest that, in central B.C., mammalian predation is rarer but has more severe impact than avian predation. Because of this, large breeding groups would not benefit from nesting close to shore, as large numbers of breeders attract more predators (see Wittenberger 1985). Since larger groups are more conspicuous by nature, nesting far from shore might reduce mammalian predation on adult and eggs.

For nests far from shore, no differences were observed in rates of egg loss between concealed and exposed nests. Either 1) vegetation does not affect predation, or 2) a critical amount of emergent vegetation must be present to offer effective nest concealment.

I suggest that nest concealment is not important to Eared Grebes, for the following reasons. First, adults often nested successfully in the absence of emergent vegetation. Secondly, adults did not nest in dead vegetation, even though dense stands were available. Instead, they delayed nest building until green shoots appeared. Nest concealment could be equally provided by dead vegetation. Preference for green shoots suggests that nest sites require greater support than can be provided by dead emergent vegetation alone. Finally, parental vigilance might reduce egg predation rates by avian predators. In the course of my study, I never observed avian predators preying upon Eared Grebe eggs.

My experiment disagrees with studies that showed that nests in increased vegetative cover are less preyed upon than more exposed nests (Bider 1968, Bowman and Harris 1980, Chasko and Coates 1982, Redmond et al. 1982). In my study, accessibility of nests and impact of predators varied with vegetative cover. In wetlands, exposed nests inaccessible to predators may experience lower predation rates than concealed nests in more accessible habitats. Nest predation rates should be interpreted with respect to impact and accessibility of nests to predators.

There are probably anti-predator benefits derived from anchoring nests to emergent vegetation, but my experiment failed to document them. Different tests could be conducted to determine if vegetation

reduces nest predation. First, one could place artificial nesting platforms with and without vegetation on breeding lakes. Because artificial platforms with and without emergent vegetation provide the same nest support, the type of platforms selected by nesting pairs would indicate the importance of emergent vegetation. A different approach would consist in repeating my experiment with artificial platforms with different levels of emergent vegetation, to determine if and when nest concealment decreases predation rates on eggs.

Overall, I interpret nest site characteristics in terms of a trade-off between predation and group size. Nests close to shore are more concealed and used by fewer pairs, but are more affected by nest predation. Nests far from shore are less concealed and used by larger numbers of breeders, and they are less affected by nest predation. If nest attendance deters avian predators, nest site selection would thus act to decrease exposure to predators.

Summary

Physical and chemical characteristics of breeding lakes were studied at 27 breeding lakes and were related to number of breeding pairs. Breeding took place in shallow lakes of various sizes, subject to extensive variations in water levels. Lake size was the only significant factor related (positively) to breeding abundance. Nest sites were classified into 2 categories: nest sites close to and far from shore. Nests close to shore were associated with shallower waters, smaller lakes and fewer breeding pairs than nests far from shore. Availability of nesting areas close to shore is less predictable than far from shore, and lakes with breeding areas close to shore were less consistently used than lakes with nesting areas far from shore. For unattended nests, nest predation was higher far from shore than close to shore. If nest attendance can decrease avian predation rates, lower frequency of occurrence and lower impact of predators away from shore might explain why most birds nested far from shore. Nest site selection can thus be approached as a trade-off between breeding group size, nest concealment and nest predation, with nests close to shore maximizing concealment by nesting in small groups in dense vegetation, while nests far from shore decrease exposure to mammalian predators by nesting in large groups away from shore.

CHAPTER 4: COLONIALITY AND FACTORS AFFECTING REPRODUCTIVE SUCCESS

IN EARED GREBES COLONIES

Introduction

Nesting colonies are sites where groups of individuals or pairs nest at a more or less centralized location from which they recurrently depart in search of food (Wittenberger and Hunt 1985). Three ideas have been used to explain avian coloniality: 1) colonies form from aggregation at limited resources; 2) individuals nesting in colonies enjoy foraging benefits; and 3) colonies form to decrease predation (Alexander 1971; Krebs 1978; Wittenberger and Hunt 1985; Kharitonov and Siegel-Causey 1988).

Coloniality can result from aggregation at limiting resources such as breeding sites (Lack 1968). Nest sites are often more densely packed than required by nest site availability alone [see Coulson (1971) and Birkhead (1976) in Wittenberger and Hunt 1985], so other advantages (such as increased foraging success and lower predation) may be associated to nesting close to conspecifics.

Coloniality could enhance foraging in different ways. If food availability varies both spatially and temporally, individuals would minimize distances to foraging sites by nesting in central locations (Horn 1968). Foragers might also use colonies to obtain information on food location and abundance (Ward and Zahavi 1973). There is little evidence to support the latter hypothesis [Wittenberger and Hunt 1985, but see Brown (1986; 1988a)].

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There is extensive evidence that coloniality reduces nest predation. Colonies can 1) enhance predator detection, 2) "swamp" predators by providing spatially and temporally overabundant food supply, 3) provide communal mobbing of predators and 4) increase the probability that predators will attack other group members (from reviews in Caraco et al. 1980; Findlay and Cooke 1982; Shields 1984; Wittenberger and Hunt 1985; Brown and Hoogland 1986; Brown and Brown 1987). Finally, nest location within colonies has been shown to have an effect on predation rates (e.g. Patterson 1965; Coulson 1968; Tenaza 1971; Dexheimer and Southern 1974; Gross and McMillan 1981).

Eared Grebes are good for studying coloniality and breeding success. First, the grebe family shows a range of breeding sociality (see Palmer 1962). Secondly, Eared Grebes nest at different densities in B.C. (Chapter 2), with breeding abundance ranging from 1 pair to 590 pairs per lake in 1985 and 1986. Small breeding groups are common and constitute a non-negligible portion of the breeding population. Finally, breeding chronology varies widely from colony to colony (Munro 1941; McAllister 1956; 1958).

Because colonies are found close to one another, it can be assumed that neighbouring colonies are subject to similar pressure from predators. Differences in reproductive success across colonies

should then solely reflect differences in group size and habitat selection and not differences in predator abundance.

My results (Chapter 3) suggest that nest site availability is not limiting and that there are few foraging advantages to nesting in groups. This chapter will focus on nest predation rates and reproductive success at Eared Grebe colonies. I assume that benefits from colonial nesting are translated into higher reproductive success (and not into higher adult survival), and I investigate correlates of reproductive success. Because early-nesters often enjoy higher reproductive success than late-nesters (Lack 1968), I consider how chronology affects reproductive success. There is also evidence that percentage of successful nests increases with nesting synchrony (e.g. Darling 1938; Veen 1977; Emlen and Demong 1975; Gochfeld 1980). I also looked for this.

Components of reproductive success are used to determine which part(s) of the breeding cycle is(are) responsible for differences in reproductive success. Three hypotheses will be considered: higher reproductive success is related to 1) higher clutch size; 2) higher nest productivity; or 3) to greater post-hatching survival.

I first describe breeding chronology and breeding success. Then I investigate relationships between breeding success and: 1) nesting chronology, 2) nesting synchrony and 3) colony size. I then use a

multivariate approach to determine the relative importance of these 3 influences on reproductive success. Finally, I use observations on marked individuals to discuss colony selection in Eared Grebes. Pairs breeding alone are referred to as colonies of 1 pair.

Methods

1- Study site

Breeding phenology was studied at Riske-Creek, B.C. The study area covered roughly 10 km^2. The area is part of the Cariboo-Aspen-Lodgepole Pine-Douglas Fir Parkland biogeoclimatic Zone of Krajiina (1969; 1973), and consists of rolling savannah upland dominated by *Agropyron spicatum* and stands of *Populus tremuloides* and *Pinus contorta* (Cannings and Scudder 1978). The area is also under the influence of the rainshadow effect of the Coast Mountains (Beil 1974).

My study area included 10 lakes used by breeding Eared Grebes in 1985 and 9 lakes in 1986. Lakes ranged in size from 0.7 to 27.2 ha, and were used by 1 to 81 pairs per lake. Together they accounted for approximately 200 nesting pairs each year.

2- Surveys

In both 1985 and 1986, shore counts of adults and young were conducted every 2 to 4 days from late April to early August. Nesting areas were searched every 4 days, starting when adults were repeatedly seen carrying vegetation in their bills. Nesting areas were mapped during each visit except on the lake used by 81 pairs in 1985, where too much disturbance would have been caused by long visits to the nesting area. Visits to nests stopped after all eggs had hatched or when adults stopped visiting the nesting area. Eggs were individually marked with permanent felt markers, and their presence was recorded at each visit.

3- Colony size

Colony size was defined as the maximum number of active nests observed simultaneously during a breeding season. On most colonies, maximum active nest count agreed exactly with half the maximum number of adults surveyed throughout the summer.

4- Reproductive biology

Nesting chronology, nesting synchrony, clutch size and reproductive performance were measured in 1985 and 1986. Laying date was derived from the number of eggs at the nest and shell

color. Laying interval between consecutive eggs is roughly 1 day, and average clutch size is 3.48 eggs (McAllister 1958). Visits every 4 days were therefore sufficient to estimate laying by back-dating one day for each egg present in the nest. Sequences of laying were determined from egg color. Fresh eggs are pale blue and become quickly stained by nesting material as they get older (McAllister 1958; Palmer 1962).

I calculated laying dates for both first and all nesting attempts. Date of initiation of first and all laying attempts were respectively obtained by averaging initiation dates of the first (n) nests in a colony [where (n) is the number of pairs breeding in the colony] and of all nesting attempts recorded during a breeding season. Comparisons between first and all nesting attempts were used to assess frequency of nest losses and renesting in colonies.

Nesting synchrony was defined as the Standard Deviation (SD) of 'the mean laying date of first nesting attempts in a colony.

For each colony, I measured individual reproductive performance (clutch size and number of young hatched per successful nest) and determined the number of successful nests and young fledged per colony. Fledging success could not be measured for individual pairs, because chicks are carried under the parent's wings for their

first 3 weeks (van Ijzendoorn 1944 in Palmer 1962) and forage independently past that age (Palmer 1962, Cramp and Simmons 1976).

Clutch size was defined as the highest number of marked eggs (see Chapter 2 for details) observed on 3 consecutive visits. Egg hatchability was determined from clutch survival. For calculations, disappearances of clutches were presumed to happen halfway between visits. Although Eared Grebes incubate for 20 to 21.5 days (McAllister 1956), a nest was presumed to have hatched if at least one egg survived a minimum of 19 days. The difference (i.e. 1-2 days) aimed at compensating for potential errors in estimating egg age and egg survival.

The proportion of nests that successfully hatched eggs per colony was calculated by dividing the number of nests where at least one egg was hatched by colony size. The number of young hatched per pair was defined as the number of eggs present at the last visit prior to the expected hatching date minus the number of unhatched eggs observed past it.

Fledging success was estimated from chick surveys. For each colony, fledging success was defined as the maximum number of young more than 1 month old observed throughout the breeding season divided by colony size. Because chicks become fully independent from their parents at 3 weeks of age (Palmer 1962), fledging success

could not be measured for individual pairs. I used linear regressions to determine the relationship between number of young hatched and number of young fledged.

Differences across years for any of those parameters were studied with either Kruskal-Wallis analyses or t-tests.

5- Correlates of reproductive success

I used separate analyses to relate reproductive performance (clutch size, number of young hatched per successful nest, ratio of successful nest per pair and number of young fledged per pair) to 1) nesting chronology, 2) nesting synchrony and 3) colony size. Depending on the analyses, I used either observations from individual nests or mean values per colony. All variables or their log-transformations were normally distributed, except for clutch size in 1985 and 1986; mean clutch initiation date in 1986 and nesting synchrony in 1985. The ratio of successful nests per pair was arcsine-transformed.

I used Kruskal-Wallis tests for the analyses involving non-normally-distributed variables. Analyses of variance and/or linear regressions were used with the remaining analyses.

6- Multiple stepwise regression on reproductive success

A multiple stepwise regression analysis was used to ascertain the relative importance of breeding chronology, nesting synchrony and colony size on the number of young fledged per colony. All values were normalized, except for clutch initiation date in .1986 and nesting synchrony in 1985, which were considered normally-distributed for the purpose of the analysis. Separate analyses were conducted for 1985 and 1986. Analyses were conducted for both first nesting attempts and overall nesting attempts.

7- Individual quality across colonies

I captured (Breault and Cheng in press) and used colored nasal discs on 69 adult Eared Grebes in 1985 and 1986. Surveys conducted in 1985, 1986 and 1987 were used to determine the location, breeding status and breeding success of 54 individuals observed after banding and on subsequent years (n=14 adults). I used a Chi-Square test to determine whether previous breeding success affected adult return and also determined whether adults returned to the colony they were banded on or moved to other colonies.

Results

1- Reproductive biology

A) Nesting chronology

Small numbers of birds were present on breeding lakes when field work started in April 1985 and 1986, but most birds arrived in May (Figure 7). Nests were first observed on 27 May in both 1985 and 1986 (Figure 8), but first nesting attempts began later in 1986 than 1985 [medians respectively 6 July (n=139) and 7 June (n=184)] (Kruskal-Wallis test, p<0.01). The shape of the distributions was also different across years. Median dates of clutch initiation for all nesting attempts were respectively 12 June in 1985 (n=341 nests) and 30 June in 1986 (n=195), 1986 being significantly later (Kruskal-Wallis test, p<0.01).

Adults departed from nesting lakes from mid-July on (Fig. 7), but departures were most apparent in August. Adults departed separately from young. Non-breeders and unsuccessful breeders left nesting lakes at an earlier date. Whether adults stayed in the area or migrated southwards is unknown.

B) Clutch size

Mean clutch size was 3.14 $\pm$0.06 eggs per nest in 1985 (n=191 nests) and was significantly smaller (p<0.01, Kruskal-Wallis test)
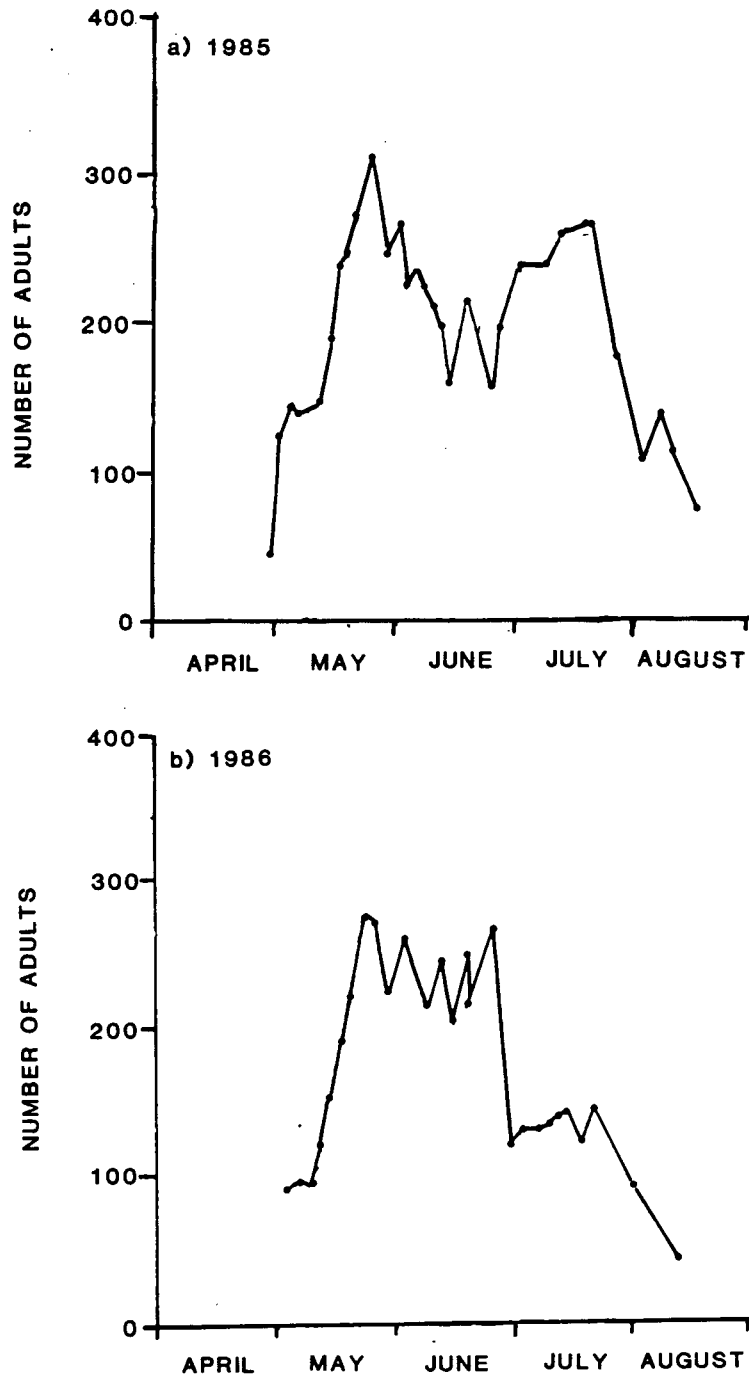
Figure 7. Adults surveys on breeding lakes in the Riske Creek area in 1985 and 1986.
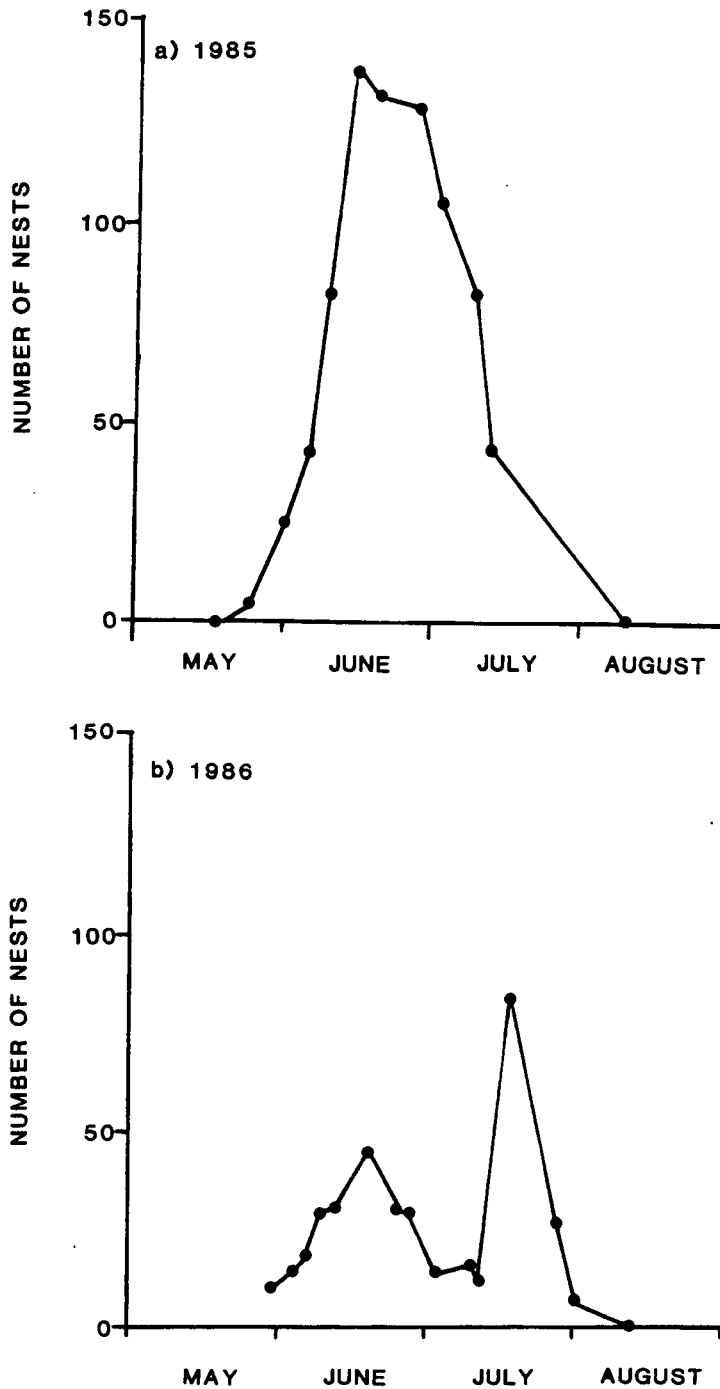
Figure 8. Date of clutch initiation for all nesting attempts in the Riske-Creek area in 1985 and 1986.

than in 1986 (3.31 ±0.06, n=99 nests).

C) Hatching success

Fewer young hatched per successful nest in 1985 (2.84 ±0.08, n=152 nests) than in 1986 (3.07 ±0.11, n=46 nests), but the difference between years was not significant (Kruskal-Wallis test, p=0.08).

D) Fledging success

The number of young fledged per pair in 1985 (1.09 ± 0.04, n=187 nests) was significantly higher than in 1986 (0.53 ± 0.06, n=139 nests) (t-test, p<0.01). Fledging success was highly correlated with number of young hatched in both 1985 (r^2=0.99, n=7, p<0.01) and 1986 (r^2=0.77, n=6, p=0.01) (Fig. 9). About 47% of eggs hatched survived to fledging (slope on Fig. 9) on both 1985 and 1986, but there was much more variation in 1986.

2- Univariate analyses of factors affecting reproductive success

A) Breeding chronology

Earlier clutches were significantly larger than late clutches in 1985 (Kruskal-Wallis test, n=191, p=0.02) (Fig. 10a), but not in 1986 (Kruskal-Wallis test, n=99, p=0.13) (Fig. 11a). The number of nests successfully hatching eggs per pair was inversely correlated with mean date·of first clutch initiation in 1985 (r^2=0.40, n=10,

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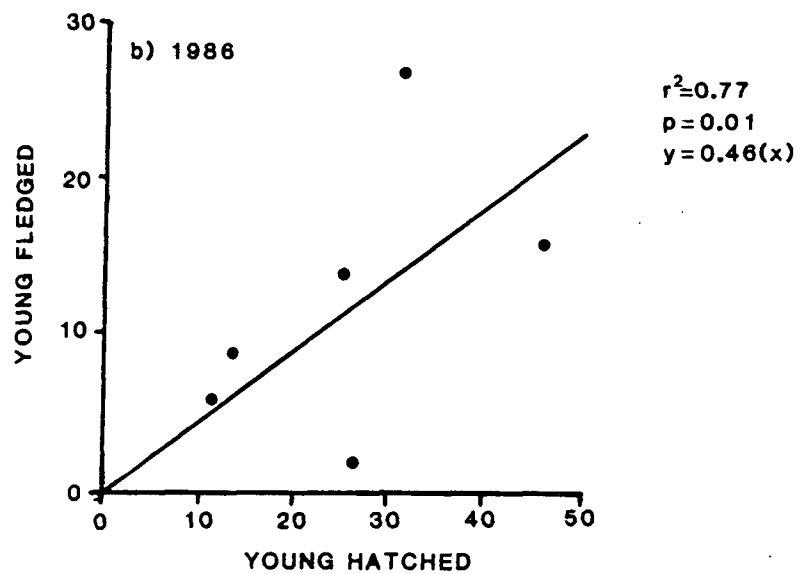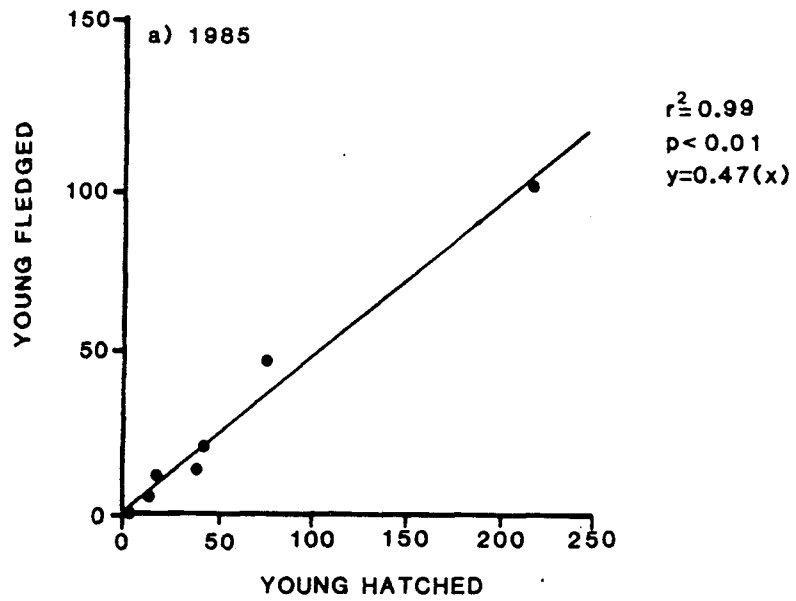
Figure 9. Correlation between number of young hatched and number of young fledged in 1985 and 1986.
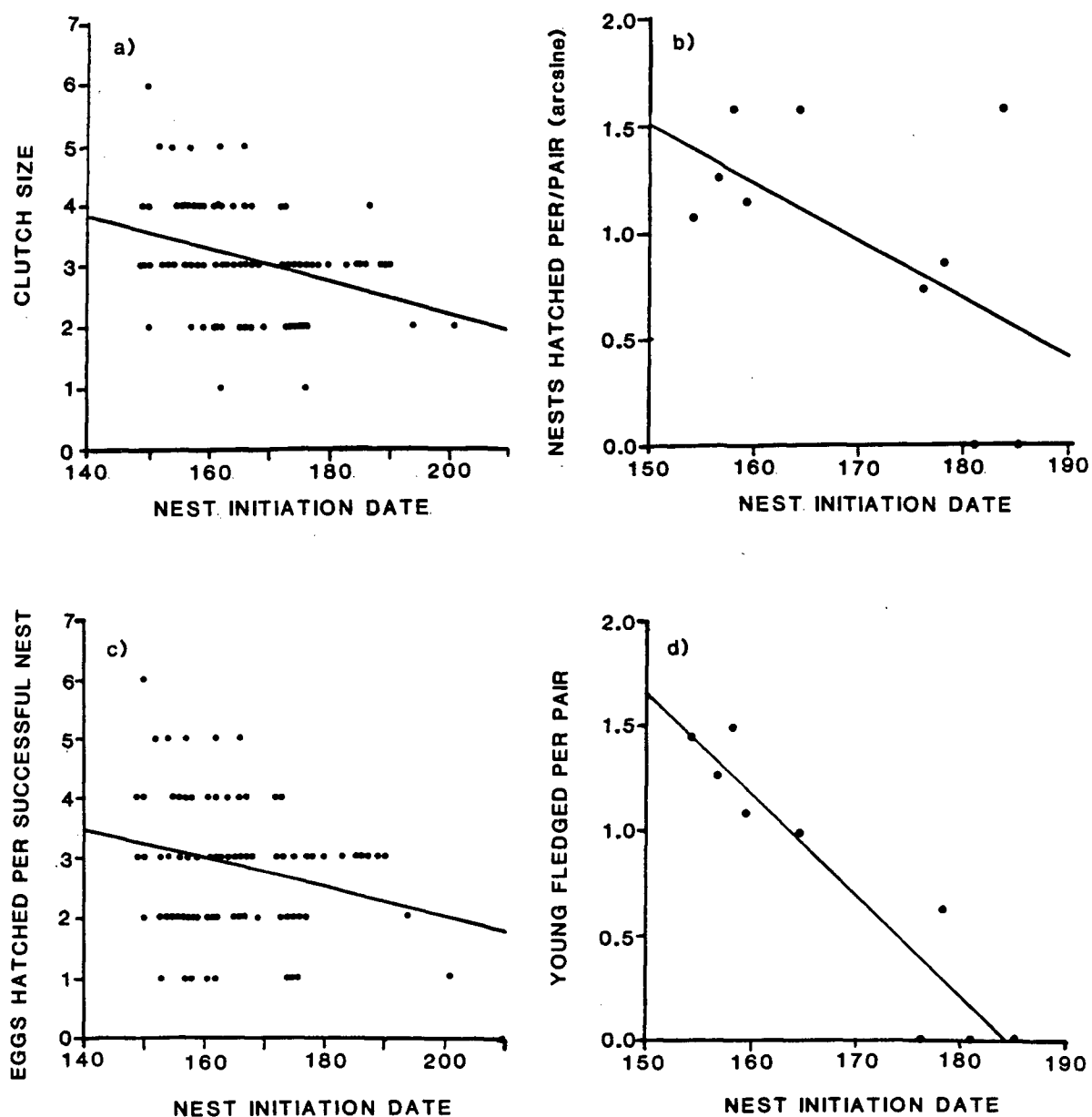
Figure 10. Relationships between clutch initiation date and a) clutch size, b) number of nests hatched per pair, c) number of eggs hatched per successful nest and d) number of young fledged per pair in 1985.
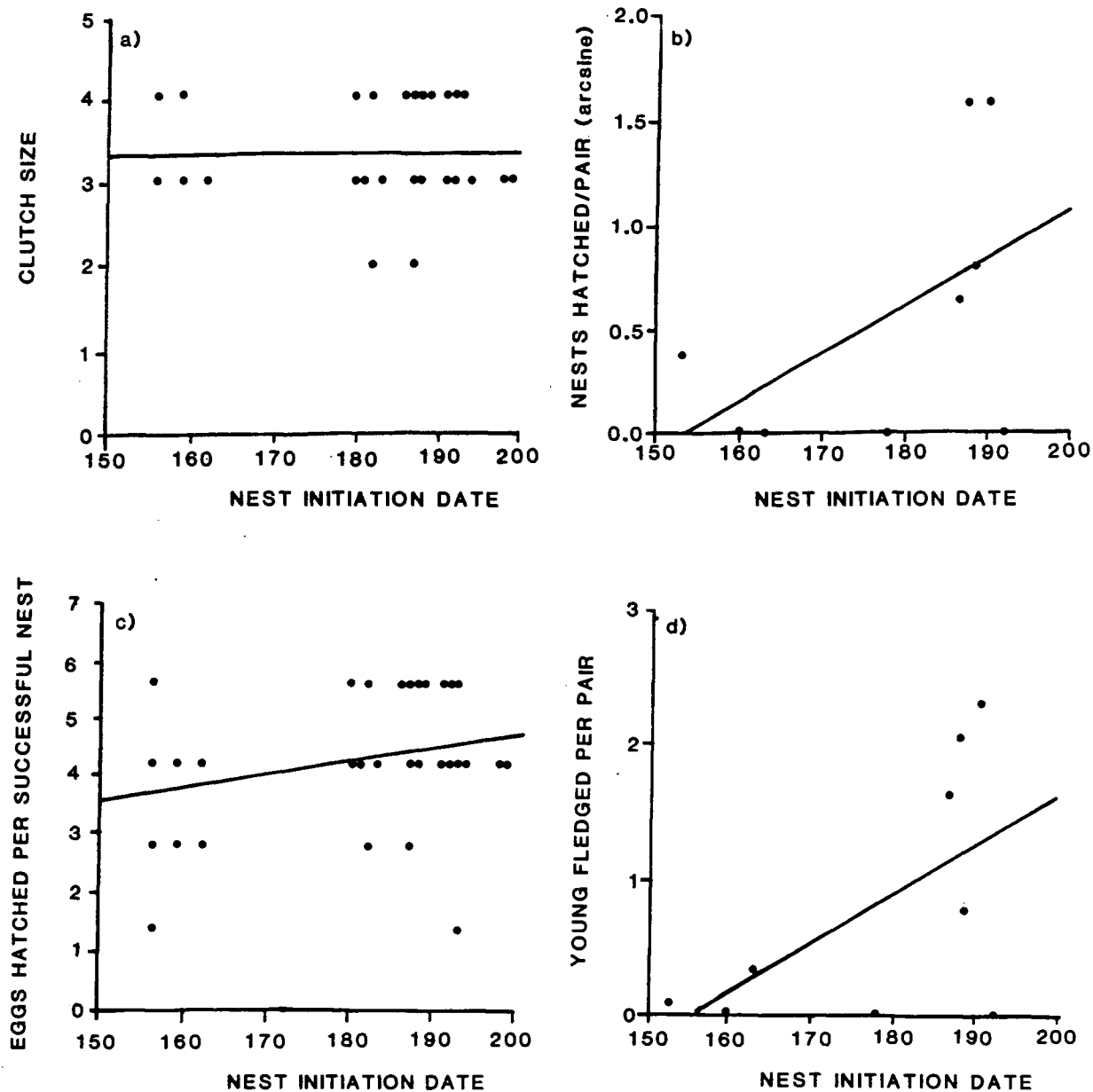
Figure 11. Relationships between clutch initiation date and a) clutch size, b) number of nests hatched per pair, c) number of eggs hatched per successful nest and d) number of young fledged per pair in 1986.

p=0.05) (Fig. 10b), but not in 1986 (r^2=.27, n=9, p=0.16) (Fig. 11b). The number of young hatched per successful nest did not vary significantly with mean clutch initiation date of successful nests in 1985 (Kruskal-Wallis test, n=152, p=0.15) (Fig. 10c) and 1986 (Kruskal-Wallis test, n=46, p=0.80) (Fig. 11c). Early nests fledged significantly more young per pair than late nests in 1985 (r^2=.90, p<0.00) (Fig. 10d), but not in 1986 (Kruskal-Wallis test, p=0.43) (Fig. 11d).

B) Synchrony

No significant relationships were observed between nesting synchrony and clutch size in 1985 (Kruskal-Wallis test, n=8, p=0.43) and 1986 (r_2=.55, n=7, p=0.06), even though higher synchrony appeared to be correlated with larger clutches in 1986. There were no differences between nesting synchrony and 1) the number of nests hatched per pair in 1985 (Kruskal-Wallis test, n=9, p=0.43) and 1986 (r^2=0.16, n=8, p=0.33); 2) the number of young hatched per successful nest in 1985 (Kruskal-Wallis test, n=7, p=0.42) and 1986 (r^2=0.13, n=5, p=0.56) and 3) the number of young fledged per pair in 1985 (Kruskal-Wallis test, n=9, p=0.43) and 1986 (r^2=0.08, n=8, p=0.51).

C) Colony size

Clutch size was significantly smaller in nests from smaller colonies than in larger ones in 1985 (Kruskal-Wallis test, n=191,

p<0.01) (Fig. 12a) but not significantly so in 1986 (Kruskal-Wallis test, n=99, p=0.09) (Fig. 13a). The distribution of laying dates was different across colony sizes. There were no relationships between colony size and 1) the number of nests successfully hatched per pair in 1985 ($r^2=0.05$, n=10, p=0.53) (Fig. 12b) and 1986 ($r^2=0.00$, n=9, p=0.97) (Fig. 13b); 2) the number of young hatched per successful nest in 1985 ($r^2=0.00$, n=7, p=0.95) (Fig. 12c) and 1986 ($r^2=0.57$, n=5, p=0.14) (Fig. 13c); and 3) fledging success per pair in 1986 ($r^2=0.02$, n=9, p=0.75) (Fig. 13d). Fledging success per pair in 1985 was positively correlated to colony size ($r^2=0.56$, n=10, p=0.01) (Fig. 12d).

3- Multiple stepwise regression on fledging success

Mean clutch initiation date was the only predictor of fledging success in 1985 ($r^2=0.89$, n=9, p<0.01), and no significant predictors were found for the 1986 data.

4- Individual quality across colonies

Of the 54 marked individuals for which sufficient data was available, adults that had a brood on the previous year were more likely to return (6 of 14) than adults without broods (8 of 46) ($X^2=3.85$, p<0.05). Marked individuals were repeatedly observed on the same breeding lakes prior to onset of laying, indicating that

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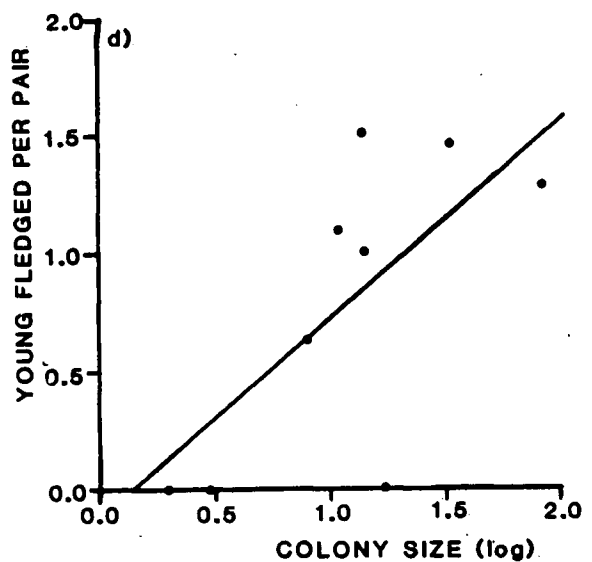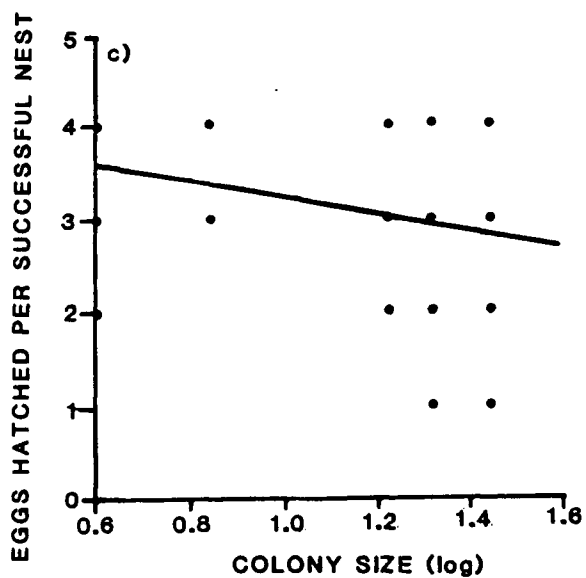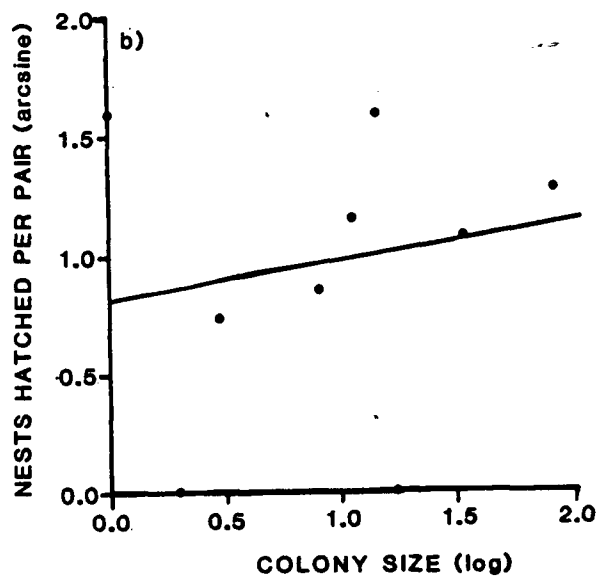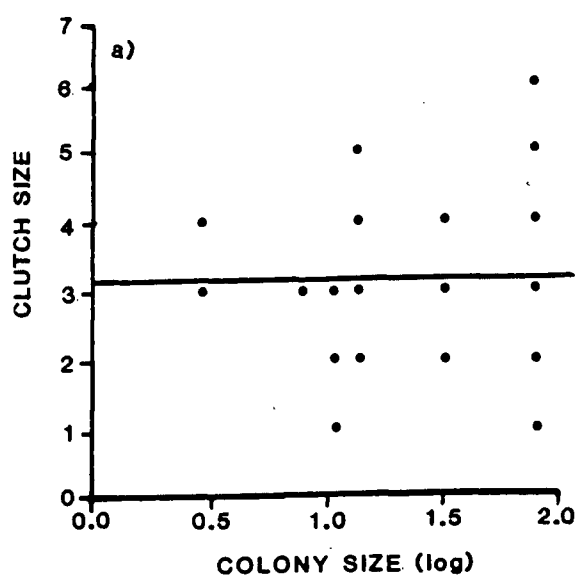
Figure 12. Correlation between colony size and a) clutch size, b) number of nests hatched per pair, c) number of eggs hatched per successful nest and d) number of young fledged per pair in 1985.

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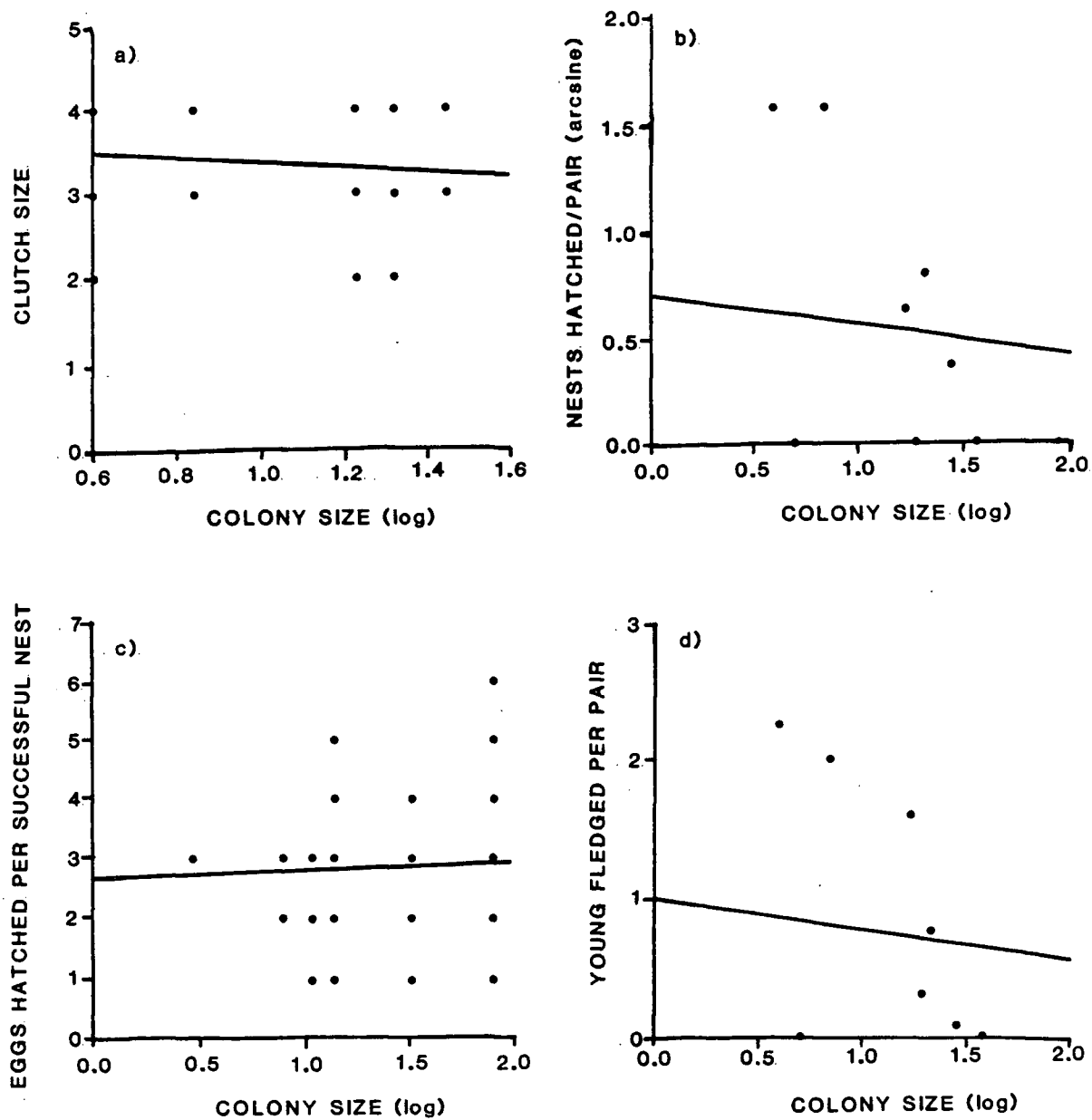
Figure 13. Correlation between colony size and a) clutch size, b) number of nests hatched per pair, c) number of eggs hatched per successful nest and d) number of young fledged per pair in 1986.

late-breeders are not birds attempting renesting. Six of the birds caught in colonies of more than 25 pairs returned to the same colony, while 7 individuals caught in smaller colonies moved to larger colonies on subsequent years, even though the colonies where they were originally banded were still active. One individual moved repeatedly between lakes. No birds moved to smaller colonies.

Discussion

1- Breeding chronology

Extensive variations in breeding chronology have been reported across North America. Clutches are laid from late April on in the southern third of the U.S.; from early May well into June in the northern U.S.; and well into June in Canada (Palmer 1962). In Washington State, nesting begins in mid-May and the bulk of the nests are started near 1 June (Yocom et al. 1958). In British Columbia, clutches were begun on 27 June in 1955; 22 June in 1956 (McAllister 1956); on 20 May 1941; and on 16 July 1940 (Munro 1941). Breeding chronology in central British Columbia fit with the data available for Washington State and B.C., with nests initiated from 27 May on in 1985 and 1986, and median first clutch initiation date of 7 June in 1985 and 6 July in 1986. However, laying was observed

into August in both 1985 and 1986 (Fig. 8), later than reported elsewhere.

2- Reproductive success

Proportionally fewer renesting attempts were initiated in 1986 than in 1985. Clutch sizes from both years are still smaller than the 3.48 eggs per nest reported by McAllister (1958). This might be because clutch size can vary with colony size, and McAllister studied colonies larger than the ones used in this study. Other possible explanations include differences in breeding chronology, in the number of renesting attempts or differences in nest parasitism.

No quantitative information on breeding success is available for the Western Palearctic (Cramp and Simmons 1977). Of 223 eggs laid in South Africa, only 12 young left the nest (Broekhuisen and Frost 1968b). In North America, accounts of reproductive success consist of estimates of young per adult during the breeding season. Yocom *et al.* (1958) estimated roughly one young per adult in late July in Washington State colonies. Munro (1941) presented young counts at selected lakes throughout the summer, but young were not aged, so it is difficult to assess the number of young surviving to fledging. Young counts do not however indicate true reproductive success, because they do not consider failed breeding attempts. My

study appears to be the first one quantifying both reproductive failure and reproductive success in Eared Grebe colonies.

My study could not find consistent differences in nest productivity across colonies. However, differences in the number of nests hatched per pair suggest that nest predation is the major factor affecting differences in reproductive success. Some of that difference could be due to differences in nest site selection (see Chap. 3). Although nest predation can be reduced through communal mobbing (Gotmark and Andersson 1984), I could not find any field or published evidence of communal mobbing in Eared Grebes. I suggest that differences in nesting habitat are responsible for differences in nest predation rates.

3- Coloniality and factors affecting reproductive success

A) Effects of colony size

This study did not support the hypothesis that group size affects reproductive success. Reproductive success is only higher for colonial than for solitary birds in species with communal defense (Andersson and Wiklund 1978; Wiklund and Andersson 1980; Gotmark and Andersson 1984). My results showed that reproductive success increased with colony size in 1985, but there is no evidence from field observations or from the literature that communal mobbing takes place in Eared Grebes.

B) Multivariate approach to reproductive success

Because of effects of both colony size and chronology on nesting success, I used a multiple stepwise regression to show that only clutch initiation date accounted for variations in nesting success. Early nesters did better than late ones, irrespective of colony size. Overall, laying took place roughly 2 weeks later than in 1985 than in 1985, and there was a trend for late nesters in 1986 to do better than early nesters. This seems to indicate that benefits of early nesting are not consistent across years.

Even though differences in reproductive success have been associated with breeding chronology (Burger 1979; Spaans *et al.* 1987), only one study has considered chronology effects on reproductive success across colonies (Haas 1985). Haas argued that colony size has different effects on nesting success with changes in environmental conditions (e.g. vegetative cover). Early broods benefit only from colony size, while late broods are affected by both differences in vegetative cover and predator behavior.

Comparative studies of coloniality should test for effects of chronology, synchrony and group size on nesting success. Absence of correlations between group size and reproductive success in other studies might be explained by differences in nesting chronology (Haas 1985). For example, swallows have been shown to have

extensive variations in nesting chronology and nesting success (Snapp 1976; Brown and Brown 1987; Møller 1987). The study by Emlen and Demong (1975) on the relationship between synchrony and reproductive success could have not taken into consideration correlations between chronology and synchrony. This raises the possibility that many studies on benefits of group size could have been biased by effects of chronology or synchrony.

C) Anti-predator benefits of coloniality

Different mechanisms have been proposed to explain how colonial nesting could decrease predation rates. Colonies could enhance predator detection (e.g. Pulliam 1973; Hoogland and Sherman 1976; Hoogland 1979; Caraco *et al.* 1980; Brown and Brown 1987); predators could be "swamped" by spatially and temporally overabundant food supply (Kruuk 1964; Nisbet 1975; Findlay and Cooke 1982); colonies could be defended through communal mobbing (e.g. Kruuk 1964; Lubcke 1975; Hoogland and Sherman 1976; Andersson and Wiklund 1978; Shields 1984); groups could form to dilute predation (Hamilton 1971; Burger 1979); or to avoid peak of predator activity (Wittenberger and Hunt 1985). Although my study did not explicitly consider any of those mechanisms, I will use incidental observations to discuss them.

Eared Grebes colonies might benefit from increased predator detection in 2 ways: because of increased group size (more eyes to detect predators), and because less dense vegetation in larger

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colonies (away from shore) makes predators more visible. Increased group size and increased predator visibility may both play a role in increasing predator detection. I do not believe that predator swamping or dilution effect occurs in Eared Grebe colonies, as predation can result in large egg losses (see Somerville 1985) or adult casualties (Breault *et al.* 1988). Mobbing behaviour was not observed in my study, and there is no published evidence that it occurs. Peaks of predator activity might not avoided by nesting early. I observed higher nest losses early in the season than late, and work done in the Riske-Creek area by Somerville (1985) also indicated lower predation rates for late nesters. I suggest that anti-predator benefits of coloniality in Eared Grebes are mostly related to increased predator detection.

Some predictions from the anti-predator hypothesis were not supported. The number of nests hatched per pair and the number of young hatched per successful nest did not increase with group size nor with nesting synchrony. The absence of documented anti-predation benefits of colony size might have been caused by the low number of colonies investigated. Data collected on nest predation rates in various nesting habitats (see chapter 3) suggested anti-predation benefits from nesting in large groups, but I was unable to document those benefits.

D) Net benefits of early nesting

Early nesters enjoyed higher reproductive success than late nesters. If there are reproductive benefits to be gained from nesting early, why nest late? Three factors could produce late nesters: habitat differences, renesting attempts and variations in individual quality (such as age or previous breeding experience).

Habitat differences could cause differences in food availability and distribution across breeding lakes and affect breeding chronology. Eared Grebe breeding lakes in the Peace River region could be used to study the effect of habitat differences, as colonies of different sizes are found on some lakes. The breeding synchrony observed among colonies on the same lake (colonies sharing the same resources) indicates that breeding chronology is likely to be a function of habitat. Conversely, differences in nesting chronology between colonies suggest variations in individual quality. That study has not yet been conducted.

E) Individual quality in different colonies

Differences in bird quality across colonies could explain differences in breeding chronology and colony composition (Veen 1977). Observations on marked adults indicated that late breeders were not birds attempting renesting. Only birds from large colonies stayed in the colonies where they were originally banded, while birds from smaller colonies moved to larger ones. This suggests age-

related differences between colonies of different sizes. Banding returns were insufficient to consider effects of previous breeding experience and reproductive success on colony selection. Further adult and young marking is needed to understand qualitative differences across colonies.

Summary

Adults arrived to nesting lakes in April and May in 1985 and 1986; started nesting on 27 May on both years and most departed from nesting lakes in July and August. Median clutch initiation date was later in 1986. Number of young fledged per pair declined with laying date in 1985, but tended to increase with laying date in 1986. Number of young fledged per pair increased with colony size in 1985. Nest predation was the major cause of nest losses. Number of young fledged per pair was positively correlated with the number of eggs hatched.

In a multiple stepwise regression, only nesting chronology correlated with differences in reproductive performance, with early nesters enjoying higher reproductive success. I discuss 3 hypotheses to explain the presence of late nesters: late nesters are 1) adjusted to local resource availability; 2) birds attempting renesting and 3) individuals that cannot nest early. Observations on marked adults showed that late nesters were not renesters, but were consistent with qualitative differences related to age across colonies.

CHAPTER 5: GENERAL DISCUSSION

In this thesis, I describe breeding biology and coloniality of Eared Grebes nesting in British Columbia. I discuss findings in 5 sections: 1) breeding biology; 2) habitat predictability; 3) models of coloniality; 4) nesting chronology and synchrony and 5) conservation and management.

1- Breeding biology of Eared Grebes

This section summarizes information on breeding distribution, abundance, and breeding biology of Eared Grebes in British Columbia.

A) Distribution and abundance

My surveys located 1761-4474 breeding pairs distributed over 47 lakes in B.C. Breeders were concentrated in the central Interior and the Peace River regions, with the Southern Interior and Northern Okanagan/Kamloops regions supporting substantially smaller breeding populations. Breeding abundance ranged from 1 to roughly 500 pairs per lake and was positively correlated to lake size. This is probably because larger lakes provide more abundant or different resources (Faaborg 1976) than smaller ones.

My study on distribution and abundance of Eared Grebes (Breault *et al.* 1988) constitutes a baseline against which future fluctuations in breeding abundance can be measured. However,

because I surveyed only 421 wetlands, further surveys are necessary to characterize status and abundance of regional populations. Surveying should focus on the Central and Southern Interior regions, which were least surveyed. These 2 regions include the highest number of productive wetlands in British Columbia (Canadian Land Use survey map, Environment Canada). Most suitable wetlands found in the Peace River and Northern Okanagan/Kamloops regions were surveyed and/or monitored by Ducks Unlimited, so further surveys should not be conducted in those areas.

B) Nesting habitat

Nesting took place on shallow, highly productive lakes of various sizes. Most nests were anchored to emergent vegetation, presumably because of increased support and resistance to wave action (Broekhuisen and Frost 1968b). Two types of nest sites were observed: nests close to shore and nests far from shore. Nests close to shore were located in shallower water and associated with smaller, shallower lakes than nests far from shore.

Nesting lakes were subject to extensive seasonal and annual environmental changes. Water levels decreased by roughly 25% between 1985 and 1986, perhaps affecting food abundance and definitely affecting availability of nesting habitat. Environmental changes have been linked to shifts of colony location across years (Werschkul 1979, Pratt and Winkler 1985). In Eared Grebes, 20% of

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breeding lakes surveyed on 2 consecutive years (n=25) were not used on both years. All lakes not used on consecutive years had nesting areas located in shallow water near shore, where nest sites are subject to the most extreme variations in water levels.

My data suggest that Eared Grebes use 2 types of breeding lakes: isolated lakes supporting large breeding populations (not extensively studied in this work) and areas with a high density of smaller lakes supporting smaller breeding populations (e.g. Riske-Creek area). Large lakes appeared able to buffer environmental variations and Eared Grebes using them probably show high philopatry (see below). Habitat variability has a more severe impact on smaller breeding lakes, and grebes nesting there are likely less philopatric. Differences in breeding biology and reproductive success between large lakes and small wetland systems remain to be documented.

2- Importance of habitat predictability

Many authors have discussed the importance of habitat variability and predictability on colonial nesting, mostly with respect to resource distribution and social foraging (see Wittenberger and Hunt 1985; Kharitonov and Siegel-Causey 1988). I believe that habitat predictability is also important at a deeper

level, and I will discuss its implications for distribution and philopatry in Eared Grebes.

A) Distribution

Habitat predictability can affect distribution in different ways. First, it directly affects habitat availability. In Eared Grebes, lakes subject to higher decreases in water levels were less consistently used than less affected lakes. Indirect effects could also take place. As suitable habitat size decreases, species become locally extinct (Pielou 1979). For Eared Grebes, this would translate into small populations or populations using small habitats running greater risks of becoming locally extinct. Small isolated populations should be rare, as small local populations would become extinct faster than large populations. I rarely observed isolated small colonies of Eared Grebes, even though groups of small connected colonies were repeatedly observed. Large isolated colonies (used by hundreds of breeding pairs) were repeatedly observed.

B) Philopatry

Philopatry should increase with habitat predictability. Species with predictable nest sites (e.g. swallows, terns, gulls, herons, marine birds) are highly philopatric (Wittenberger and Hunt 1985). Conversely, if nest sites are not predictable, there should be low philopatry to nesting areas. This suggests that, within

populations, gradients in nest site predictability are correlated to gradients in philopatry, which is supported by my observations on marked individuals.

Low philopatry could influence community structure, which could in turn influence reproductive success and breeding chronology. Colonies formed of exclusively young birds would likely nest later and experience lower reproductive success than colonies made of older birds. This could occur if breeding adults group themselves based on their readiness to lay, where age would be correlated with readiness to lay. There is evidence that breeding chronology varies with age (see Coulson and White 1960). Anti-predator and foraging benefits would likely favor highly synchronized nesting, with late nesters subject to more resource depletion. Extensive adult movements prior to nesting might have resulted in adult grouping based on body condition or some other qualitative factor.

3- Coloniality in Eared Grebes

I observed both colonial and solitary nesting in Eared Grebes, with colonies ranging in size from 1 to 343 pairs. Many lakes (mostly in the Peace River and Central Interior regions) supported more than 1 colony.

Although evolutionary causes of coloniality in Eared Grebes are unknown, current factors maintaining it can be studied. I compared reproductive success in a dense group of colonies in the Central Interior to assess current reproductive benefits of coloniality. As mentioned earlier, 3 groups of hypotheses have been proposed to explain the evolution of colonial nesting in birds: 1) colonies arise from clumping at limiting resources, 2) colonies increase the efficiency in obtaining resources and 3) colonies help decrease predation (Alexander 1974; Wittenberger and Hunt 1985). Those 3 hypotheses will be discussed with respect to my data.

A) Resource limitation hypothesis

Birds might aggregate to take advantage of limiting resources such as nest sites (Wittenberger and Hunt 1985). The nest site limitation hypothesis is partially supported by the fact that breeding abundance was positively correlated with lake size, but such a relationship cannot by itself explain why nests are aggregated at colonies as opposed to being uniformly or randomly distributed over the breeding area. I interpret the lack of relationships between lake characteristics (other than nest site location ones) and breeding abundance as indicating that breeding lakes are of similar nature. The difference in nest site selection on otherwise similar lakes, combined with a significantly different number of breeders at each type of nest site also support the resource limitation hypothesis.

Nest sites do not, however, appear to be limiting. Although not quantitatively studied, emergent vegetation was very abundant on most lakes, and could probably have supported more breeding pairs than observed. Colonies also regularly moved to new areas after nest failure, and pairs often successfully hatched eggs at the new location. If nest sites are limiting, relocation should not take place, or reproductive success at new sites should be low because adults settled down in suboptimal habitat. I suggest that nest site limitation cannot explain colonial nesting in Eared Grebes.

B) Foraging benefits

A second hypothesis is that colonies can evolve if individuals gain foraging benefits from being in groups. Foraging gains could arise from individuals independently taking advantage of food distribution and predictability (Horn 1968) or from transfer of information about foraging areas at colonies (Ward and Zahavi 1965).

Neither argument is likely to apply to Eared Grebes. Horn's geometrical model assumes a cost for getting to and from patchy food. Eared Grebes forage solely on breeding lakes (pers. obs.), and foraging costs are probably low on most/all lakes. On regularly-shaped lakes, information transfer could take place in the absence of nesting colonies: nests evenly distributed on the lake edge would allow direct observation of foragers anywhere on the

lake. Further, Eared Grebes forage independently from one another (pers. obs.), while one would expect aggregation at good food patched in the presence of information transfer. I conclude from those observations that there are no foraging benefits of coloniality in Eared Grebes.

C) Anti-predation benefits

Nest predation is a primary cause of nesting mortality in many bird species (Ricklefs 1969; Somerville 1985). My study showed that most of the variation in reproductive success across colonies occurred during incubation, showing the importance of predation at nest. Nest site location influenced nest predation rates. Attended artificial nests close to shore were subject to more predation than attended artificial nests far from shore, but predation rates on unattended nests were higher far from shore than close to shore. This suggests that attendance at nest or nest defense plays an important role on nest predation rates, and that attendance at nest was more effective on nests far from shore than on nests close to shore. My experiment could not fully account for effects of group size on nest defense, even though it was observed that nesting areas close to shore were used by fewer pairs than nesting areas far from shore.

Avian predators (e.g. corvids, hawks, eagles) are common in my study area (Somerville 1985; pers. obs.), but nest defense or

mobbing might be effective against them. However, mobbing or nest defense by Eared Grebes have not been reported in the literature. On the other hand, mammalian predators (e.g. Mink, Coyote) are usually found at much lower densities than avian predators, but their impact is more severe and they cannot be fended off. Because of easier access to nests, impact of mammalian predation should be most severe close to shore. This could explain why nests were more concealed close to shore than far from shore. Nest site location can be considered in terms of trade offs between group size, nest concealment, and exposure to predators. Larger groups might use exposed sites (because concealment would be ineffective) where exposure to predators is reduced. Smaller breeding groups, using sites more accessible to predators, would opt for maximum nest concealment.

4- Breeding chronology and synchrony

On a year with normal (i.e. non-drought) conditions (i.e. 1985), reproductive success was higher for individuals nesting early. If nesting early increases reproductive success, why nest late? I considered 3 hypotheses: late nesters are 1) taking advantage of local habitat; 2) renesting birds from different colonies and 3) birds that cannot nest early (because of body condition, age or previous breeding experience).

Earlier breeding has been reported in older Kittiwakes (Rissa tridactyla) (Coulson and White 1958; 1960; 1968). Late-nesting young Kittiwakes and Shags (*Phalacrocorax aristotelis*) experienced lower reproductive success than old individuals (Coulson and White 1956, 1960, Snow 1960), while experienced gull pairs are more successful than newly established pairs (Coulson 1966, Mills 1973). Veen (1977) suggested that birds seek out pairs that are at a similar reproductive state. Colonies could breed late because they contain a large proportion of young birds with little breeding experience (Coulson and White 1960).

Breeding chronology could also be affected by resource distribution. Separating effects of age and resource distribution on breeding chronology could be accomplished by comparing chronology in colonies sharing similar resources. In Eared Grebes, this could be accomplished by studying lakes in the Peace River region, which supports multiple nesting colonies. Because colonies on a given lake share the same set of resources, the resource distribution hypothesis predicts synchronized nesting across colonies, while the individual quality hypothesis predicts non-synchronized nesting across colonies. The study remains to be conducted.

Synchronization within colonies can increase individual fitness by reducing the period for which vulnerable prey items are available to predators (Evans 1982). Higher synchrony within colonies than

across colonies has been demonstrated in Bank Swallows (Emlen and Demong 1975), and there is evidence of additional synchrony in neighbourhoods within colonies (Hoogland and Sherman 1976).

Anti-predator benefits of within-colony synchrony might not be detectable if predation is seasonal and nesting is not synchronized. Synchronized colonies nesting at different times would suffer different predation rates because of seasonal differences in predator activity. Seasonal variations in predation rates have been observed with egg predators in the Riske Creek area (Somerville 1985), and I showed that nesting chronology varied extensively across colonies. This could explain the apparent lack of anti-predator benefits of within-colony synchrony.

5- Conservation and management

Conservation and management of rare and endangered wildlife is based on data on abundance, distribution, habitat protection, reproductive success and national and international significance of regional populations [Committee On Status of Endangered Wildlife in Canada ranking criteria]. My study tried to gather information on the above points. This section will briefly discuss 1) surveying techniques used and 2) management priorities derived from my work.

A) How to survey Eared Grebes

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Multiple adult, nest and young counts were used throughout the breeding season to derive number of breeding pairs per lake. The above surveys suggest that breeding abundance can be derived from a small number of surveys. The best method is to conduct adult and nest counts from mid to late June. Most pairs are nesting by then, and fall migration has not yet begun. Estimates based on adult and nest counts should match closely. If only one type of survey is possible, either adult or nest counts should be used. Adult surveys are most efficient in late May, prior to nesting, because all spring migrants have arrived on the breeding lakes and breeding pairs spend their time on open water, where they can easily be counted. Nest counts are most efficient from mid-June to early July, when most nests are active. Surveys should not be conducted at times other than indicated above, due to biases associated with nest failures, predation, migrations, and differences in breeding chronology.

B) Management priorities

I have provided extensive information on distribution and biology of Eared Grebes in British Columbia, and used it to identify key breeding areas for protection (Breault *et al.* 1988). Conservation efforts should be directed towards lakes with large breeding populations, because these lakes comprise the bulk of the known breeding population, and they are less affected by environmental fluctuations than lakes with small breeding populations.

environmental fluctuations than lakes with small breeding populations.

I showed that fluctuations in water level play an important role in the reproductive biology of Eared Grebes. Because nest-site availability is unpredictable, many breeding areas shift location across years. Small lakes with nesting areas in shallow water close to shore are most affected. Protecting those lakes would be less effective, because they are not consistently used by breeders. However, if smaller colonies contain younger individuals, as some of my data suggest, smaller colonies should be also protected. Water controls on major breeding lakes should not be considered at the moment, because their impact on emergent and submerged vegetation is unknown.

Emergent vegetation might provide concealment, protection and support for the nest. The presence of successful self-supporting nests (not associated with emergent vegetation) suggests that emergent vegetation may merely support the nest. If this is the case, artificial structures providing nest support might also be used by breeding pairs. I placed a total of 50 artificial platforms on 5 lakes used by breeding Eared Grebes in 1985. Eared Grebes built nests and laid eggs in 5 of those platforms, while I observed partially or completed nests (without eggs) on another 10 artificial platforms (unpubl. data). Artificial nesting platforms might help

rare), and could also be used to study nest site selection and coloniality in Eared Grebes.

Most of the findings of this study have management implications because little was known on the breeding biology of Eared Grebes both locally and world-wide. However, it also revealed further needs for research covering 1) status and size of local populations; 3) effects of resource abundance (food) on distribution, breeding chronology and reproductive success; 4) potential benefits of coloniality and 5) the suspected age differences between colonies. Savard (1986) pointed out that studies of waterfowl ecology can address theoretical questions, and that the answers to those questions have important management implications. I attempted to integrate both theoretical (coloniality) and management considerations in the design and implementation of this project, because I believe that Eared Grebe conservation depends on a good understanding of both aspects.

LITERATURE CITED

Alexander, R.D. 1974. The evolution of social behaviour. Annu. Rev. Ecol. Syst. 5:325-383.

Anderson, G. 1981a. Influence of fish on waterfowl communities. Anser 20:21-34.

Anderson, S.H. 1981b. Correlating habitat variables and birds. Studies in Avian Biology 6:538-542.

Andersson, M. and C.G. Wiklund. 1978. Clumping versus spacing out: experiments on nest predation in fieldfares (*Turdus pilaris*). *Anim. Behav. 26:1207-1212.*

Arnold, T.W. and E.K. Fritzell. 1987. Food habits of prairie mink during the waterfowl breeding season. Can. J. Zool. 65:2322-2324.

Ashmole, N.P. 1971. Sea bird ecology and the marine environment. *In* "Avian biology" (D.S. Farner and J.R. King, eds.), Vol. 1, pp.224-286. Academic Press, New York.

Beil, C.E. 1974. Forest associations of the southern Cariboo Zone, British Columbia. Syesis 7:213-233.

Bellrose, F.C. 1978. Ducks, geese and swans of North America. Stackpole Books. Harrisburg, Pa.

Bengston, S.-A. and D. Bloch. 1983. Island land bird population densities in relation to island size and habitat quality in the Faroe Islands. Oikos 41:507-522.

Bent, A.C. 1919. Life history of North American diving birds. U.S. Nat. Mus. Bull. 130:34-35.

Bider, J.R. 1968. Animal activity in uncontrolled terrestrial communities as determined by a sand transect technique. Ecol. Monogr. 38:269-308.

Bowman, G.B. and L.O. Harris. 1980. Effects of spatial heterogeneity on ground-nest depredation. J. Wildl. Manage. 44:806-813.

Boyd, W.S. 1982. Preliminary priority migratory bird species list for the Pacific and Yukon Region. Regional Report, Canadian Wildlife Service, Pacific and Yukon Region.

Boyd, W.S. and J-P.L. Savard. 1987. Abiotic and biotic characteristics of wetlands at Riske Creek, British Columbia - a

data report. Technical Report Series No. 16. Canadian Wildlife Service, Pacific and Yukon Region, British columbia.

Breault, A.M. and K.M. Cheng. 1988. Surplus killing of Eared Grebes, *Podiceps nigricollis*, by Mink, *Mustela vison*, in Central British Columbia. Can. Field-Nat. 102:738-739.

Breault, A.M., K.M. Cheng and J-P.L. Savard. 1988. Distribution and abundance of Eared Grebes (*Podiceps nigricollis*) in British Columbia. Techn. Rep. Ser. No. 51. Canadian Wildlife Service, Pacific and Yukon Region, British Columbia.

Breault, A.M. and K.M. Cheng. in press. Use of submerged mist nets to capture diving birds. J. Field Ornithol.

Broekhuisen, G.J. 1963. Does Black-necked Grebe cover its eggs? Bokmakiere 14:2-4.

Broekhuisen, G.J. and P.G.H. Frost. 1968a. Nesting behaviour of the Black-Necked Grebe *Podiceps nigricollis* in Southern Africa. II: Laying, clutch size, egg size, incubation and nesting success. Ostrich 39:242-252.

Broekhuisen, G.J. and P.G.H Frost. 1968b. Nesting behaviour of the Black-Necked Grebe *Podiceps nigricollis* in Southern Africa. II: Laying, clutch size, egg size, incubation and nesting success. Ostrich 39:242-252.

Brown, C.R. 1986. Cliff Swallow colonies as information centers. Science 234:83-85.

Brown, C.R. 1988a. Enhanced foraging efficiency through information centers: a benefit of coloniality in Cliff Swallows. Ecology 69:602-613.

Brown, C.R. 1988b. Social foraging in cliff swallows: local enhancement, risk sensitivity, competition and the avoidance of predators. Anim. Behav. 36:780-792.

Brown, C.R. and M.B. Brown. 1987. Group-living in cliff swallows as an advantage in avoiding predators. Behav. Evol. Sociobiol. 21:97-107.

Brown, C.R. and J.L. Hoogland. 1986. Risk in mobbing for solitary and colonial swallows. Anim. Behav. 34:1319-1323.

Buckley, F.G. and P.A. Buckley. 1980. Habitat selection and marine birds. Pp. 69-111 in: Behavior of marine animals: current perspective in research. Vol. 4: Marine birds. C.J. Burger, B.L. Olla and H.E. Winn, Eds. New York, Plenum Press.

Bull, 1981. Indirect estimates of abundance of birds. Studies in Avian Biology 6:76-81.

Burger, J. 1973. Competition between American Coots and Franklin's Gulls for nest sites and egg predation by the Coots. Wilson Bull. 85:449-451.

Burger, J. 1979. Colony size: a test for breeding synchrony in Herring Gull (*Larus argentatus*) colonies. Auk 96:694-703.

Campbell, R.W. and H.M. Garrioch. 1978. Waterbirds nesting on South Westwick Lake, British Columbia. Unpubl. report. British Columbia Provincial Museum, Victoria, B.C.

Campbell, R.W., R.J. Cannings, S.G. Cannings and R.A. Cannings. 1979. A proposal for an ecological reserve at Rock Lake, Becher's Prairie, British Columbia. Unpubl. proposal. B.C. Provincial Museum, Victoria, B.C.

Campbell, R.W., N.K. Dawe, I. McTaggart-Cowan, J.M. Cooper, G.W. Kaiser and M.C.E. McNall. in press. The birds of British Columbia, Vol. 1. Royal British Columbia Museum. Victoria, B.C.

Cannings, R.A and G.G.E. Scudder. 1978. The littoral Chironomidae (Diptera) of saline lakes in central British Columbia. Can. J. Zool. 56:1144-1155.

Caraco, T., S. Martindale and H.R. Pulliam. 1980. Avian flocking in the presence of a predator. Nature 285:400-401.

Chasko, G.G. and J.E. Coates. 1982. Avian habitat suitability along a transmission-line corridor in an oak-hickory forest region. Wildl. Monogr. 82:41pp.

Cody, M.L. 1971. Bird communities. Princeton University Press, Princeton, New Jersey.

Cooper, S.D., Winkler, D.W. and R.H. Ley. 1984. The effect of grebe predation on a brine shrimp population. J. Anim. Ecol. 53:51-64.

Cooperidder, A.Y., R.J. Boyd and H.R. Stuart, eds. 1986. Inventory and monitoring of wildlife habitat. U.S. Dept. Inter., Bur. Land Manage. Service Center. Denver, Co. 858pp.

Coulson, J.C. 1968. Differences in the quality of birds nesting in the centre and on the edges of a colony. Nature 217:478-479.

Coulson, J.C. 1971. Competition for breeding sites causing segregation and reduced young production in colonial animals. *In:* "Dynamics of populations: proceedings of the advanced study

institute on 'Dynamics of numbers in populations', Oosterbeek, the Netherlands, 7-18 September 1970" (P.J. den Boer and G.R. Gradwall, eds.), pp. 257-268. Pudoc. Wageningen, the Netherlands.

Coulson, J.C. and E. White. 1956. A study of colonies of the Kittiwake *Rissa tridactyla*. Ibis 98:63-79.

Coulson, J.C. and E. White. 1958. The effect of age on the breeding biology of the Kittiwake *Rissa Tridactyla*. Ibis 100:40-51.

Coulson, J.C. and E. White. 1960. The effect of age and density of breeding birds on the time of breeding of the Kittiwake *Rissa Tridactyla*. Ibis 102:71-86.

Cramp, S. and K.E.L. Simmons, (eds). 1977. The Birds of the Western Palearctic: Vol. 1. Oxford Univ. Press, Oxford.

Crook, J.H. 1964. The evolution of social organization and communication in the weaverbirds (Ploceinae). Behav. Suppl. 10.

Crook, J.H. 1965. The adaptive significance of avian social organizations. Symp. Zool. Soc. London. 14:181-218.

Crook, J.H. 1972. Sexual selection, dimorphism, and social organization in the primates. *In:* Sexual selection and the descent of man. 1871-1971, ed. B.Campbell, 231-281. Chicago: Aldine.

Croze, H. 1970. Searching image in Carrion Crows - hunting strategy in a predator and some anti-predator devices in camouflaged prey. Z. Tierpsychol. Suppl. 5:5-85.

Darling, F.F. 1938. Bird flocks and the breeding cycle, a contribution to the study of avian sociality. Cambridge University Press, Cambridge.

DesGranges, J-L. and J. Brodeur, 1985. Effets de l'acidite des lacs et de la competition avec les poissons sur l'alimentation et la croissance de deux especes de canetons du Bouclier laurentien: Premier etape. Pages III-1 to III-41 in J-L. DesGranges (red.). L'acidite des lacs et les canards: Premier etape. Rapport technique prepare dans le cadre du programme "Environnement 2000" par Canards Illimites et le Service Canadien de la Faune.

Dexheimer, M. and W.E. Southern. 1974. Breeding success relative to nest location and density in Ring-billed Gulls colonies. Wilson Bull. 86:288-290.

Eadie, J.McA. and A. Keast. 1982. Do Goldeneye and perch compete for food? Oecologia 55:225-230.

Emlen, S.T. and N.J. Demong. 1975. Adaptive significance of synchronized breeding in a colonial bird: a new hypothesis. Science 188:1029-1031.

Eriksson, M.O.B. 1979. Competition between freshwater fish and Goldeneye Bucephala clangula (L.) for common prey. Oecologia 41:99-107.

Evans, R.E. 1982. foraging-flock recruitment at a Black-billed Gull colony: implications for the information center hypothesis. Auk 99:24-30.

Faaborg, J. 1976. Habitat selection and territorial behavior of the small grebes of North Dakota. Wilson Bull. 88:390-399.

Findlay, C.S. and F. Cooke. 1982. Synchrony in the Lesser Snow Goose (Anser caerulescens caerulescens). II. The adaptive significance of reproductive synchrony. Evolution 36:786-799.

Forbes, L.S. 1985. Nesting of Eared Grebes at Duck Lake, near Creston, British Columbia. Murrelet 66:20-21.

Gochfeld, M. 1980. Mechanisms and adaptive value of reproductive synchrony in colonial seabirds. In: Burger, J., B.L. Olla and H.E. Winn (eds) Behaviour of marine animals, current perspectives in research. Plenum Press, New York, pp. 207-270.

Gollop, J.B. and W.H. Marshall. 1954. A guide for aging duck broods in the field. Miss. Flyway Counc. Tech. Sect. 14p.

Gotmark, F. and M. Andersson. 1984. Colonial breeding reduces nest predation in the Common Gull (Larus larus). Anim. Behav. 32:485-492.

Green, R.E. 1985. Estimating the abundance of breeding Snipe. Bird Study 32:141-149.

Green, R.J., J. Hawell and T.H. Johnson. 1987. Identification of predators of wader eggs from egg remains. Bird Study 34:87-91.

Gross, M.R. and A.M. McMillan. 1981. Predation and the evolution of colonial nesting in Bluegill Sunfish (Lepomis macrochirus). Behav. Ecol. Sociobiol. 8:163-174.

Guiguet, C.J. 1954. The birds of British Columbia: Diving birds and tube-nosed swimmers. British Columbia Provincial Museum Handbook No. 29, Victoria, B.C.

Haas, V. 1985. Colonial and single nesting in Fieldfares *Turdus pilaris* L.; a comparison of nesting success in early and late broods. Behav. Ecol. Sociobiol. 16:119-124.

Hamilton, W.D. 1971. Geometry for the selfish herd. J. Theor. Biol. 36:361-382.

Harrisson, C. 1978. A field guide to the nests, eggs and nestlings of North American birds. Collins, Cleveland, Ohio, 416pp.

Hoogland, J.L. 1979. Aggression, ectoparasitism and other possible costs of Prairie Dog (Sciuridae: *Cyonomis* spp.) coloniality. Behav. 69:1-35.

Hoogland, J.L. and P.W. Sherman. 1976. Advantages and disadvantages of Bank Swallow (*Riparia riparia*) coloniality. Ecol. Monog. 46:33-58.

Horn, H.S. 1968. The adaptive significance of colonial nesting in the Brewer's Blackbird (*Euphagus cyanocephalus*). Ecology 49:682-694.

Jehl, J.R. Jr. 1988. Biology of the Eared Grebe and Wilson's Phalarope in the nonbreeding season: a study of adaptations to saline lakes. Studies in Avian Biology No. 12.

Jehl, J.R. Jr. and S.I. Bond. 1983. Mortality of Eared Grebes in winter of 1982-83. Amer. Birds 37:832-385.

Kadlec, J.A. 1962. Effects of a drawdown on marsh impoundment. Ecology 43(2):267-281.

Kharitonov, S.P. and D. Siegel-Causey. 1988. Colony formation in seabirds. In: *Current Ornithology, Vol. 5.* Plenum:New York. pp. 223-271.

Krajina, V.J. 1969. Ecology of forest trees in British Columbia. Ecol. West. N. America 2:1-46.

Krajina, V.J. 1973. Biogeoclimatic zones of British Columbia. Map published by British Columbia Ecological Reserves Committee, British Columbia Dept. Lands, Forests and Water Resources.

Krebs, J.R. 1978. Colonial nesting in birds, with special reference to Ciconiiformes. In: Wading birds. Ed. by A. Sprunt IV, J.C. Ogden and S.Winkler. Res. Rep. No. 7. Nat. Audubon Soc.

Kruuk, H. 1964. Predators and anti-predator behaviour of the Black-Headed Gull (*Larus ridibundus* L.). Behav. Suppl. 11:1-129.

Lack, D. 1968. Ecological adaptations to breeding in birds. London, Methuen. 409 pp.

Lancaster, J. 1985. Structure of arthropod communities in some saline lakes of central British Columbia. M.Sc. Thesis, Dept. Zool., Univ. of British Columbia, Vancouver, Canada, 192pp.

Leys, H.N. and J.J.F.E. de Wilde. 1971. Het voorkomen van de fuut *Podiceps cristatus* in Nederland. Limosa 44:133-183.

Liversidge, R. and G.R. McLachlan. 1957. Breeding notes on the Black-Necked Grebe *Podiceps nigricollis* Brehm. Ostrich 28:233-234.

Loiselle, B.A. and W.G. Hoppes. 1983. Nest predation in insular and mainland lowland rainforest in Panama. Condor 85:93-95.

Lubcke, W. 1975. Zur Okologie und Brutbiologie der Wacholderdrossel (*Turdus pilaris*). J. Ornithol. 116:281-296.

McAllister, N.M. 1956. Reproductive Behaviour of the Eared Grebe. M.Sc. Thesis, Univ. of British Columbia, Vancouver, B.C.

McAllister, N.M. 1958. Courtship, hostile behaviour, nest establishment and egg laying in the Eared Grebe (*Podiceps caspicus*). Auk 75:290-311.

McTaggart Cowan, Ian. 1939. The Vertebrate Fauna of the Peace River district of British columbia. Occ. Pap. No. 1. British Columbia Provincial Museum.

Meeks, R.L. 1969. The effect of drawdown date on wetland plant succession. J. Wildl. Manage. 33(4):817-821.

Mills, J.A. 1973. The influence of age and pair-bond on the breeding biology of the Red-Billed Gull (*Larus novaehollandiae scopulinus*). J. Anim. Ecol. 42:147-162.

Møller, A.P. 1987. Advantages and disadvantages of coloniality in the swallow, *Hirundo rustica*. Anim. Behav. 35:819-832.

Munro, J.A. 1941. The Grebes: Studies of Waterfowl in B.C. B.C. Prov. Mus. Occ. Pap. No. 3, Victoria, B.C.

Munro, J.A. 1942. Observations of Waterfowl in British Columbia. Unpublished Report, Canadian Wildlife Service, Pacific and Yukon Region.

Nelson, J.B. 1970. The relationship between behaviour and ecology in the Sulidae with reference to other seabirds. Ocean. Mar. Biol. Annu. Rev. 8:501-574.

Nilsson, S.G. 1981. Census methods for breeding ducks in South Sweden. Proc. Second Nordic Congr. Ornithol. 1979:118-126.

Nisbet, I.C.T. 1975. Selective effects of predation in a tern colony. Condor 77:221-226.

Northcote, T.G. and P.A. Larkin. 1956. Indices of productivity in British Columbia lakes. J. Fish. Res. Bd. Canada 13:515-540.

Palmer, R.S. 1962. Handbook of North American birds. Volume 1. Loons through Flamingos. New Haven, Yale Univ. Press.

Parsons, J. 1976. Nesting density and breeding success in the Herring Gull *Larus argentatus*. Ibis 118:537-546.

Patterson, I.J. 1965. Timing and spacing of broods in the Black-headed Gull *Larus ridibundus*. Ibis 107:433-459.

Picman, J. and J-C. Belles-Isles. 1988. Interspecific egg pecking by the Black-capped Chickadee. Wilson Bull. 100:664-665.

Pielou, E.C. 1979. Biogeography. John Wiley and Sons, New York. 351pp.

Pratt, H.M. and D.W. Winkler. 1985. Clutch size, timing of laying, and reproductive success in a colony of Great Blue Herons and Great Egrets. Auk:102:49-63.

Pulliam, H.R. 1973. On the advantages of flocking. J. Theor. biol. 38:419-422.

Rearden, J.D. 1951. Identification of waterfowl nest predators. J. Wildl. Manage. 15:386-395.

Redmond, G.W., D.M. Keppie and P.W. Herzog. 1982. Vegetative structure, concealment, and success at nest of two races of Spruce Grouse. Can. J. Zool. 60:670-675.

Ricklefs, R. 1969. Analysis of mortality in birds. Smiths. Contrib. Zool. 9:1-48.

Riske, M.E. 1975. Environmental impact upon grebes breeding in Alberta and British Columbia. Ph.D. Thesis. Univ. of Calgary, Calgary, Alberta.

Savard, J-P.L. 1985. Territorial behaviour, nesting success and brood survival in Barrow's Goldeneyes and its congeners. Ph.D. Thesis. University of B.C. (Vancouver). 212pp.

Schaeff, C. and J. Picman. 1988. Destruction of eggs by Western Meadowlark. Condor 90:935-937.

Shields, W.M. 1984. Barn Swallow mobbing: self defence, collateral kin defence, group defence, or parental care? Anim. Behav. 23:504-508.

Shields, W.M. and J.R. Crook. 1987. Barn Swallow coloniality: a net cost for group breeding in the Adirondacks? Ecology: 68:1373-1386.

Shields, W.M., J.R. Crook, M.L. Hebblewaithe and S.S. Wiles-Ehmann. 1988. Ideal free coloniality in the swallows. *In:* The ecology of social behavior, C.N. Slobodchikoff (ed.). San Diego: Academic Press. pp. 189-228.

Simberloff, D.S. 1974. Equilibrium theory of island biogeography and ecology. Ann. Rev. Ecol. Syst. 5:161-182.

Snapp, B.D. 1976. Colonial breeding in the Barn Swallow (*Hirundo rustica*) and its adaptive significance. Condor 78:471-480.

Snow, B.K. 1960. The breeding biology of the Shag (Phalacrocorax aristotelis) on the island of Lundy, Bristol Channel. Ibis 102-554-575.

Somerville, A.J. 1985. Advantages to late breeding in Ruddy Ducks. M.Sc. thesis. Univ. of B.C. (Vancouver). 104pp.

Sonerud, G.A. 1985. Nest hole shift in Tengmalm's Owl *Aegolius funerus* as defence against nest predation involving long-term memory in the predator. J. Anim. Ecol. 54:179-182.

Spaans, A.L., A.A.N. de Wit and M.A. van Vlarrdingen. 1987. Effects of increased population size in Herring Gulls on breeding success and other parameters. Studies in Avian Biol. 10:57-65.

Storer, R.W. and J.R. Jehl, Jr. 1985. Moult patterns and moult migration in the Black-necked Grebe (Podiceps nigricollis). Orn. Scand. 16:253-260.

Tenaza, R. 1971. Behaviour and nesting success relative to nest location in Adelie Penguins (*Pygoscelis adeliae*). Condor 73:81-92.

Tinbergen, N., M. Impekoven and D. Franck. 1967. An experiment on spacing-out as defence against predation. Behav. 28:307-321.

Topping, M.S. 1985. Effect of environmental factors on standing crop of plankton in British Columbia lakes. Verh. Int. Ver. Limnol. 18:524-529.

van Vessem, J. and D. Draulans. 1986. The adaptive significance of colonial breeding in the Grey Heron *Ardea cinerea:* inter- and intra-colony variability in breeding success. Orn. Scand. 17:356-362.

Veen, J. 1977. Functional and causa aspects of nest distribution in colonies of the Sandwich Tern (*Sterna s. sandvicensis* Lath.). Behav. Suppl. 20:1-93.

Ward, P. and A. Zahavi. 1973. The importance of certain assemblages of birds as 'information centres' for food finding. Ibis 115:517-534.

Werschkul, D.F. 1979. Nestling mortality and the adaptive significance of early locomotion in the Little Blue Heron. Auk 96:116-130.

Wetzel, R.G. 1975. Limnology. Philadelphia: W.B. Saunders Co. 743pp.

Wiklund, C.G. 1982. Fieldfare (*Turdus Pilaris*) breeding success in relation to colony size, nest position and association with Merlins (*Falco colombarius*). Behav. Ecol. Sociobiol. 11:165-172.

Wiklund, C.G. and M. Andersson. 1980. Nest predation selects for colonial breeding among Fieldfares Turdus Pilaris. Ibis 122:363-366.

Wilkinson, L. 1989. SYSTAT: the system for statistics. Evanston, IL: Systat, Inc.

Winkler, D.W. and S.D. Cooper. 1986. Ecology of migrant Black-necked Grebes (*Podiceps nigricollis*) at Mono Lake, California. Ibis 128:483-491.

Wittenberger, J.F. and G.L. Hunt, Jr. 1985. The adaptive significance of coloniality in birds. In: *Avian Biology. Vol. 8* (Ed. by D.S. Farmer, J.R. King & K.C. Parkes), pp. 1-78. New York: Academic Press.

Woolhead, J. 1987. A method for estimating the number of breeding pairs of Great Crested Grebes *Podiceps cristatus* on lakes. Bird Study 34:82-86.

Yocom, C.R., S.W. Harris and H.A. Hansen. 1958. Status of grebes in Eastern Washington. Auk 75:36-47.

Appendix 1. Calculation of breeding abundance from chick counts

Age specific survival rates were obtained from a detailed study of 174 nests surveyed in 1985 and 1986 at Riske-Creek. Clutch size (3.48 eggs per nest) (McAllister 1958) was assumed to indicate the number of chicks hatched. The maximum number of chicks 2 weeks of age or older was compared to the number of eggs laid in breeding lakes used by a known number of breeders. The survival rate for that period was 32.4%. Survival from 2 weeks to 1 month old was similarly derived by comparing the number of chicks 1 month old or older with the number of chicks 2 weeks old or more. Survival was 84%. Fledging rates could not be measured directly due to movements of fledged chicks between lakes. Because of the short interval between 1 month old and fledging, I assumed that survival from 2 weeks to 1 month was identical to survival from 2 weeks to fledging. This information produced the following equation, used to obtain the number of breeding pairs from chick counts:

$$BP = [(Y_1/S_1) + (Y_2/S_2)]/C_s$$

where BP = number of breeding pairs

       Y_1 = number of chicks less than 2 weeks old

       Y_2 = number of chicks more than 2 weeks old

       S_1 = survival from 0 to 2 weeks old (%)

       S_2 = survival from 2 weeks old to fledging (%)

       C_s = clutch size (3.48 eggs/nest) (McAllister 1958)

Appendix 2. Estimated number of Eared Grebe pairs in the

Northern Okanagan/Kamloops area.

Lake	Location	Estimate*
	(mercator coordinates)	
Separation South	10.6918-56063	0-48
Separation North	10.6917-56072	0-18
Stump	10.6845-55786	74-(100)
Rawling	11.3663-55705	4-24
Kamloops A (Mitchell)	10.6934-56113	9-(10)
Munson	unknown	2-9
McKay's	unknown	8-9
Lew (Campbell)	10.7060-56040	6-22
Hamilton Corrals	unknown	1
Douglas	10.6990-55600	2
Round	11.3345-55885	2-(10)
Golden	unknown	1-2
Deer	unknown	1
Duck	unknown	0-20
Osoyoos	unknown	1
Spectacled	11.3128-54390	1
White	unknown	1
Tunkwa	10.6528-56067	0-1
Total		109-280

* Presents the minimum and maximum estimates obtained from the 2 most recent years of surveys. Some maximum values are personal inferences and are presented in parentheses.

Appendix 3. Estimated number of Eared Grebe pairs in the Peace River area.

Lake	Location (mercator coordinates)	Estimate*
Fort St. John Potholes	10.6377-62383	0-33
Boundary	10.6850-62480	83-295
Boudreau A	10.6030-62250	120-(700)
Cutbank	10.6840-61340	0-(50)
German	10.6820-62520	0-11
Cecil	10.6490-62450	62-(500)
"Bob Emery"	10.6302-62655	33
Whispering Pine	10.6240-62725	0-24
McQueen's slough	10.6775-61872	23-63
Sloane's slough	10.6388-61868	0-7
Boudreau B	10.5970-62255	20-(50)
Charlie	10.6260-62400	1-5
Huhn's slough	10.6393-62465	0-2
Scott	10.6310-61965	0-2
Total		342-1775

* Presents the minimum and maximum estimates obtained from the 2 most recent years of surveys. Some maximum values are personal inferences and are presented in parentheses.

Appendix 4. Estimated number of Eared Grebe pairs in the Southern Interior area.

Lake	Location (mercator coordinates)	Estimate*
Meadow Lake	10.5860-56910	37-164
Green Lake A	10.6147-56858	3-4
Green Lake B	10.6150-56853	9-19
Green Lake C	10.6151-56856	0-2
Little White Lake	10.5915-56815	590-(700)
4403 lakes	10.5890-56906	36-46
43 miles	unknown	1-5
Total		676-940

* Presents the minimum and maximum estimates obtained from the 2 most recent years of surveys. Some maximum values are personal inferences and are presented in parentheses.

Appendix 5. Estimated number of Eared Grebe pairs in the Central
             Interior area.

Lake	Location (mercator coordinates)	Estimate*
6 (Rock)	10.5400-57580	37-(82)
11	10.5387-57605	21-33
12	10.5390-57609	2-24
16 (Separating)	10.5344-57588	11-28
24	10.5386-57616	1-15
26	10.5387-57619	0-11
28	10.5375-57615	0-3
S. of 40	10.5338-57639	5-15
SS. of 40	10.5337-57637	0-13
42	10.5332-57643	17-21
53	10.5380-57626	3-5
Westwick	10.5580-57600	206-243
Sorenson	10.5570-57610	0-19
Coyote	10.5445-57910	8-9
McMurray	10.5415-57877	358-(450)
Elkhorn	10.4874-57386	96-262
8432 North	10.4817-57767	41-86
Upper Dry	10.4995-57450	0-57
Lower Dry	10.5005-57445	0-35
Dry 3	10.4984-57452	0-5
Jamieson Meadow	10.5212-57353	6-19
Golden Pond	10.4887-57381	3
Soda I & J	10.6130-58369	5
Rush	10.7110-55710	1-5
5 mi East of 100 Mile	unknown	11
Stum	10.4990-57900	2
Tachick	10.4200-59780	2-7
Near Bonds	unknown	1-3
Duncan	unknown	2-3
Alkali	10.5500-57365	1-5
Total		634-1479

* Presents the minimum and maximum estimates obtained from the 2
most recent years of surveys. Some maximum values are personal
inferences and are presented in parentheses.