



EVOLUTION OF COLONIALITY IN BIRDS: A TEST OF HYPOTHESES WITH THE RED-NECKED GREBE (*PODICEPS GRISEGENA*)

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ABSTRACT.—Group breeding is perplexing, because individuals incur density-dependent fitness costs to breed in groups, yet no universal benefit appears to explain its evolution. Coloniality in birds, defined as dense nesting within limited territories, is a striking example of group breeding. Adaptive explanations for coloniality are diverse, and several research approaches have emerged. Here, we test models for the evolution of coloniality with a population of Red-necked Grebes (*Podiceps grisegena*). We distinguish habitat models from conspecific models for explaining the adaptive evolution of coloniality. Habitat models propose that the fitness benefits of colonial breeding are gained through the characteristics or location of the colony site, whereas conspecific models posit that the benefits of colonial breeding are gained solely from nesting near conspecifics. Red-necked Grebes are waterbirds that typically nest in a dispersed fashion, only rarely nesting in colonies. Both dispersed and colonial nesting co-occurred in the study population, and aquatic nests were found in three distinct habitat types. We gathered detailed demographic data and used analyses of covariance to test whether variation in habitat type or conspecific aggregation best explained differences in breeding success across the population. We further used fitness, genetic, and spatial data to test whether kin selection, sexual selection, or conspecific reproductive-success cueing may drive colony formation. The data provided strong support for a habitat-based model and inconsistently supported conspecific models. Our results suggest that colonial individuals of this population gain selfish benefits from relatively rare, high-quality habitat rather than from proximity of conspecifics. *Received 23 August 2004, accepted 4 June 2006.*

Key words: aggregation, coloniality, commodity selection, habitat, *Podiceps grisegena*, Red-necked Grebe.

Evolución de la Colonialidad en las Aves: Una Evaluación de las Hipótesis en *Podiceps grisegena*

RESUMEN.—La nidificación grupal es asombrosa, ya que los individuos soportan costos denso dependientes en términos de su adecuación biológica al nidificar en grupo. A pesar de esto, no parecen haber beneficios generales que expliquen la evolución de este rasgo. La colonialidad en las aves, definida como una nidificación densa dentro de territorios limitados, es un excelente ejemplo de cría en grupo. Las explicaciones adaptativas de la colonialidad son diversas y han surgido diversos enfoques de investigación al respecto. En este estudio, evaluamos los modelos de

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evolución de la colonialidad en una población de *Podiceps grisegena*. Separamos los modelos de hábitat de los modelos coespecíficos para explicar la evolución adaptativa de la colonialidad. Los modelos de hábitat proponen que los beneficios en términos de adecuación biológica de la cría colonial se manifiestan a través de las características o de la localización del sitio de la colonia, mientras que los modelos coespecíficos destacan que los beneficios de la cría colonial se manifiestan sólo por el hecho de nidificar cerca de los individuos coespecíficos. *Podiceps grisegena* es una especie de ave acuática que típicamente nidifica de modo disperso y sólo en raras ocasiones nidifica en colonias. Tanto la nidificación dispersa como colonial se presentan conjuntamente en la población de estudio, y los nidos acuáticos fueron encontrados en tres tipos de ambientes diferentes. Recolectamos datos demográficos detallados y usamos análisis de covarianza para evaluar si la variación en el tipo de hábitat o la agregación de individuos coespecíficos explicaba mejor las diferencias en el éxito reproductivo a lo largo de la población. Luego empleamos datos de adecuación biológica, genéticos y espaciales para evaluar si la selección de parentesco, la selección sexual o el éxito reproductivo de los coespecíficos podrían determinar la formación de la colonia. Los datos apoyaron de manera contundente un modelo de hábitat y sólo apoyaron débilmente a los modelos coespecíficos. Nuestros resultados sugieren que los individuos coloniales de esta población se beneficiaron de su presencia en ambientes relativamente raros y de alta calidad, más que de la proximidad a individuos coespecíficos.

THE ORIGIN OF group living in animals is an evolutionary puzzle. Although automatic costs are often associated with group living, there appear to be no automatic or universal benefits (Alexander 1974, Danchin and Wagner 1997). Individuals that join groups may benefit from access to a limited resource, such as food or predator-safe sites; may gain social benefits, including group feeding (Richner and Heeb 1996) and increased access to multiple mates (Wagner 1993); and can benefit from conspecifics' knowledge of habitat quality (Wagner and Danchin 2003). However, theory and empirical study suggest that group members always incur density-dependent costs (Alexander 1974, Wittenberger and Hunt 1985). These costs may include competition for resources, including mates, and increased disease transmission. Our purpose here is to address one form of group living: colonial breeding in birds. We investigated multiple models for colonial breeding in a population of birds that exhibits both clumped and dispersed nesting.

Colonial breeding in birds occurs when a group of females or pairs nests in a localized area from which they must depart regularly for food (Wittenberger and Hunt 1985). Coloniality, defined as aggregated nesting regardless of whether individuals display cooperative behavior (Alexander 1974), appears to be an

evolutionarily derived state in birds, whereas the ancestral condition is dispersed, solitary nesting (Coulson and Dixon 1979, Coulson 1985, Wittenberger and Hunt 1985, Rolland et al. 1998). Aggregation of nests in a colony can occur at different levels. Nest clustering, defined as habitat-mediated aggregation, can track local variation in habitat quality; or nests can be more or less clustered than expected from habitat variation alone, which is defined as additive aggregation (Danchin and Wagner 1997).

Colonial nesting occurs in 13% of avian species and is concentrated in marine birds, 98% of which are colonial (Lack 1968). Phylogenetic analysis indicates that coloniality has evolved at least 20 times in the avian lineage (Rolland et al. 1998). Existing data suggest that more than one evolutionary route to coloniality exists and that multiple ecological conditions may favor its evolution (Siegal-Causey and Kharitonov 1990, Rolland et al. 1998).

Two main frameworks have been used to explain the evolution of colonial nesting in birds. The first is the functional or cost-benefit approach (Alexander 1974, Wittenberger and Hunt 1985, Lauder 1986), in which benefits and costs of coloniality are weighed against each other and the benefits with the greatest positive effects (on fitness) are proposed to be key selective forces. Second, commodity-selection

has emerged as a complementary framework (Shields et al. 1988, Danchin and Wagner 1997). Commodity-selection considers how individuals choose breeding sites using various sources of information, especially from conspecifics, and how these choices affect aggregation. Important sources of information include the presence and location (including past location) of conspecific breeding sites, reproductive success of conspecifics, and group size (Ward and Zahavi 1973, Buckley 1997, Danchin and Wagner 1997, Wagner et al. 2000). Here, we investigated coloniality in a population of Red-necked Grebes (*Podiceps grisegna*), employing methods of both the functional and commodity-selection approaches.

THE FUNCTIONAL APPROACH

The functional approach examines the costs and benefits of nesting in a colony to understand the selective forces at work. Two types of functional models have been distinguished in past research: (1) habitat models predict that colonially breeding individuals benefit from the characteristics or location of the colony site and (2) conspecific models predict that the benefits of coloniality can be attributed solely to the presence of nearby conspecifics. Both types of models have been suggested in various forms (see below) and were tested in our analysis.

Habitat models propose that the main benefit of colonial breeding is access to the limited resource of a high-quality nesting site (Lack 1968, Wittenberger and Hunt 1985). Quality of a site is conferred by any combination of the following: protection from predators because of inaccessibility (Buckley and Buckley 1980); protection from abiotic forces such as wind, waves, and heat; or proximity to a plentiful supply of food or nesting material (Horn 1968). The benefits of high-quality habitat may occur independently of the presence of conspecifics. For example, Burger (1985) found that reproductive success of colonial gulls was highest at the most protected colony sites, irrespective of nesting density.

Conspecific models propose that the benefits of colonial nesting are gained from the presence of conspecifics. Such benefits are, by definition, independent of the physical characteristics or location of the colony site and include group protection from predators, as well as the benefits

of feeding or breeding in aggregation. Predator protection was proposed early as favoring coloniality in birds (Lack 1968) in two ways. First, with "dilution effects," per-capita nest loss to predators is lowered simply as a "byproduct-benefit" of increased group size (Hamilton 1971, Sachs et al. 2004). However, some studies show a positive correlation between group size and predation risk (reviewed in Wittenberger and Hunt 1985), and one model predicts equal risk across prey densities (Hugie and Dill 1994), so there appears to be no universal rule (Davies 1978, Danchin and Wagner 1997). Second, group protection from predation may derive from behavior such as warning calls or predator mobbing (Charnov and Krebs 1975).

Feeding benefits may also select for aggregated nesting. For example, Brown and Brown (1996) analyzed the costs and benefits of coloniality in Cliff Swallows (*Petrochelidon pyrrhonota*) and concluded that the main benefit of colonies was group feeding. However, group-feeding benefits, as well as predator protection, often rely on cooperation and should be considered cautiously, because they may be secondary adaptations that maximize the benefits of colonial nesting once it is already in place (Siegal-Causey and Kharitonov 1990).

THE COMMODITY-SELECTION APPROACH

The commodity-selection approach focuses on breeding-site selection and its influence on nesting dispersion. Perhaps the first hypothesis using this approach was the ideal-free distribution (Fretwell and Lucas 1969), which proposes that individuals select breeding sites on the basis of intrinsic habitat quality. This hypothesis predicts roughly equal fitness for all individuals because areas of high habitat quality are subsequently most crowded. By contrast, the despotic distribution (Brown et al. 1990) predicts that dominant individuals take a disproportionate share of the high-quality habitat. Commodity-selection hypotheses predict that colony formation can be driven by sexual selection (Wagner 1993), reproductive-success cueing among conspecifics (Boulinier and Danchin 1997, Danchin and Wagner 1997, Danchin et al. 1998, Doligez et al. 2003), and kin selection (Hamilton 1964a, b), as well as by conspecific attraction (Stamps 1988).

The sexual-selection hypothesis predicts that the potential to acquire multiple mates can drive

colony formation. Pierotti (1981) posited that colonial individuals may benefit from increased opportunity to pursue extrapair copulations (EPCs), and Wagner (1993) proposed the hidden-lek hypothesis, in which female pursuit of EPCs drives colony formation. Empirical work supports female benefit from EPCs in colonies of Bearded Tits (*Panurus biarmicus*; Hoi and Hoi-Leitner 1997). The conspecific-reproductive-success hypothesis predicts that individuals use information gathered about the reproductive success of conspecifics to guide breeding-site selection (Boulinier and Danchin 1998, Doligez et al. 2003). Brown et al. (2000) found empirical support for this hypothesis: colonial Cliff Swallows choose nesting sites based on the reproductive success of neighbors. Finally, colonies might form when first-time breeders return to nest near their parents or other kin (Hamilton 1964a, b; Rodman 1981).

A COMBINED APPROACH

We investigated a population of Red-necked Grebes that exhibited both solitary and colonial nesting. We tested habitat and conspecific models of the functional approach by comparing nesting success among pairs breeding at different levels of aggregation and in different habitat types. We also used the commodity-selection approach to investigate hypotheses about colony formation: we tested whether colony formation was driven by the pursuit of multiple mates, by conspecific cueing on reproductive success, by kin selection, or whether individuals were spaced in an ideal-free distribution.

METHODS

Study site and field methods.—The natural history of Red-necked Grebes and our field-site description and census techniques were detailed in Nuechterlein et al. (2003). That study analyzed the spatiotemporal patterns of nesting in this population and found that overall success of solitary versus aggregated nesting strategies varied from year to year. Here, we analyze these data to specifically test functional and commodity-selection models for the evolution of colonial breeding. Field methods and natural history are described briefly, with a focus on data analysis.

Demographic census data were gathered on Red-necked Grebes at Lake Osakis, Minnesota, for the summers of 1995–1998. Red-necked Grebes are large migratory waterbirds that typically breed solitarily in small lakes or ponds, with a pair defending a pond from other diving waterbirds (Cramp and Simmons 1977). Females and males cooperatively build floating aquatic nests of marsh grasses and algae in water that is usually ~1 m deep. Rarely, Red-necked Grebes form colonial groups with nests ≤ 10 m apart (Munro 1941, Cramp and Simmons 1977, Stout and Nuechterlein 1999). Our study population occupies a 2,537-ha windblown lake and includes pairs of Red-necked Grebes that nest in the typical dispersed fashion, with internest distances of 50–100 m or more, as well as in clustered or colonial fashion, where individuals have as many as 12 neighboring nests within 50 m. In this fish-rich lake, both dispersed and colonial individuals feed solitarily and spend little time feeding, often reaching satiation after catching several large fish (Nuechterlein et al. 2003, Klatt et al. 2004). Therefore, food finding or availability is unlikely to be a major cost or a benefit to coloniality and is not considered further.

For each nest, we gathered data on nest initiation date, egg-laying and hatching dates, date and cause of nest failure, and nest location on a coordinate system. Nest fate was classified as hatching (one or more eggs hatched), depredated (nest intact but egg fragments found), destroyed by weather (nest was missing or partially sunken after a storm), or abandoned (nest and eggs intact but eggs remained cold for a full day). We used hatching success as our main estimator of fitness. We attempted to confirm chick survival by later identifying parents with their young, but these data were scant. However, because we are investigating the fitness consequences of nesting strategies, hatching success is a more appropriate measure than chick survival. Parents leave the nesting area with their chicks after the eggs are hatched and move to nondefended open-water areas. Chick survival after nest departure is unlikely to be tightly correlated with differences in nesting habitat or nesting aggregation.

We recorded nest location by marking all nests at the end of each season, taking aerial photos of the lake, and aligning photos with marked nests to U.S. Geological Survey maps (Nuechterlein et al. 2003). Eighty-seven individuals in the population were captured, color banded, and

bled for genetic analysis. Sachs and Hughes (1999) developed microsatellite markers for this species. Nuechterlein et al. (2003) analyzed population-genetic structure, kin selection, and rates of extrapair matings. Nuechterlein et al. (2003) concluded that this population has no detectable population-genetic structure. Extrapair matings were relatively uncommon: of 20 offspring analyzed, only 2 (at one nest) shared loci with their mother but not her social mate (Sachs 1998).

Nesting aggregation and habitat analysis.—To analyze conspecific models, an index of nesting aggregation from Nuechterlein et al. (2003) was used for all nesting attempts. The aggregation index (AI) averages the number of active conspecific nests within 50 m of a focal nest per day of focal nest activity (Nuechterlein et al. 2003). In addition to using AI, some of our analyses of nest fate divided nests into three aggregation classes: dispersed (0 neighbors within 50 m), intermediate (0.1–1.9 neighbors within 50 m), and colonial (≥ 2 neighbors), following Nuechterlein et al. (2003). Aggregation classes were always complemented by analysis of the continuous variable (AI).

To test habitat models, nesting habitat was divided into three distinct types: large cattail islands (LI), small cattail islands (SI), and shoreline (S). All nests were assigned to one of these habitat types, using digitized overhead photos of the lake with the nests marked on them and the following criteria: LI consisted of offshore floating masses of cattail roots (*Typha angustifolia*) anchored to the lake bottom and had continuous axes ≥ 25 m (32–45 m). Small cattail islands were smaller emergent islands without a foundation of floating cattail root mass and with maximum continuous axes < 25 m (3–11 m). The LI axes were measured from edges of permanent floating material and did not include emergent material that surrounded islands. Shoreline areas included the shallow-water emergent vegetation of cattail, bulrush (*Scirpus acutus*), and phragmites (*Phragmites communis*) skirting the lake's edge.

The habitat classifications followed from expectations that nests at LI, SI, and S might be exposed to different ecological pressures. An experiment with artificial nests at Lake Osakis showed that shoreline habitat is more vulnerable to raccoons (*Procyon lotor*) and other terrestrial predators than offshore sites (Nuechterlein et al.

2003). Island habitat was subdivided on the basis of size and structural characteristics: LI were composed of cattail mats originating from the shoreline and torn off during the spring thaw. Small cattail islands were composed of emergent vegetation that grew patchily in shallow water. Large cattail islands persisted for several years before they disintegrated, whereas SI appeared to vary each season. Shoreline habitat contained the most dispersed nests, with AI means between 0.30 and 0.67 in 1996–1998. However, in 1995, there was a long peninsula of shoreline that contained aggregated nests, and the mean AI for S nests was 2.90. Large cattail islands and SI had AI means between 2.40 and 4.27 and between 1.04 and 1.86, respectively, in the four years of the study. Roughly similar numbers of individuals nested at each of the three habitat types: mean numbers of nesting attempts per season were 34 for LI, 39 for S, and 55 for SI. Resighting data revealed that ~45% of marked birds nested within 50 m of the previous year's nest, and ~85% within 150 m (Nuechterlein et al. 2003).

Statistical analysis.—We used the functional approach to test the fitness benefits of conspecific aggregation versus the different nesting habitats. The following estimators of breeding success and timing were analyzed: number of chicks successfully hatched, dates of nest initiation and first egg laid (Julian dates), number of nesting attempts per breeding pair in a season, and mean number of incubation days for the first chick hatched. We used analyses of covariance (ANCOVA) to simultaneously test for the effects of habitat type and AI and their interaction. The ANCOVAs combined a one-way analysis of variance (ANOVA, analyzing habitat types), a regression (analyzing AI), and an interaction factor. This approach yields an explicit evaluation of whether habitat type or conspecific aggregation best explains the variation in the nesting data. Because ANCOVAs can be conservative, we also analyzed the effects of habitat and aggregation on fitness measures separately (using ANOVAs with *post-hoc* comparisons and regression analysis, respectively).

We analyzed the importance of habitat versus aggregation for the following categorical (nest fate) data: proportion of nests successfully hatched, depredated, destroyed by weather, or abandoned by parents. For habitat types, we used chi-square analyses coupled with likelihood-ratio tests to assign significance. For conspecific

aggregation, we used a logistic regression that fit all nesting attempts onto a plane with the four nest outcomes categorized on the *y* axis and AI on the *x* axis (fit *y* by *x*, contingency analysis of JMP 5.01). A maximum-likelihood model was then used to calculate whether nest outcome was significantly affected by AI. We also divided nests into aggregation classes (described above) and used chi-square analyses coupled with likelihood-ratio tests to assign significance. Aggregation classes were used to compare the frequencies of each of the different nest fates among nests of similar aggregation.

We employed the commodity-selection approach to test hypotheses about colony formation. (1) We tested for the presence of an ideal-free distribution (Fretwell and Lucas 1969) and (2) for reproductive-success cueing (Boulinier and Danchin 1997). (3) The hidden-lek hypothesis (Wagner 1993), wherein coloniality is driven by females' pursuit of EPCs, was not considered, given the low frequency of extrapair matings found in the previous analysis of this population (Nuechterlein et al. 2003). (4) Kin-structured colonies (Hamilton 1964a, b; Rodman 1981) were ruled out using genetic and spatial data from previous analyses (Sachs and Hughes 1999, Nuechterlein et al. 2003).

Individual nesting attempts were considered as independent data. Using color bands to track pairs, we also analyzed data using a subset of known pairs. Data from 46 such pairs where both birds were marked showed that none was resighted with new partners within a season, so we assume that a pair with only one marked bird remains the same pair within a season. The known-pairs data set avoids nonindependence by comparing multiple nesting attempts of pairs equally. Because results were similar between data sets, we report only the data from individual nesting attempts.

RESULTS

Effect of habitat versus conspecific aggregation on estimates of fitness.—Hatching success varied among habitat types in three of the four years, 1996–1998 (ANCOVA, 1996, *P* = 0.046; 1997, *P* = 0.011; 1998, *P* = 0.002), but not in 1995 (Table 1). We also compared hatching rates among habitat types for the successful nests (hatching ≥1 egg) using a one-way ANOVA and a student's *t*-test for *post-hoc* comparisons (Fig. 1). The hatching

TABLE 1. Analyses of covariance (ANCOVA) results of fitness component data. Significance values (*P*) are shown for ANCOVA by habitat type, aggregation index, and interaction effect. Fitness components analyzed include number of chicks hatched per nesting attempt (Hatch), date of nest initiation (Date init.), and date of first egg hatched (Date hatch). Significant results (*P* < 0.05) are indicated by an asterisk.

	Habitat			Aggregation			Interaction		
	Hatch	Date init.	Date hatch	Hatch	Date init.	Date hatch	Hatch	Date init.	Date hatch
1995 (<i>n</i> = 102)	0.241	0.045*	0.216	0.879	<0.001*	0.379	0.372	<0.001*	0.296
1996 (<i>n</i> = 141)	0.046*	0.033*	0.248	0.252	0.381	0.879	0.409	0.933	0.722
1997 (<i>n</i> = 146)	0.011*	<0.001*	0.001*	0.463	0.133	0.499	0.037*	0.719	0.035*
1998 (<i>n</i> = 121)	0.002*	0.654	0.019*	0.895	0.246	0.208	0.056	0.033*	0.027*

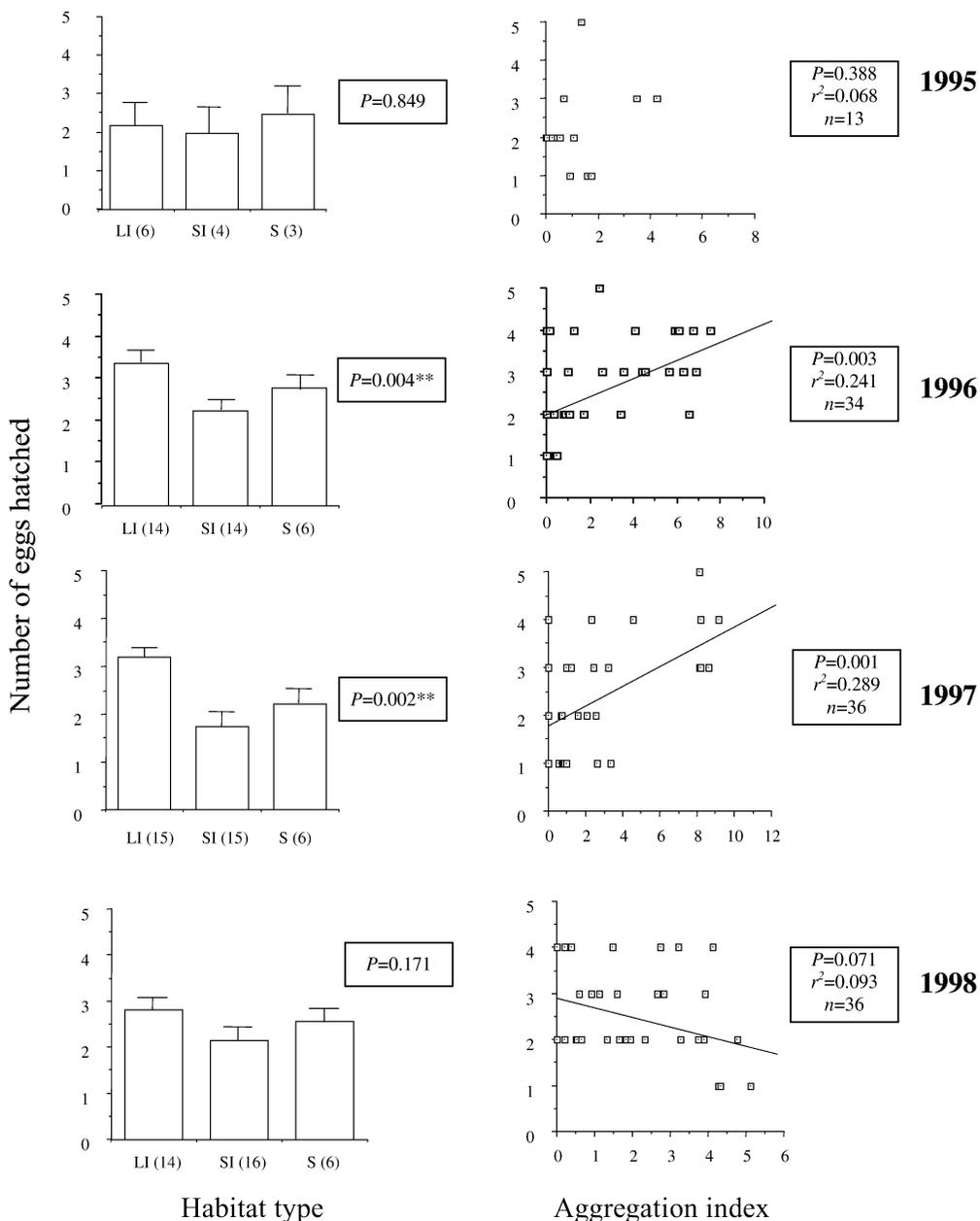


FIG. 1. Hatching success of nesting pairs that hatched at least one egg analyzed separately by habitat type (left) and aggregation index (right). (Left) Mean number of eggs hatched per nest in each habitat classification is shown, with error bars indicating standard error (SE). Significant differences between habitat types (one-way ANOVA, $P < 0.05$) are indicated by an asterisk. Double asterisks indicate that LI hatched significantly more eggs than both S and SI (*post-hoc* analysis; student's multiple pairwise *t*-test). Sample sizes for each habitat type (n) are reported in parentheses under each graph. (Right) Nonparametric regression analyses (Kendall's tau, JMP 5.01) of number of eggs hatched against AI. Values for r^2 , significance value (P), and sample size (n) are listed. Regression lines are shown when $P < 0.1$.

rate was significantly higher for LI than S or SI nests in 1996 and 1997. Analyses of covariance revealed no significant effect of conspecific aggregation in any year of the study (Table 1), though a significant interaction effect between habitat type and aggregation index was found in 1997 ($P = 0.037$), and a marginal effect in 1998 ($P = 0.056$). There was a positive correlation between hatching rate and AI in 1996 ($P = 0.003$) and 1997 ($P = 0.001$), a marginally significant negative correlation in 1998 ($P = 0.071$), and no detectable correlation in 1995 (nonparametric regression; Fig. 1).

Nest initiation date varied significantly among habitats in 1995–1997 (ANCOVA, 1995, $P = 0.045$; 1996, $P = 0.033$; 1997, $P < 0.001$) and not in 1998 (Table 1). Mean date of nest initiation was earliest for LI nests in 1995–1997 (ANOVA; Fig. 2), and *post-hoc* comparisons revealed that LI nests were initiated significantly earlier than SI nests but not S nests. Conspecific aggregation had a significant effect on nest initiation date only in 1995, with a significant interaction effect with habitat ($P < 0.001$). This correlation was negative; aggregated nests were initiated earlier ($r^2 = 0.118$, $P < 0.001$). Finally, there was a significant interaction effect between aggregation and habitat in 1998 ($P = 0.033$).

Habitat type had a significant effect on date of first hatching in 1997 (ANCOVA, $P = 0.001$) and 1998 ($P = 0.035$), and a significant interaction effect with aggregation in both years (1997, $P = 0.019$; 1998, $P = 0.027$; Table 1). Large cattail island pairs had the earliest mean date of first hatching in 1995–1997 (ANOVA), though *post-hoc* comparisons did not reveal that LI nests hatched earlier than SI and S in any year of the study. Conspecific aggregation did not affect hatching date in any year of the study (ANCOVA).

Neither habitat nor conspecific aggregation accounted for significant variation in nesting attempts or duration of incubation in any year of the study.

Effects of habitat versus aggregation on nest fate.—Nest fate differed among habitat type in all years of the study (chi-square analyses; 1995, $P = 0.004$; 1996, $P = 0.002$; 1997, $P = 0.007$; 1998, $P = 0.005$; Table 2). The LI had the lowest rates of weather-related destruction in three of the four seasons, though this difference was statistically significant only in 1996 ($P = 0.02$) and 1998 ($P = 0.02$; Table 3). Predation was lower in island

nests than shoreline in two years of the study, and this was statistically significant in 1997 ($P < 0.01$). Nests at small islands suffered the lowest predation levels in three of the four years, but this was statistically significant only in 1997 ($P < 0.01$; Table 3). The hatching rate was significantly higher for LI than for the other habitat types in three of the four years (1996–1998; Table 3).

Nesting aggregation affected nest fate in 1995 ($P = 0.010$) and 1998 ($P < 0.001$; Table 2). In 1995, predation was highest among the most clustered nests ($P < 0.01$). In 1998, the hatching rate was highest among the most clustered nests ($P = 0.01$), likely because clustered nests also suffered from lower rates of weather-related destruction ($P = 0.03$; Table 3).

Commodity-selection hypotheses.—The ideal-free distribution (Fretwell and Lucas 1969), which predicts no mean difference in fitness among individuals in different habitat types, was rejected because fitness differed significantly across habitat types (see Table 1). The conspecific reproductive-success cueing hypothesis (Boulinier and Danchin 1997), which predicts that individuals choose to breed near others that bred successfully in past years, was also unsupported by our data. To test this hypothesis, we compared the AI of pairs hatching at least one egg in that successful year (mean AI = 2.51) to their AI in the following year (mean AI = 2.09). If reproductive-success cueing occurs, breeding pairs are predicted to have more neighbors, on average, the year after a successful hatch than the previous year (see Brown et al. 2000). An analysis of 47 pairs over the study revealed no significant difference in aggregation ($P = 0.48$) and, hence, provides no evidence to support conspecific reproductive-success cueing.

DISCUSSION

Habitat versus conspecific aggregation.—Our results are most consistent with a habitat-based model for the adaptive significance of coloniality. The hatching-success data and data on nest timing suggest that Red-necked Grebes nesting at one particular habitat type (large cattail islands) had higher fitness than birds nesting elsewhere. The main selective benefits of nesting at these colonial sites were protection from wind storms and open-water protection from predation that led to more eggs hatched (Tables 2 and

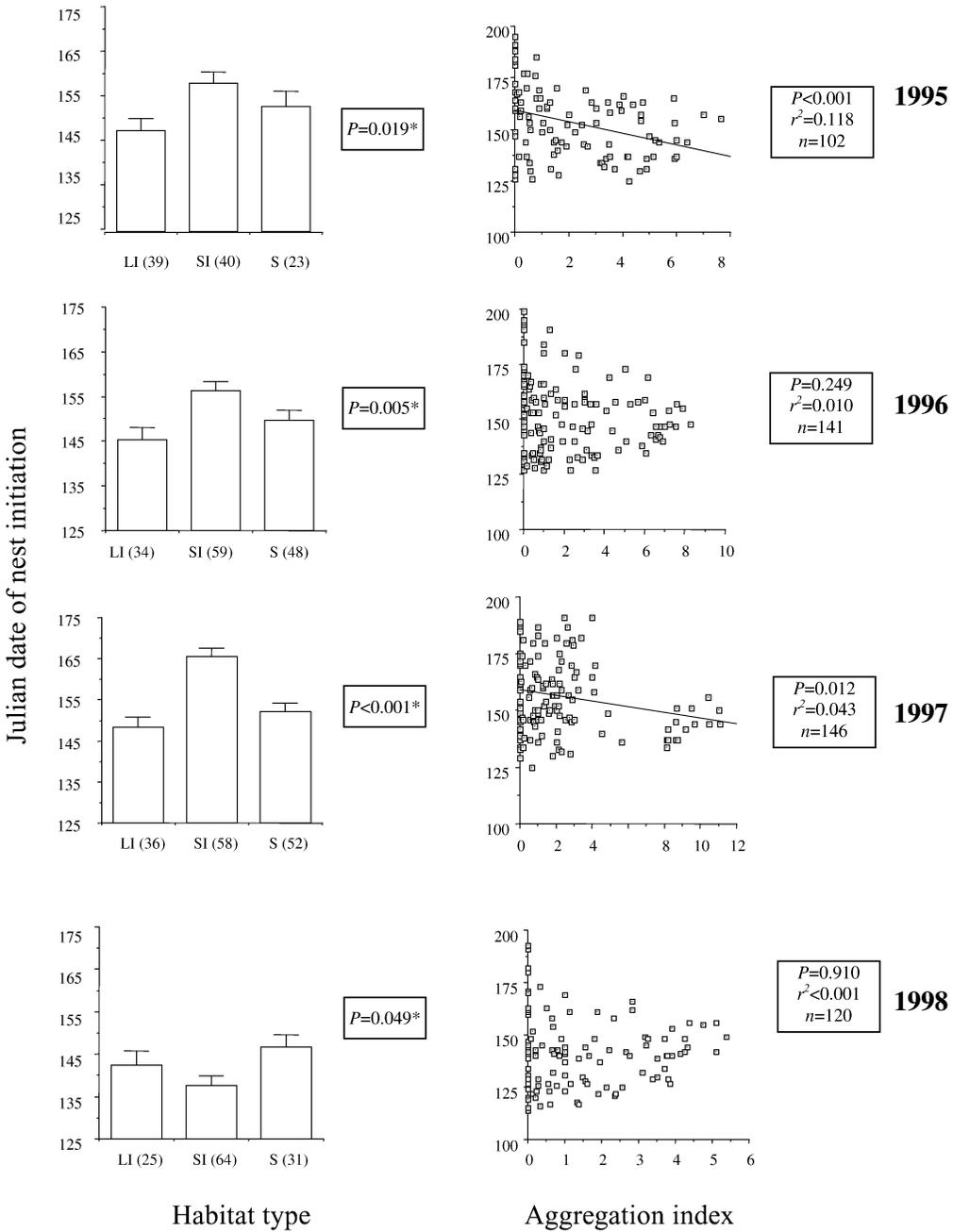


FIG. 2. Nest initiation date analyzed by habitat type (left) and aggregation index (right). (Left) Mean Julian date of nest initiation for each habitat classification is shown with error bars indicating standard error. Significant differences between habitat types (one-way ANOVA, $P < 0.05$) are indicated by an asterisk. Sample size for each habitat type is listed (n) in parentheses under each graph. (Right) Regression analyses of number of date of nest initiation against AI are shown. Values for r^2 , significance value (P), and sample size (n) are listed. Regression lines are shown when $P < 0.1$.

TABLE 2. Chi-square analysis of nest fate by habitat type and aggregation class.

Year	n	Habitat type						Aggregation Class					
		All	H	Pr	W	A	All	H	Pr	W	A		
1995	102	P	0.004*	0.411	0.078	<0.001* ^a	0.299	0.010*	0.084	0.015* ^b	0.060	0.442	
		r ²	0.071	0.023	0.046	0.137	0.018	0.042	0.120	0.094	0.038	0.039	
1996	141	P	0.002*	0.002* ^c	0.201	<0.023* ^a	0.095	0.317	0.078	0.944	0.153	0.944	
		r ²	0.057	0.083	0.026	0.039	0.036	0.010	0.009	0.007	0.020	0.037	
1997	146	P	0.007*	0.004* ^c	0.006* ^d	0.444	0.906	0.633	0.532	0.816	0.215	0.480	
		r ²	0.047	0.066	0.077	0.008	0.002	0.005	<0.001	0.013	0.008	0.023	
1998	121	P	0.005*	0.007* ^c	0.058	0.020* ^a	0.296	<0.001*	0.007* ^e	0.204	0.002* ^f	0.020* ^g	
		r ²	0.028	0.068	0.056	0.047	0.028	0.061	0.051	0.020	0.042	0.04	

Nest fates: All = combined; H = number hatched; Pr = predation; W = weather; A = abandoned. n = sample size; P = significance value; r² = square of correlation coefficient. *P < 0.05.

^a Large cattaal islands (LI) had the lowest rate of weather destruction.

^b Predation increases with aggregation.

^c Large cattaal islands (LI) had the highest number of eggs hatched.

^d Small cattaal islands (SI) had the lowest rate of predation.

^e Hatching increases with aggregation.

^f Weather destruction decreases with aggregation.

^g Abandonment increases with aggregation.

TABLE 3. Nest fates. Percentage of individual nesting attempts are shown for each of the four outcome categories: hatched (H), predation (Pr), weather (W), and abandoned (A). Two chi-square analyses (χ^2) are shown for each year of the study. The left divides the nesting outcomes by habitat category and the right by aggregation category. Values for r^2 and significance values (P) are shown; the latter was calculated using the likelihood-ratio. Habitat categories are (1) large islands (offshore floating cattail root mats >25 m in diameter), (2) small islands (offshore emergent cattail islands <25 m in diameter), and (3) shoreline (emergent cattail growth contiguous with the shore). Aggregation categories are (1) territorial (no neighbors within 50 m), (2) intermediate (0–1.9 neighbors within 50 m), and (3) colonial (two or more neighbors).

Year	Habitat	H	Pr	W	A	Aggregation	H	Pr	W	A
1995	Large islands	15%	33%	18%	33%	Territorial	6%	6%	33%	56%
	Small islands	8%	13%	45%	35%	Intermediate	26%	15%	33%	26%
	Shoreline	17%	26%	4%	52%	Colonial	4%	38%	16%	42%
	r^2	0.02	0.05	0.14	0.02	r^2	0.12	0.09	0.04	0.04
1996	P (χ^2)	0.31	0.08	<0.01*	0.30	P (χ^2)	<0.01*	<0.01*	0.11	0.07
	Large islands	41%	26%	27%	9%	Territorial	20%	20%	35%	25%
	Small islands	10%	10%	54%	25%	Intermediate	21%	17%	53%	9%
	Shoreline	29%	19%	38%	15%	Colonial	30%	13%	37%	20%
1997	r^2	0.08	0.03	0.04	0.04	r^2	0.01	0.01	0.02	0.04
	P (χ^2)	<0.01*	0.20	0.02*	0.10	P (χ^2)	0.48	0.65	0.15	0.09
	Large islands	42%	11%	33%	14%	Territorial	26%	23%	37%	14%
	Small islands	28%	9%	47%	17%	Intermediate	24%	16%	49%	10%
1998	Shoreline	12%	31%	42%	15%	Colonial	26%	13%	39%	22%
	r^2	0.07	0.08	<0.01	<0.01	r^2	<0.01	0.01	<0.01	0.02
	P (χ^2)	<0.01*	<0.01*	0.44	0.91	P (χ^2)	0.98	0.41	0.45	0.23
	Large islands	56%	4%	20%	20%	Territorial	15%	21%	56%	8%
1998	Small islands	25%	14%	51%	11%	Intermediate	31%	15%	46%	8%
	Shoreline	20%	26%	48%	7%	Colonial	44%	9%	27%	21%
	r^2	0.07	0.06	0.05	0.03	r^2	0.05	0.02	0.04	0.04
	P (χ^2)	<0.01*	0.06	0.02*	0.30	P (χ^2)	0.02*	0.36	0.03*	0.18

* $P < 0.05$.

3). Earlier nest initiation at LI may have yielded higher-quality offspring, with more time to grow and mature before migration (Fig. 2).

We found little evidence for selective forces arising solely from conspecific aggregation. The ANCOVAs of our aggregation index produced only one significant effect (Table 1). In 1995, AI was correlated with earlier nest initiation (a significant interaction with habitat type was also found). This suggests that early nesting grebes may have been cueing-in on each other at the clustered sites. An interaction effect for nest initiation was found in 1998 as well. Interaction effects between habitat type and aggregation were also found for hatching rate in 1997 and 1998 (marginal significance in 1998), yet aggregation had an opposite relationship with hatching success in each of these years (Fig. 1). Finally, although the ANCOVA did not detect an effect of aggregation in 1996, a regression analysis of successful nests showed a positive relationship between aggregation and hatching rate. The ANCOVAs often have higher *P* values than the separate ANOVAs and regressions (Figs. 1 and 2), because multiple tests are being performed simultaneously and the significance level is adjusted accordingly.

There were 4 separate examples (4 of 16) in the four-year study where nest fate was correlated with nesting aggregation. Two of these were potential costs of coloniality: nesting aggregation was positively related to higher predation rates in 1995 and higher rates of nest abandonment in 1998. There were also two beneficial associations found: nesting aggregation was associated with a higher proportion of successful nests in 1998 and wind damage was also lowest in these nests. These latter data suggest that individuals may be using the presence of conspecifics to cue-in on habitat that is available early in the nesting season or that is protected from strong winds. Windstorms are a major cause of nest destruction for many grebe species, and nests at Lake Osakis were preferentially located on the leeward side of LI and in bays protected from the predominant northwesterly storms.

The costs of aggregation we detected included increased predation and increased levels of nest abandonment, though evidence for these costs was inconsistent over the duration of the study. However, Klatt (2003) found significantly higher levels of aggression at the

colony sites of this population, which signifies a potential energetic cost to coloniality. Hill et al. (1997) and Hotker (2000), in comparable studies, found similar costs of aggregated nesting in Eared Grebes (*P. nigricollis*) and American Avocets (*Recurvirostra americana*), respectively. The benefits of nesting colonially in our population outweighed any of these potential costs in most years.

Two lines of evidence support a habitat-based model over conspecific models in this population: (1) there are consistent fitness differences between birds nesting at distinct habitat types in this population, with the highest fitness often found at colony sites; and (2) there was no consistent link between nesting aggregation and fitness. The fitness differences between habitat types were pronounced. In three of the four study years, the birds nesting on LI had significantly higher fitness than the rest of the population because they experienced lower rates of weather destruction, predation, or both. In 1995, the year that we did not detect this pattern, there was one nesting region that did not fit well into our classification scheme. It was the large peninsula of shoreline, which was similar in some respects to an LI. The peninsula consisted mainly of a large floating cattail root mass connected to the shoreline by a thin neck of vegetation. A comparison of the habitat types in 1995 with the twelve "peninsula" nests analyzed separately from LI, S, and SI was consistent with peninsula nests sharing some characteristics of both LI and S nests. Peninsula nests had rates of predation similar to those of shoreline nests, which suggests that connectedness to the mainland may be critical (Nuechterlein et al. 2003). On the other hand, the peninsula nests had weather destruction rates and mean dates of nest initiation that were similar to LI.

Commodity selection.—Our use of the commodity-selection approach yielded mostly negative results. There was no clear link between presence of conspecifics and adaptive choice of breeding location. Proximity to conspecifics was not significantly correlated with relatedness (Nuechterlein et al. 2003), nor was prior-year reproductive success of conspecifics an apparent cue for breeding-habitat choice. Brown et al. (2000) used a comparable analysis and found evidence for reproductive-success cueing in Cliff Swallows. We did not specifically test

whether simply the presence of conspecifics was an important cue for habitat choice. However, site fidelity was high: individuals moved little between years, even though habitat and aggregation were dynamic in the same time range (Nuechterlein et al. 2003). This was dramatically illustrated by several birds that had nested in the aforementioned peninsular region in 1995 and that attempted to nest in that region in the following year, even though a windstorm had destroyed all usable habitat there. A critical missing piece of information is how juvenile Red-necked Grebes make their first breeding-habitat choices. We were unable to ascertain the degree to which offspring disperse from the natal area. Young Red-necked Grebes stay on their parents' backs for several weeks and are extremely hard to color-band without significant risk to them. The lack of population-genetic structure suggests that young do not nest directly near parents (Nuechterlein et al. 2003).

We cannot reject conspecific cueing, in which individuals use the presence of conspecifics to select breeding sites; however, we found scant evidence of it. Commodity-selection theory predicts that conspecific cueing is beneficial when the environment is patchy yet predictable (Boulinier and Danchin 1997, Danchin et al. 1998, Doligez et al. 2003). Although habitat was indeed patchy at Lake Osakis, predictability was apparently low. The LI varied in size and shape between years and disintegrated after the study. The peninsula disappeared after one year, and shoreline habitat varied in water depth and wind vulnerability among years (Nuechterlein et al. 2003). Temporal variation in habitat was driven mainly by movement of large, drifting sheets of ice during spring melt. However, in support of conspecific cueing, there were LI that existed during the study that were never observed with nesting Red-necked Grebes. These LI were indistinguishable (by us) from the LI on which we monitored nests, which suggests that this habitat type is not limited and that conspecific cueing could have an effect on initial habitat selection.

Conclusions.—Both the functional and the commodity-selection framework must be applied with caution. Classic studies of coloniality in highly social species face the difficulty of untangling the confounded factors responsible for the maintenance of coloniality with those operating at its evolutionary origin (Siegal-

Causey and Kharitonov 1990). For example, many highly social species, such as gulls (Laridae), are members of mostly colonial taxa, which indicates that this state is ancestral. This suggests that there may have been long periods during which adaptations that minimize the costs or maximize the benefits of the social environment could have evolved. Our study largely avoids this difficulty; because Red-necked Grebes are solitary, their conspecific interactions are mainly territorial in nature. There is no cooperative nest defense, even though colonies are conspicuous. There is a high level of aggression at the colony (Klatt 2003), and there is no cooperative feeding.

Red-necked Grebes may represent the earliest stages of coloniality. Our results support the view that the benefits of high-quality habitat best explain colonial nesting in our population. Overall, we found that birds nesting colonially had higher fitness than others in the population, which supports the idea that aggregated nesting is adaptive in this case.

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