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Colony choice in birds: models based on temporally invariant site quality

Abstract We propose two stochastic models to explain how birds choose colonies. In the resource choice model, birds settle at each site at a rate proportional to the total resources the site contains. In the reduced resource choice model, a smaller cohort of birds enters sites at a rate determined by the total resources at each, and the remaining individuals enter sites at a rate that is linearly proportional to the total number of birds already nesting at each site. Thus, a fraction of birds chooses sites based on the resources present, and the remainder are attracted to a site by the presence of other birds. Colony site quality is assumed not to vary between years. Both models result, on average, in an ideal free distribution of colony sizes if the birds' settlement rate is linearly related to the resources in a site, if resources are distributed equally among individuals within sites, and if individuals with equal resources have equal fitness. We applied these models to long-term data on colony sizes and site usage of cliff swallows in southwestern Nebraska. A test of the resource choice model suggested that the swallow population as a whole did not choose sites based strictly on site quality or the total resources contained at each site. However, a test of the reduced resource choice model suggested that a smaller fraction of the individuals in each colony may have based their choice of site on local resource availability, with the remaining birds aggregating at those sites based on the number of birds already settled there. Tests of these models may provide insight into how individuals choose colony sites and why colonies vary in size.

Key words Cliff swallow · Coloniality · Habitat selection · Ideal free distribution · Social behavior

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Introduction

Most colonially breeding animals occupy fixed colony sites that are distributed nonrandomly through a habitat. Different sites may vary in overall physical size (Lack 1968), quantity of suitable nesting substrate (Hoogland and Sherman 1976; Shields et al. 1988; Burger and Gochfeld 1993), proximity to food sources (Gibbs et al. 1987; Gibbs 1991), extent of overwintering ectoparasite infestations (Brown and Brown 1986; Loye and Carroll 1991), accessibility to predators (Robinson 1985), and other biotic and abiotic features. Most species of colonial birds are distributed such that colony sizes among the breeding sites vary widely in a population (Brown et al. 1990). This variation suggests that colony sites may differ in their suitability as nesting locations. However, differences in reproductive success among individuals in different-sized colonies have usually been interpreted as due to the various social costs and benefits resulting from a given group size (e.g., Hoogland and Sherman 1976; Robinson 1985; Brown and Brown 1986; 1987; in press; Møller 1987; Shields and Crook 1987, Brown 1988) or the degree of relatedness among colony residents (Giraldeau and Caraco 1993; Higashi and Yamamura 1993; Rannala and Brown 1994). There have been few attempts to model colony choice based strictly on colony site characteristics. Explicit models of how animals choose colonies should prove useful in helping to explain why colonies vary in size, why some sites are perennially used and others rarely, and what cues individuals use to select colony sites.

The ideal free distribution

Fretwell and Lucas (1970) presented a general model relating the average fitness of individuals to their distribution among habitat patches. The model assumes that individuals are "ideal" in that they consistently

settle in the habitat that maximizes their fitness, and that they are "free" in their choice of a habitat site, so that all individuals within a habitat have an equal expected fitness. Fretwell and Lucas use the terms "suitability" and "success rate" when they appear to mean fitness, and we use that term instead. An explicit assumption of the ideal free model is that fitness is a monotonically decreasing function of population density, so that there is no resource enhancement due to density (Allee et al. 1949), and an increase in group size never benefits individuals in the group enough to outweigh the costs associated with such an increase. Thus, the ideal free distribution model is most accurate for describing species that live in groups mainly due to an aggregation of resources (i.e., a non-uniform habitat), rather than those species forming groups as a result of particular benefits associated with group-living (e.g., information transfer, predator avoidance) that are increasing functions of population density over some range (see Brown et al. 1990).

Fretwell and Lucas (1970) derived the following result for an ideal free distribution,

$$S_1 = S_2 = \cdots = S_m, \tag{1}$$

where S_1 is the average suitability (= average fitness) in the ith colony, and there are m colony sites in total. In this paper, we will refer to a distribution as ideal free if Eq. 1 is satisfied. If K_i is a measure of the total resources contained in the ith site, and the resources are distributed with uniform density among the n_i individuals in that site, then the average amount of resources received by each individual is,

$$\frac{K_i}{n_i}. \tag{2}$$

If individuals with equal resources have an equal fitness, a situation we will term *fitness equivalence* among individuals, then Eq. 2 provides the average fitness of individuals in the ith colony. In this case, if the distribution is ideal free, Eqs. 1 and 2 imply,

$$\frac{K_i}{K_1 + K_2 + \cdots + K_m} = \frac{n_i}{N} \tag{3}$$

where N is the total number of individuals in m colony sites (i.e., the total population size). Thus, the fraction of individuals in a site, on average, should reflect the total resources present in that site under this model. Whether the ideal free requirement of Eq. (2) is satisfied depends on the process that generates the distribution of birds among colony sites. If the expected number of birds in a site is a linear function of the resources contained in that site, under the above model of within-site resource allocation the distribution will be ideal free on average. In this paper, we consider two models of the process of colony choice that may, in certain cases, result in an ideal free distribution.

Limited theory has been developed to explain how individuals actually go about choosing habitats (Partridge 1978), but for birds one habitat-based colony choice hypothesis was developed by Shields et al. (1988) which they termed the "traditional aggregation hypothesis" (TAG). In the case of barn swallows (*Hirundo rustica*), Shields et al. (1988) argued that colony sites varied in suitability (as in an ideal free model), and birds used the presence of nests remaining from a previous breeding season to gauge the suitability of a site and the probability of successful reproduction there. Individuals aggregated at sites with many existing nests, which were indicators of breeding success the previous year. This kept large colonies perennially large, and caused the birds to avoid potential sites with few or no existing nests.

The temporal invariance hypothesis

The TAG hypothesis, as outlined by Shields et al. (1988), implicitly assumes that colony site quality is either temporally invariant, or highly correlated, between breeding seasons. That is, whatever determines a site's suitability one year determines it similarly the following year, enabling animals to predict site quality based solely on the presence of nests from previous years. Though not recognized by Shields et al. (1988), in this model the process of change may ultimately be described as a Markov chain with zero nests as an absorbing state. Thus, small colonies will tend to be unused more often than large ones, the nests will disappear completely from these sites, and the birds will ultimately accumulate at a single site. The nest-based choice hypothesis (Shields et al. 1988) therefore cannot account for a range of colony sizes, unless the system is far from equilibrium and the distribution has been determined initially by some other mechanism.

However, if we retain the assumption, implicit in the TAG hypothesis, that site quality is temporally invariant, it may be reasonable to expect that some species of birds choose nesting sites based on an evaluation of the total resources available at or near each site. The number of birds in each site might then approach a steady-state distribution over time. For example, eastern kingbird (*Tyrannus tyrannus*) territories appear to be somewhat consistent from year to year in their expectation of breeding success, and birds apparently assess potential territories based on a suite of currently available resources, although not necessarily on past breeding performance per se (Blancher and Robertson 1985). In this paper, we develop a stochastic model of colony choice in which birds settle in a particular site at a rate proportional to the total available resources that are contained in that site.

In addition, we consider a more complex model in which only a fraction of the total individuals are "choosers" (i.e., they enter sites at a rate determined

by the available resources) and the remaining individuals enter a site at a rate determined by the number of individuals already settled there. This second model incorporates the "conspecific attraction" hypothesis (Stamps 1988; Smith and Peacock 1990; Reed and Dobson 1993) and may be realistic for certain species in which experienced individuals choose sites based on resource availability and inexperienced individuals choose sites based on the number of conspecifics present (e.g., Burger 1988).

The models we present provide an explicit formulation of the temporal invariance hypothesis as applied to colony choice, and relate the ideal free distribution to the colony choice process. Probabilistic models based on continuous-time stochastic processes have previously been used to describe group formation in a number of animals (Cohen 1971, 1972, 1975; Morgan 1976). To our knowledge, the models presented in this paper represent the first stochastic models to be developed for studying choice of breeding colony in birds. We apply the models to colonial cliff swallows (*Hirundo pyrrhonota*) to illustrate the potential insights into colony choice that this approach may offer.

Probability models of colony choice

Consider a population subdivided into discrete colonies of individuals, with the segregation of individuals into colony sites occurring in continuous time during the course of a breeding season. Each colony site contains a fixed amount of resources, and this amount is temporally invariant for particular sites. We consider two ways that individuals may distribute themselves among colony sites. In the *resource choice* model individuals settle in a particular colony site with a rate determined by the resources that the site contains. We use the term "resources" in a general sense, and these may include nesting spaces, food sources, nest-building materials, and other properties of a site. In the *reduced resource choice* model a smaller fraction of individuals are resource-based "choosers," being distributed as in the resource choice model, with the remaining individuals settling in colony sites at a rate that is linearly proportional to the total number of individuals that have settled at each site. It is assumed that the system of populations is "open" in that the flux of individuals through the local breeding region remains constant, and the arrival rates of individuals at each colony do not vary with time. Both models predict that, in certain special cases to be considered below, individuals will settle in colony sites in such a way that each individual, on average, receives an equal fraction of the total resources available in the collection of sites as a whole. If individuals have an equal fitness, given an equal share of the resources, the resulting distributions are ideal free (*sensu* Fretwell and Lucas 1970).

Resource choice model

Consider a colony site i that individuals colonize according to a Poisson process with rate K_i. It is assumed that the value of K_i is linearly proportional to the resources available in the ith site and is invariant over time. Each individual that has settled in the site leaves with probability μ in unit time. During a small interval of time dt, the probability that a single arrival occurs in the ith colony site is $K_i dt$, and the probability that a single departure occurs is $N_i \mu dt$, where N_i is the number of birds in the ith colony. It is assumed, in all cases, that the probability of two or more events occurring in an infinitesimal interval of length dt is of order $o(dt)$ and may be neglected. This model is equivalent to the well-known stochastic immigration-death process (see Renshaw 1991, p. 43) and has a steady-state distribution of population size that is Poisson with density,

$$P(N_i = n) = \frac{\exp\left[-\frac{K_i}{\mu}\right]\left(\frac{K_i}{\mu}\right)^n}{n!} \quad . \tag{4}$$

In this case, the expectation and variance are both simply K_i/μ, and if μ does not vary among sites then the expectation of the distribution of individuals among sites is linearly proportional to the resources in each site and, given a uniform distribution of resources within sites and fitness equivalence, is ideal free on average.

Reduced resource choice model

Consider a colony site i that receives individuals that choose based on resources with a rate K_i, and let additional individuals enter with a rate λN_i which is independent of the resources in the ith site, but is linearly dependent on the total number of individuals that have settled in the site. Each resident individual leaves the site with probability μ in unit time. During a small interval of length dt, the probability of a single arrival for the ith colony is

$$(K_i + \lambda N_i)dt, \tag{5}$$

and the probability of a single departure is $N_i \mu dt$. This model is equivalent to a stochastic birth, death and immigration process (see Kendall 1948, 1949), and has a steady-state distribution of population size (for $\lambda < \mu$) that is negative binomial,

$$P(N_i = n) = \binom{\frac{K_i}{\lambda} + N_i - 1}{N_i}\left[1 - \frac{\lambda}{\mu}\right]^{\frac{K_i}{\lambda}}\left[\frac{\lambda}{\mu}\right]^{N_i}, \tag{6}$$

with expectation,

$$E[N_i] = \frac{K_i}{\mu - \lambda}, \tag{7}$$

and variance,

$$\text{Var}[N_i] = \frac{K_i \mu}{(\mu - \lambda)^2}; \tag{8}$$

Thus, the expected number of individuals in the ith site is again linearly proportional to the resources contained in the ith site, if μ and λ are constant among sites. The expectation of the distribution of individuals among sites, given a uniform distribution of resources within sites and fitness equivalence, is ideal free.

Properties of the models

Several properties of the resource choice and reduced resource choice models are apparent. First, the distribution of individuals is, on average, ideal free if μ and λ do not vary among sites, K_i is a linear function of the resources in a site, resources are uniformly distributed among individuals, and fitness equivalence exists. Second, the reduced proportion of resource-based "choosers" in the second model increases the variance of the distribution, and therefore decreases the "efficiency" of the colony choice process in achieving the ideal free state. We also note, from Eq. 6, that the overdispersion parameter of the negative binomial distribution, k_i, is equal to K_i/λ under the reduced resource choice model. The parameter k_i may then be estimated for particular colony sites, and will indicate the relative magnitudes of these two parameters if the model is correct. Thus, if a site contains few resources, and each individual's presence has a large influence in attracting other individuals to the site, k will tend to be small. Alternatively, if a site has a large resource base, and the individuals present have little influence in attracting others to the site, k will tend to be large.

Another useful relationship is that between the expectation of the population size in the ith site and k_i. If a regression is made of the mean population size versus k for each colony site, the value of K_i factors out of the regression and has no effect. Assuming λ and μ are constant among sites, the expected slope of the regression is $\lambda/(\mu - \lambda)$. Thus, variations in λ and μ among sites will cause deviations about the regression line. Large deviations suggest variation in one or both of these parameters among sites. This is important, because both parameters must remain constant among sites in order for the distribution of individuals to be ideal free on average.

Colony site choice in cliff swallows

Statistical tests of the models

The resource choice model predicts that any particular colony site will have a population size, among years, that is an independent and identically distributed Poisson random variable. Thus, we may test the fit of this model by fitting the annual colony sizes across years at each site to a Poisson distribution. We used the dispersion index for this test (see Southwood 1978), which is defined as

$$ID = \frac{s_i^2(n-1)}{\bar{x}_i}, \tag{9}$$

where, for the ith colony site, $\bar{x}_i$ is the mean population size among years, s_i^2 is the variance in population size among years, and n is the number of years that the population counts were made. The ID statistic is χ^2 distributed with $n-1$ degrees of freedom.

The reduced resource choice model predicts that a particular colony will have a size that is an independent and identically distributed negative binomial random variable among years. Thus, we may test the fit of this model by fitting the annual colony sizes across years at each site to the negative binomial distribution. To test this fit, we first applied the maximum likelihood estimator to find k_i, the overdispersion parameter, for the ith colony site,

$$\sum_{l=1}^{n_i} \sum_{j=0}^{n_{il}-1} \left(\frac{1}{k_i+j}\right) = n_i \log\left(1+\frac{\bar{x}_i}{k_i}\right), \tag{10}$$

where n_i is the number of years that the ith site was observed, n_{il} is the population size of the ith site in year l, and $\bar{x}_i$ is the mean observed population size, among years, for the ith site. Equation 10 was solved numerically to estimate k_i. The fit of the cliff swallow data to the reduced resource choice model was tested by calculating the statistic, based on the difference between the observed and expected skew (from Evans 1953),

$$T_i = \gamma_i + s_i^2 - \frac{2(s_i^2)^2}{\bar{x}_i}, \tag{11}$$

where γ_i is an estimate of the skew, and s_i^2 is an estimate of the variance, among years, in population size for the ith site. If the observed value of the statistic T_i exceeded its predicted standard error, calculated using the formula given by Evans (1953, p. 205) with the value of k_i estimated from Eq. 10, then the observed distribution of colony size, in the ith site, was taken to be significantly different from a negative binomial distribution, and therefore not to fit the predictions of the reduced resource choice model.

Applying the models

Our test of these models for cliff swallows is based on colony site occupancy data collected over a 13-year period, 1982–1994, at our study site in southwestern Nebraska. Within an area of approximately 150×50 km along the North and South Platte rivers, centered near Ogallala, we scored whether each cliff swallow colony site was used each year, and if so, the approximate or exact number of active nests. Active nests were defined as those in which at least one egg was laid. We visually inspected the contents of nests at some sites and got

exact counts of active nests, and at other sites estimated the number of active nests based on counts within colony sections or (at inaccessible sites) the number of birds present on a daily basis. Estimated colony sizes agreed closely (to within about 3% on average) with exact counts of nests for a sample of 23 colony sites where we used both methods (Brown and Brown in press).

An empirical test of the models requires only that the colony size at each site each year be known. We used 65 colony sites for which size and usage were known for ≥ 10 years during the study. We did not include other potential sites which were either discovered by us in later years or were added to the study area in later years by the construction of new highway bridges (on which cliff swallow colonies are often located).

Dispersion indices (Eq. 9) (Table 1) indicated that cliff swallow colony sizes across the span of years sampled did not fit a Poisson distribution. For each colony site the dispersion index differed significantly from that expected under the resource choice model (Table 1). Values of the T statistic (Eq. 11) for the same colony sites (Table 1) indicated that cliff swallow colony sizes more closely matched those predicted from the negative binomial distribution. At 55 of 65 sites (85%) the T statistic did not differ significantly from that expected under the reduced resource choice model (Table 1).

There appeared to be no relationship between colony size and the likelihood of a site's fitting the reduced resource choice model (Table 1). However, there was a relationship between colony size and the overdispersion parameter, k: the value of k increased significantly with colony size (Fig. 1). This positive correlation was either due to an increase in the resources contained in a site with size, or a decrease in the relative effect each individual had in attracting others to a colony site as the colony there became larger. More importantly, the deviations about a mean-versus-k regression line increased with the mean population (colony) size, with more variation among the larger colony sites. This sort of variation in λ or μ suggests that the distributions of cliff swallows among sites were not ideal free.

Inferences about colony choice

The application of the resource and reduced resource choice models to cliff swallows yielded insight into colony choice that would not otherwise have been possible. The observation that the distributions of colony sizes at each site differed so much from those expected under the resource choice model indicated that this model, and the temporally invariant resource hypothesis that it is based upon, did not adequately explain colony site choice in cliff swallows. The model provided a quantitative test of whether birds distributed themselves among colonies based on the total resources in each, and allowed us to reject a simple resource-based
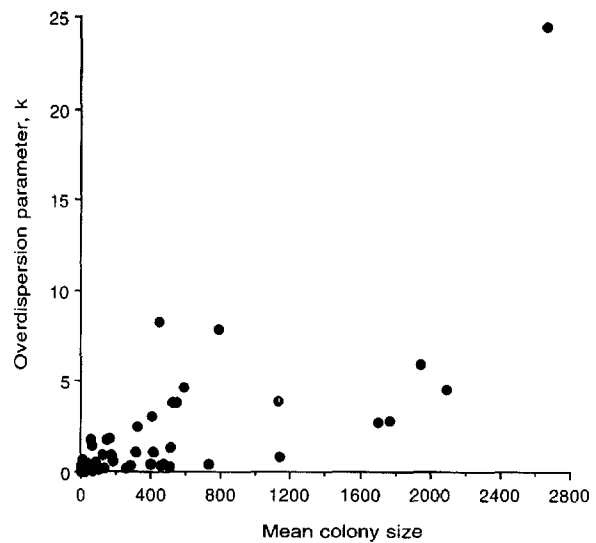

Fig. 1 Overdispersion parameter, k, as a function of mean cliff swallow colony size per site. The value of k increased significantly with colony size ($r_s = 0.78$, $P < 0.001$, $n = 65$ sites). Overlapping dots where colony size is less than 200 represent a total of 41 colony sites (see Table 1)

colony choice hypothesis of this form (*sensu* Shields et al. 1988) as an explanation for how cliff swallow colonies are chosen and why colonies vary in size. Cliff swallows apparently do not assess and select colony sites based solely on the total resources (e.g., nesting sites, food, nest-building materials, predators) present at each site.

The reduced resource choice model suggested, however, that some birds in the population may have actively chosen colony sites based on characteristics of the local resources at each site, with other individuals aggregating at each colony site at a rate determined by the number of birds that had already settled there. The fit for the reduced resource choice model agrees with our biological observations that cliff swallows often seemed to be attracted to occupied colonies. Some prospecting potential colony residents likely have their attention initially drawn to a site by the conspicuousness of the bird traffic around an active colony. Birds who base their choice of colony solely on the number of existing settlers at a site probably spend less time searching for other sites within the habitat and may begin nesting sooner. Early nesting provides a variety of fitness advantages in cliff swallows, but non-choosers must pay the cost of relying on other individuals to assess local resources accurately. The substantial individual variation in the number of colonies visited by different radiotagged cliff swallows early in the season when selecting colonies (Brown and Brown in press) suggests that individual birds may indeed choose colonies in different ways. Colony selection of the sort predicted by the reduced resource choice model may also occur in colonial least terns (*Sterna antillarum*) (Burger 1988).

The relationship between the overdispersion parameter, k_i, and mean colony size (Fig. 1), and in

Table 1 Statistical fit of cliff swallow colony usage data to the Poisson distribution, and negative binomial distribution, as expected under the "resource choice" and "reduced resource choice" models, respectively, for 65 colony sites. Mean colony size is in number of nests and calculated across all years of data for each site (*SD* standard deviation of colony size; *ID* index of dispersion, *k* estimate of the overdispersion parameter, *T* test statistic for the negative binomial distribution, *SE(T)* standard error of T, *n* number of years of data for each site)

Site	Mean size	SD	ID	k	T	SE(T)	n
1	0.15	0.55	24.00*	0.07	1.89	2.24	13
2	0.38	1.39	60.00*	0.03	−14.49	435.42	13
3	0.62	1.33	34.25*	0.19	−6.62	15.55	13
4	1.25	4.33	165.00*	0.02	−541.10	44,643.30	12
5	1.36	4.52	150.00*	0.02	−590.72	60,594.30	11
6	1.92	6.93	300.00*	0.02	−2,352.95	156,810.00	13
7	2.00	3.49	67.00*	0.18	−134.91	783.49	12
8	2.73	9.04	300.00*	0.02	−4,824.81	487,292.00	11
9	3.15	6.01	137.51*	0.32	−790.11	748.99	13
10	3.36	7.65	174.38*	0.14	−1,984.93	7,401.97	11
11	5.50	5.76	66.37*	0.66	−366.10	782.74	12
12	5.77	15.22	481.57*	0.22	−18348.50*	11,644.70	13
13	5.77	7.89	140.04*	0.20	−1,923.99	10,907.20	13
14	7.31	17.15	483.16*	0.06	−23,396.90	566,933.00	13
15	7.46	19.58	616.66*	0.06	−39,022.30	603,571.00	13
16	8.00	14.64	321.50*	0.21	−11,268.80	34,986.30	13
17	11.62	24.86	638.56*	0.20	−65,160.90	121,084.00	13
18	14.00	21.24	354.43*	0.19	−28,616.40	250,107.00	12
19	16.91	22.27	293.27*	0.27	−28,589.10	199,419.00	11
20	20.85	30.53	536.39*	0.14	−82,369.60	1.66 e6	13
21	21.92	37.88	785.42*	0.17	−186,399.00	1.21 e6	13
22	24.55	26.54	287.01*	0.51	−39,732.60	139,642.00	11
23	27.31	96.97	4131.80*	0.02	−6.47 e6	2.87 e8	13
24	28.08	44.14	832.60*	0.10	−268,380.00	9.22 e6	13
25	32.50	40.93	566.92*	0.11	−170,978.00	1.18 e7	12
26	37.00	44.85	543.68*	0.33	−216,719.00	1.31 e6	11
27	50.00	109.54	2400.00*	0.05	−5.75 e6	3.11 e8	11
28	58.45	48.86	408.27*	1.76	−192,538.00*	131,979.00	11
29	62.73	145.88	3392.75*	0.03	−1.44 e7	2.18 e9	11
30	66.83	71.33	843.66*	0.20	−775,298.00	2.49 e7	12
31	69.83	55.71	488.90*	1.38	−272,828.00	355,890.00	12
32	73.17	55.71	651.85*	0.45	−509,534.00	4.76 e6	12
33	85.77	65.85	3335.02*	0.49	−1.32 e7*	6.06 e6	12
34	96.82	154.39	1854.13*	0.10	−6.64 e6	4.12 e8	13
35	101.69	212.67	5336.85*	0.13	−4.02 e7	2.45 e8	11
36	120.75	111.23	1127.16*	0.93	−2.52 e6	4.27 e6	12
37	136.54	197.80	3438.73*	0.14	−2.24 e7	5.03 e8	13
38	151.92	121.03	1157.01*	1.74	−2.81 e6*	2.21 e6	13
39	162.73	134.45	1110.87*	1.85	−4.00 e6*	2.61 e6	11
40	177.00	135.17	1238.14*	0.91	−3.76 e6	1.36 e7	13
41	181.25	134.39	1096.03*	0.54	−3.58 e6	4.79 e7	12
42	261.25	326.69	4493.61*	0.20	−8.71 e7	1.45 e9	12
43	281.80	283.63	2569.27*	0.35	−4.59 e7	5.33 e8	10
44	316.25	294.72	3021.21*	1.06	−4.76 e7	5.80 e7	12
45	320.45	242.59	1836.52*	2.48	−2.16 e7*	1.12 e7	11
46	397.69	522.05	8223.39*	0.44	−3.73 e8	7.75 e8	13
47	409.62	170.64	853.05*	3.02	−4.11 e6	1.48 e7	13
48	414.58	223.98	1331.03*	1.07	−1.21 e7	1.28 e8	12
49	445.83	145.18	520.02*	8.21	−1.97 e6	3.31 e6	12
50	457.90	525.51	5427.99*	0.35	−3.33 e8	2.29 e9	10
51	470.00	352.92	2385.11*	0.40	−6.59 e7	1.78 e9	10
52	504.62	473.47	5330.94*	0.23	−1.99 e8	7.59 e9	13
53	518.91	318.10	1950.02*	1.36	−3.94 e7	1.59 e8	11
54	521.15	294.01	1990.41*	3.81	−2.86 e7*	1.98 e7	13
55	545.83	274.86	1522.52*	3.78	−2.08 e7	2.40 e7	12
56	593.18	331.30	1850.38*	4.66	−4.05 e7*	2.20 e7	11
57	728.85	727.00	8701.85*	0.42	−7.66 e8	5.32 e9	13
58	786.54	294.15	1320.05*	7.87	−1.89 e7	1.89 e7	13
59	1,129.17	594.85	3447.05*	3.86	−2.21 e8*	2.05 e8	12
60	1,139.38	778.72	6386.69*	0.83	−6.45 e8	4.42 e9	13
61	1,700.00	1,031.38	7508.82*	2.72	−1.33 e9*	1.30 e9	13
62	1,770.83	1,061.83	7003.65*	2.79	−1.43 e9	1.46 e9	12
63	1,941.67	799.38	3620.17*	5.92	−4.20 e8	4.85 e8	12
64	2,092.50	986.16	4182.83*	4.51	−9.03 e8	1.08 e9	10
65	2,670.83	542.07	1210.22*	24.50	−6.45 e7	1.20 e8	12

*$p \leqslant 0.05$

particular the deviations about the expected regression, suggest that an ideal free distribution of colony sizes is rarely achieved in cliff swallows, even if the reduced resource choice model is correct. This is consistent with direct empirical observations of reproductive success (Brown and Brown 1986, in press) that imply major differences in fitness among birds occupying different colony sites. Thus, another possible explanation for the observed distribution of cliff swallow colony sizes is that choice of colony site is based on the expected social costs and benefits of living in groups of particular sizes independent of site characteristics or site quality per se (Brown and Brown in press). A process of colony choice based on density-dependent social effects will typically result in distributions that are not ideal free, because the fitness function will normally not monotonically decrease with density. If fitness increases with density over some interval, then a unique distribution of birds among sites that maximizes average fitness need not exist (Fretwell and Lucas 1970). One outcome of testing the resource choice model is that its rejection underscores the possibility that cliff swallows may choose colonies based largely on density-dependent social effects. Unfortunately, the form of the distribution of colony sizes that is expected under a colony choice model based on density-dependent social effects is not presently known.

Although cliff swallows as a whole did not fit a simple model of resource-based colony choice, other colonial species may be more likely to choose colonies in the manner predicted by the resource choice model. Seabirds that occupy perennially used colony sites and live in large colonies (e.g., Gaston and Nettleship 1981; Coulson and Thomas 1985; Nettleship and Evans 1985; Spendelow and Patton 1988; Brooke 1990) would be good candidates. This may be especially the case when colonies are so large that the relevant social costs and benefits of group living (e.g., ectoparasitism, increased foraging efficiency, predator avoidance) level off at smaller group sizes, leaving the truly huge colonies to form mostly in response to local resources and colony site quality.

The reduced resource choice model also is likely to apply to other colonial species. It might be expected to describe especially well instances in which young and inexperienced birds settle at colonies following the cue of older individuals that have colonized the sites. First-time breeders in a variety of colonial species typically arrive at sites later than older birds and this may act to enhance the influence of older birds in determining the sites that are used (Coulson and White 1958; Harrington 1974; Massey and Atwood 1981; Brooke 1990; Brown and Brown in press). Individuals that have never bred before may be more likely to aggregate at existing colonies and less likely to move among a large number of colony sites, some of which may be unoccupied and difficult for a naive bird to assess.

The most problematic assumption inherent in the resource choice and reduced resource choice models is that site quality – the total resources at a site – does not change between years. Depending on the array of resources that potentially influence colony choice, an assumption of temporal invariance may or may not be realistic. If the major resource in question is simply nesting substrate, there may be little variation between years, and the resource choice model would then be appropriate (as perhaps in certain seabirds). If birds are basing their choices on local food resources around a colony, or local predator/parasite population sizes, those resources may show greater annual variability. It is thus possible that a species might in fact choose colonies based on the proportion of resources at each site and settle in an ideal free way, but annual variability in site quality would confound tests of the resource choice model.

Unfortunately, it appears unlikely that a more general model of colony choice, allowing for temporally variable site quality, will be possible. Estimation of the parameters for either model considered in this study, for example, is much more difficult if the population size each year is not an independent and identically distributed (IID) random observation from a fixed distribution (the IID property arises as a result of a colony choice process "restarting" each year with identical parameters). Furthermore, there is often no way to measure independently the resource characteristics associated with colony sites. Such a large number of variables potentially determine site quality, and usage, that an attempt to measure site quality independent of the number of birds occupying the sites will most often prove inconclusive.

We suggest that the models presented here should have broad application with many colonial animals, and we encourage other workers to test them. Even when the observed colony sizes in a population do not match those predicted under these models, we may still gain insight, by a process of elimination, into how the animals choose colony sites. Paradoxical as it may seem, a "poor" fit of empirical observations to those expected under a particular model is generally more informative than a "good" fit, because it allows one to reject the offending model as an explanation for the process. The resource choice model was clearly rejected for cliff swallows, and we can thus rule out this form of simple resource-based colony choice in these birds. On the other hand, although the cliff swallow data provided an acceptable fit to a negative binomial distribution, as predicted under the reduced resource choice model, this distribution may be generated in numerous other ways (see discussion in Southwood 1978). Until other possible models generating a similar distribution are ruled out, we cannot be certain that the reduced resource choice model is an accurate description of how cliff swallows choose colonies (see Waters 1959).

Additional models of colony choice with explicit quantitative predictions are needed, given the little we know about how animals choose colonies in nature.

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