

FORMATION AND GROWTH OF NEW SEABIRD COLONIES: THE SIGNIFICANCE OF HABITAT QUALITY

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SUMMARY

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Despite the central role that colonial breeding plays in the ecology of marine birds, few theoretical or empirical studies have addressed the process by which new seabird colonies form and grow. Documented colonization events are rare, but suggest an intriguing paradox—prospective breeders are reluctant to pioneer new colonies even when they may suffer substantial costs by recruiting into large established colonies. Once formed, however, new colonies become highly attractive to prospective breeders and grow rapidly. We evaluated the contributions of habitat quality and individual quality to processes of colony formation and growth in Black-legged Kittiwakes (*Rissa tridactyla*) using productivity and population data from 14 new colonies that formed in Chiniak Bay, Kodiak Island, Alaska, in the late 1980s. Two lines of reasoning suggest that habitat quality in established colonies was more important than individual quality in promoting formation of new colonies: new colonies exhibited greater productivity than old colonies, and new colonies formed at a time when compelling evidence existed of low habitat quality in established colonies. In addition, population modeling revealed that: i) immigration fueled rapid growth of new colonies, ii) some established breeders may have relocated from old to new colonies, and iii) Chiniak Bay did not constitute a closed metapopulation. We propose that, although inverse density dependence in small seabird colonies can explain both the reluctance of individuals to pioneer new habitat and the rapid growth of newly formed colonies, density-independent factors such as predation may also contribute to differences in habitat quality between old and new colonies.

Key words: Colony formation, colonial breeding, habitat quality, population dynamics, conspecific attraction, *Rissa tridactyla*, Black-legged Kittiwake

INTRODUCTION

Colonial breeding is a specialized form of group living in which individuals raise offspring in densely aggregated territories that contain no other resource than a breeding site (Wittenberger & Hunt 1985). This breeding system is widespread among vertebrates, occurring in fish, reptiles, mammals and birds (Rolland *et al.* 1998), and is the principal form of social organization for 98% of marine bird species (Wittenberger & Hunt 1985). Colonial breeding is a unifying characteristic of seabirds as a group and has evolved independently in each of several disparate seabird lineages as a precursor to invasion of marine habitats by these taxa (Rolland *et al.* 1998). Although much research has been directed toward understanding the evolution of avian coloniality (reviewed by Brown & Brown 2001), population regulation (Ashmole 1963, Lewis *et al.* 2001), and metapopulation dynamics (Danchin *et al.* 1998) of seabird colonies, few theoretical or empirical studies have directly addressed demographics associated with formation and growth of new seabird colonies (Kharitonov & Siegel-Causey 1988, Forbes & Kaiser 1994).

Social attraction is an important determinant in habitat selection by breeding seabirds, wherein the presence (Burger & Shisler 1980), density (Kildaw 1999) and reproductive success (Danchin

et al. 1998) of established breeders play a role. Seabird colonies are conspicuous and highly attractive to conspecific prospectors (reproductively mature individuals seeking a nesting site), and managers have successfully established new breeding colonies by using social attractants (decoys and call playbacks) to lure prospectors to unoccupied habitat (Podolsky & Kress 1989).

The prevalence of colonial breeding among seabirds and the attractiveness of established colonies to prospectors suggest that potential benefits such as predator deterrence (Birkhead 1977), enhanced ability to locate food (Buckley 1997, Burger 1997), and information regarding habitat suitability (Boulinier & Danchin 1997) outweigh costs such as competition for nest sites (Potts *et al.* 1980) or food (Furness & Birkhead 1984, Lewis *et al.* 2001), increased prevalence of disease and parasites (Boulinier & Danchin 1996), and predator attraction (Brown & Brown 1996). The net advantage of colonial breeding to seabirds must truly be great because, when faced with intense competition for limited nest sites within established colonies, potential recruits make use of lower-quality nest sites (Ashmole 1962, Kildaw 1999, Potts *et al.* 1980) or may defer breeding and join a pool of “floater” individuals (Manuwal 1974, Nelson 1978, Porter & Coulson 1987) rather than colonize unoccupied habitat that is often available nearby (Kildaw 1999, Olsthoorn & Nelson 1990, Porter & Coulson 1987).

While variation in the size of seabird colonies is usually dampened by low reproductive output, low adult mortality and high fidelity to nest sites, the formation of new colonies is critical to the persistence of seabird metapopulations: individual colonies do fluctuate in size and occasionally decline to extinction (Danchin & Monnat 1992, Heubeck *et al.* 1999, McGrath & Walsh 1996). The attractiveness of established colonies to prospectors presents a substantial impediment to formation of new colonies and highlights the central question of this paper: Which conditions induce prospecting seabirds to pioneer vacant habitat and form new colonies rather than join existing ones?

From a cost–benefit perspective, individuals should form new colonies when there is a net payoff in fitness for doing so. Information is an important resource for seabirds engaged in selecting habitat. Danchin *et al.* (1998) suggested that where factors such as food availability, predation or parasitism are spatially localized but predictable across years, prospecting individuals can use the success of conspecifics as an indicator of breeding habitat quality. Forbes and Kaiser (1994) explicitly addressed new-colony formation from a cost–benefit perspective by proposing that uncertainty regarding the quality of unoccupied habitat presents an “information barrier” to would-be pioneers. The information-barrier hypothesis is a special case of Fretwell’s (1972) “ideal Allee” model of habitat distribution, wherein habitat quality initially increases with size in small colonies, but eventually declines because of crowding and associated density-dependant costs in larger colonies. Forbes and Kaiser (1994) assumed that prospecting seabirds make ideal decisions (*sensu* Fretwell 1972) and posited that prospectors will pioneer new colonies only when the cost of joining an established colony exceeds the cost of the information barrier.

In this paper we evaluate two hypotheses to explain why 14 new kittiwake colonies formed within Chiniak Bay (Kodiak Island, Alaska) in the mid-to-late 1980s. The “Habitat Quality” hypothesis proposes that individuals should pioneer new colonies when diminished habitat quality in established colonies lowers the anticipated fitness payoff to a prospecting individual below that achievable in new, unoccupied habitat. We define habitat quality broadly to include a number of factors that may change in a density-dependent or density-independent manner: prey abundance and accessibility (Suryan & Irons 2001), nest site suitability and availability (Potts *et al.* 1980), and the prevalence of predators, diseases and parasites (Danchin 1992, Boulinier & Danchin 1996). In contrast, the “Individual Quality” hypothesis proposes that low-quality individuals form new colonies because they are poor competitors with a lower expectation of fitness in established colonies than in vacant habitat. Individuals may differ in quality because of varying abilities to compete for nest sites or food (Porter & Coulson 1987, Hamer & Furness 1991), to avoid predators, or to resist parasites and disease (Boulinier *et al.* 1997). If individuals experience different costs and benefits within established colonies (Brown *et al.* 1990), then low-quality individuals might enhance their fitness by pioneering vacant habitat.

Habitat quality and individual quality are not mutually exclusive hypotheses—their net effect may be additive or interactive. Hence, we can determine which hypothesis best agrees with our observations, but we cannot reject either hypothesis outright. We evaluated these two by comparing productivity (chicks fledged per nest attempt) of new and old colonies and by determining whether

demographic trends in established colonies indicated diminished habitat quality (suggesting the Habitat Quality hypothesis) or heightened intraspecific competition for nest sites and food (predicted by the Individual Quality hypothesis) during the time when new colonies were formed. If new colonies formed because of diminished habitat quality in old colonies, then we predict i) greater productivity of new versus old colonies, and ii) evidence of low productivity, large colony size and declining populations at the old colonies. If new-colony formation is better explained by the dispersal of low-quality individuals, then we predict i) lower productivity of new colonies versus old colonies, and ii) evidence of high productivity (attractive to prospectors and raising competition for nest sites), large colony sizes, increasing population trends and an abundance of potential recruits in old colonies.

In addition to those empirical tests, we employed deterministic population modeling to characterize the growth patterns of new colonies and to address three specific questions: i) Does immigration contribute to the growth of new colonies? ii) Did established breeders emigrate from old to new colonies? iii) Does Chiniak Bay act as a closed kittiwake metapopulation?

METHODS

We studied breeding colonies of kittiwakes in Chiniak Bay on the northeastern coast of Kodiak Island, Alaska (Fig. 1). Between 1984 and 1990, 14 new colonies formed in the bay, presenting a rare opportunity to investigate colony formation and growth within a metapopulation of seabirds. Kittiwakes nest on vertical cliff faces of numerous small islands and sea stacks scattered around the bay’s perimeter and on two mainland sites at Gibson Cove and Sealand. In some analyses, we distinguish colonies in designated “inner” and “outer” regions of Chiniak Bay (Fig. 1) because, in several years, poor weather and time restrictions permitted a complete census of only “inner” colonies.

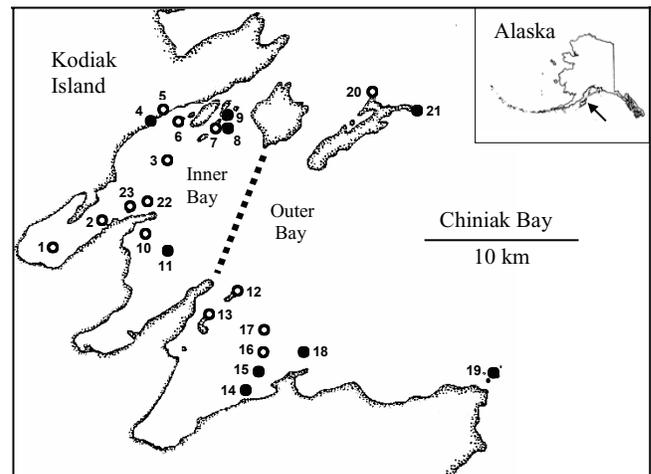


Fig. 1. Distribution of kittiwake colonies in Chiniak Bay, Alaska: (1) Mary I., (2) Blodgett I., (3) Puffin I., (4) Gibson Cove, (5) Sealand, (6) Gull I., (7) Crooked I., (8) Kulichkof I., (9) Holiday I., (10) Marathon Rock, (11) Veisoki I., (12) Queer I., (13) Kalsin I., (14) Utesistoi I., (15) Svitlak I., (16) Middle I., (17) Pinnacle Rock, (18) Kekur I., (19) Cape Chiniak Is., (20) Long I. Inner, (21) Long I. Outer, (22) Cliff I., (23) Zaimka I. Filled circles denote colonies present in 1975, open circles indicate new colonies formed mainly in the mid-to-late 1980s. The dashed line demarcates inner and outer regions of the bay.

We use counts of kittiwake nests and broods between 1975 and 2004 as indices of abundance and productivity. In all years, brood counts were conducted in early August, just before fledging of the earliest-hatched nestlings in Chiniak Bay. In most years, nest counts were conducted in mid-incubation (late June), but from 1989 through 2002, they were combined with brood counts in early August. We assume that every new colony was observed in its year of formation because white guano streaks are readily observed on generally dark cliffs within Chiniak Bay, although it is possible that colonies founded by only a few pairs evaded detection initially. All counts were made from an open skiff or small boat (<10 m) at a distance of 40–150 m using 8×–10× binoculars and tally counters. We defined a nest as any site at which a palm-sized, or larger, disk of nesting material was present, regardless of the presence or absence of a bird. During brood surveys, we kept separate counts for broods of 1, 2, or 3 chicks and also tallied recently fledged chicks seen roosting on cliff faces or on the water near the colony. We defined productivity for each colony as total nestlings divided by total nests.

Nest counts are imperfect indices of kittiwake population sizes because they are influenced by variability in breeding propensity and by the persistence of nests through the season. For example, low nest counts in 1983 and 1997/98 coincided with severe El Niño events, and likely did not reflect actual changes in population size. These short-term declines were rapidly reversed (Fig. 2[a]). Suryan and Irons (2001) concluded that brood counts underestimate chicks fledged by 23%, a correction factor that accounts for chick observability at the time of the census. We did not correct indices of productivity in most analyses because only relative productivity was important. However, we corrected productivity measures by a factor of 1.23 when modeling the growth of new colonies, because absolute values were required.

Population modeling and Monte Carlo simulations require complete time series of population and productivity measures over the spatial and temporal scales of interest. Unfortunately, no kittiwake counts are available for a number of years in the 1970s and early 1980s, and surveys of outer-bay colonies were incomplete in most years between 1983 and 1997. For a few colonies that lacked data for 1983, 1996, 1997 and 1999, we estimated nest counts based on an adjacent year and the between-years ratio obtained for colonies counted in both years. We interpolated missing nest counts for all other years using known counts from the individual colonies, ignoring the anomalous nest counts from the El Niño year of 1983.

We could not interpolate missing productivity data, because productivity was highly variable among years (Fig. 2[b]). Fortunately, productivity was highly correlated between outer and inner regions for both old ($R^2 = 0.81$) and new ($R^2 = 0.72$) colonies. We therefore estimated missing productivity data for old and new colonies in the outer bay using data from the inner bay (for old colonies, $\text{outer} = 1.14 \text{ inner} - 0.006$; for new colonies, $\text{outer} = 0.82 \text{ inner} - 0.001$). Because no productivity data were collected from any Chiniak Bay colony in 1976 or between 1979 and 1982, we estimated those missing values by regressing Chiniak Bay productivity against the average productivity of kittiwakes on Middleton Island (400 km NE of Chiniak; Hatch *et al.* 1993) and Chowiet Island (300 km SE; Larned 2004). The relation over 17 years was $\text{Chiniak} = 0.59 (\text{Middleton} + \text{Chowiet}) / 2 + 0.07$, with $R^2 = 0.63$.

Statistical analysis

We tested predictions of the Habitat and Individual Quality hypotheses by comparing mean productivity of old and new colonies using a paired-sample *t*-test ($n = 20$ years).

We further evaluated our two hypotheses by comparing the timing of new-colony formation with indicators of habitat quality and intraspecific competition in established colonies. We computed productivity, colony size, population growth, and projected abundance of potential recruits in established colonies during the year preceding establishment of each new colony. Those values were tested against null distributions generated by Monte Carlo sampling (1000 values of each parameter drawn at random from all available measures). We used data from the year preceding colony formation in these analyses because kittiwakes “prospect” for breeding sites and make decisions on where to settle in the summer preceding their first breeding attempt (Cadiou *et al.* 1994). The significance level (*P* value) of each test was the proportion of means derived from random sampling that were more extreme than our observed mean. The precise year of formation was unknown for 4 of 14 new colonies, but could be narrowed to a 3- to 4-year interval. For those colonies, we computed mean values of productivity, abundance, population trend, and number of recruits across all potential years of colonization and emulated this same process when generating the random distributions of parameters. For analysis of colony size and population growth rates, we smoothed nest counts over the anomalous data from 1983 by interpolation. In analyzing the abundance of potential recruits, we excluded one colony for which information on abundance of recruits was unavailable for its year of formation (1978, Fig. 2[c,d]).

To model population growth and to evaluate patterns of immigration and emigration within the kittiwake metapopulation in Chiniak Bay, we determined the following vital rates for each inner bay colony in every year possible:

$$\text{population growth rate } t = (\text{nests } t - \text{nests } t-1) / \text{nests } t-1 \quad (1)$$

$$\text{recruits } t = \text{nests } t-5 \times \text{productivity } t-5 \times C \times \text{SR} \quad (2)$$

$$\text{deaths } t = (\text{nests } t-1 \times 2) \times \text{SA} \quad (3)$$

$$\text{immigrants } t = (\text{nests } t - [\text{nests } t-1 \times \text{SA}]) \times 2 - \text{recruits } t \quad (4)$$

$$\text{emigrants } t = -1 \times (\text{immigrants } t) \quad (5)$$

The current year is denoted *t*, SA is annual adult survival (0.925, Golet *et al.* 1998), and SR is survival from fledging to recruitment (0.567, DBI unpubl. data). Determining a value for SR is problematic because it is an extremely difficult parameter to estimate. In equation (2), *t*–5 reflects the average of 5 years for age of recruitment in kittiwakes (DBI unpubl. data) and C corrects boat-based estimates of productivity by a factor of 1.23 (see above and Suryan & Irons 2001). We accommodated variability in survival parameters by also using a second set of vital rates: maximum SA (0.969) observed in any kittiwake population in the Gulf of Alaska (Golet *et al.* 2004) and a maximum SR (0.854) obtained by applying maximum SA over the 5-year mean age of first reproduction. The latter was the most liberal of possible estimates of survival from fledging to recruitment.

Rates of immigration, emigration and population growth are derived measures sensitive to fluctuations in breeding propensity and survival and, as such, must be treated with caution. For example, in an otherwise stable colony, a large reduction in

breeding propensity between two years will generate an apparent pulse of emigration and negative population growth. A subsequent return to normal breeding propensity will then produce an apparent pulse of immigration and positive population growth. In addition to such false signals, changes in survival or breeding propensity may obscure real episodes of immigration and emigration or real changes in population size.

We modeled individually the growth of six new inner bay colonies, each as a closed population, to determine whether chick production and projected recruitment could account for the observed growth rate. Year of formation was known for all colonies included in

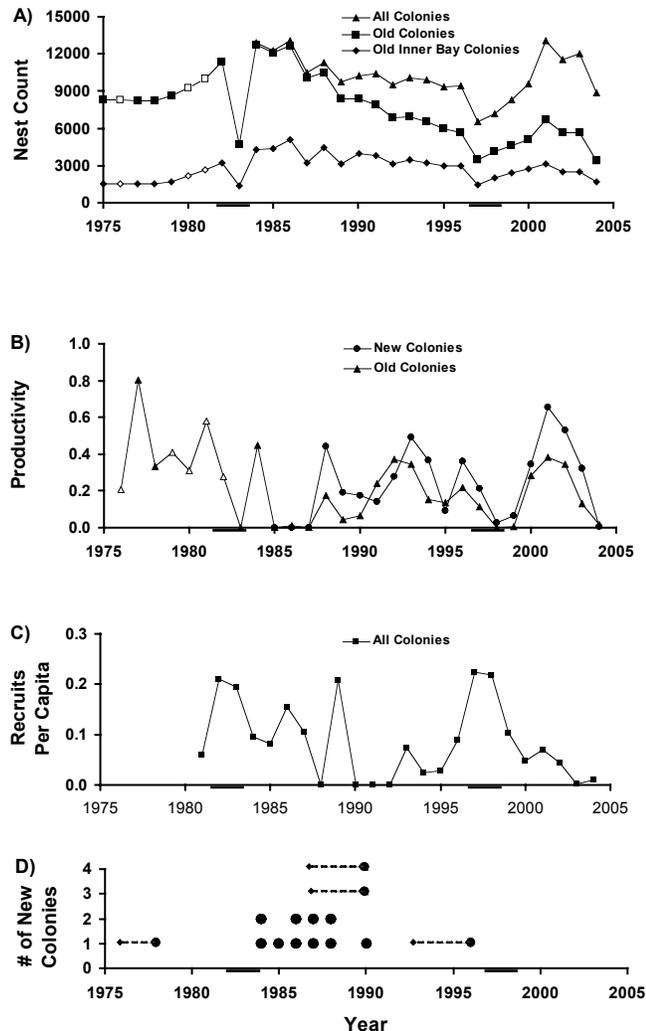


Fig. 2. Indicators of habitat quality and timing of formation of new colonies in Chiniak Bay. Thick bars beneath the x-axes indicate periods of strong El Niño conditions in the North Pacific Ocean. New colonies formed in a period characterized by (A) peak numbers but a downward population trend, (B) poor productivity in older colonies, and (C) above-average abundance of potential recruits. In (D), dots indicate the year in which each new colony was first observed; dashed “tails” indicate the potential window of formation of four colonies for which the exact year of formation was uncertain. Open symbols in (A) denote years in which nest counts for all colonies were estimated by interpolation. Open symbols in (B) denote values estimated from productivity of colonies in the Gulf of Alaska outside of Chiniak Bay.

this analysis, and each colony had nest counts and productivity data available from 1984 though 2004. We projected growth under assumptions of average and maximum survival rates using the following formula:

$$\text{projected nests } t+1 = \text{nest } t + (\text{recruits } t+1 - \text{deaths } t) / 2 \quad (6)$$

Formulae for recruits and deaths appear earlier (equations [2] and [3], respectively). Division by 2 converts individual-based recruitment and mortality statistics to nest equivalents, on the assumption of a 1:1 sex ratio.

We evaluated whether the kittiwake colonies of Chiniak Bay comprised a closed metapopulation by comparing rates of immigration into 14 new and growing colonies with rates of emigration from old colonies within the bay. For this and other analyses of emigration described below, we used average values of survival (SA and SR) and used interpolated values instead of actual nest counts for old colonies in the anomalous 1983 year.

Immigrants to new colonies came from two possible sources, dispersal of first-time breeders and dispersal of established breeders. Lacking direct evidence for breeding dispersal between colonies (i.e. observations of banded birds), we used an indirect approach (Danchin *et al.* 1998) by identifying years in which the growth of all old colonies combined was both negative and greater than the average adult mortality ($1 - SA = 0.075$). Annual growth rates of -0.075 or lower indicated years in which adults potentially dispersed from old colonies. Population decline is a conservative indicator of breeding dispersal because immigration into a colony will mask true dispersal. We assessed statistically the potential for adult dispersal from old colonies using a one-sample *t*-test that compared the annual growth rate of old colonies between 1985 and 1996 against the average rate of adult mortality. We chose these years for analysis because new colonies exhibited sustained growth and required large numbers of immigrants during this period (Fig. 3[a,b]).

In addition to the combined analysis, we also examined individually the growth rates of old colonies for evidence of dispersal of breeders. Growth rates of individual colonies were highly variable and frequently exhibited reversals in direction between years. Such fluctuations likely resulted from changes in breeding propensity and possibly nest persistence between years. We attempted to minimize such noise and identify true breeding dispersal by considering only those population declines in excess of adult mortality that were neither preceded nor followed by a positive growth rate of comparable magnitude. In addition, we excluded from this analysis those colonies with fewer than 50 nests because the smallest colonies had the greatest variability in annual growth rates.

RESULTS

In 1975, kittiwakes occupied nine colonies in Chiniak Bay and half the total population was located at the Cape Chiniak colony (Fig. 1). Over the next two decades, kittiwakes colonized 14 new sites that are distributed throughout Chiniak Bay, and 12 of them were colonized between 1984 and 1990. New colonies are interspersed amongst the old colonies and eight are located within 2 km of an old colony (Fig. 1). Despite their proximity, old and new colonies differ markedly in population trend: new colonies have grown rapidly since their inception (Fig. 4[a]), and old colonies have declined by 70% from peak numbers in 1984 (Fig. 2[a]).

The kittiwake population of Chiniak Bay exhibited periods of increasing and declining numbers, but no net change over the 30-year period, 1975–2004 (Fig. 2[a]). Abrupt declines of nest counts in 1983 and 1997 were coupled with extreme El Niño conditions, poor reproductive performance (Fig. 2[b]), and widespread mortality of kittiwakes and other seabirds via starvation in the Gulf of Alaska (Hatch 1987, Baduini *et al.* 2001). Depressed counts in those two years probably reflected reduced breeding propensity rather than a change in abundance, because numbers had largely recovered by 1984 and 1999, respectively (Fig. 2[a]).

Productivity of new kittiwake colonies ($x = 0.24$) exceeded that of old colonies ($x = 0.14$, $t_{19} = 3.79$, $P = 0.001$; Fig. 2[b]) when paired data from all years are considered. Monte Carlo simulations indicated that new colonies formed when established colonies were characterized by (Table 1) large population size ($P < 0.001$), negative population trend ($P = 0.04$), low productivity ($P < 0.001$) and an abundance of potential recruits ($P = 0.03$).

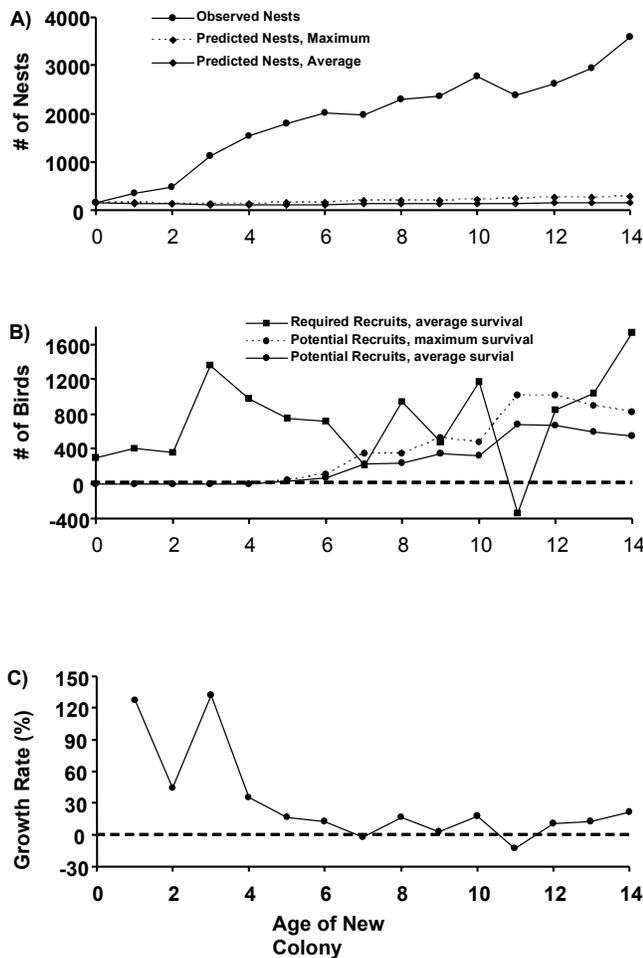


Fig. 3. Demographic patterns observed in six new colonies formed in Chiniak Bay. (A) Observed growth compared with intrinsic growth rates predicted for a closed population using maximum and average values for annual survival of adults and juveniles. (B) Recruits required to support the observed growth of new kittiwake colonies compared with the ability of new colonies to produce recruits under average and maximum rates of survival from fledging to recruitment. (C) Growth of new colonies was highest immediately after they formed but remained at 10%–15% per annum 12–14 years later.

We modeled population growth of six new inner bay colonies colonized by 148 breeding pairs ($x = 22.5$ pairs per colony, minimum = 1 pair, maximum = 41 pairs) and found that observed growth of new colonies could not have been sustained intrinsically (Fig. 3[a]). Under even the most liberal assumptions—100% natal site-fidelity and juvenile survival equal to adult survival—the projected abundance of nests in new colonies after 14 years was only 7% of that actually observed. Thus, immigration must have contributed greatly to the growth of new colonies. Further analysis indicated that immigration—the difference between growth of new colonies and the production of potential recruits by new colonies—was greatest during the first six years after colony formation. It was

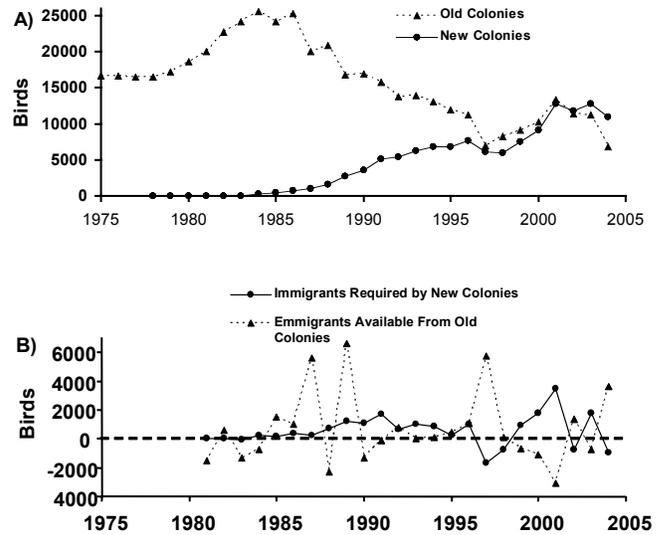


Fig. 4. Population trends in new and old kittiwake colonies in Chiniak Bay and estimated numbers of immigrants and emigrants. (a) Trends of old and new colonies, parallel since 1997, were opposite between 1984 and 1996, a period of formation and rapid growth of new colonies. (b) In the early 1990s and in 1999–2001, estimated immigration into new colonies exceeded the supply of emigrants available from old colonies, suggesting immigration from outside of Chinak Bay.

TABLE 1

Mean (+ standard error) values of population abundance, population growth rate, productivity, and abundance of potential recruits in established colonies during the years immediately preceding formation of each new kittiwake colony in Chiniak Bay (observed). For comparison, mean (+ standard error) values were calculated for 1000 samples of observations drawn randomly from n established colonies, including data from all available years (random). P values are the proportion of 1000 random means that were more extreme than the observed mean

Source	Mean colonies (n)			
	Population abundance	Population growth rate	Productivity	Potential recruits, per capita
Observed	11349 ± 384 ($n=14$)	-0.030 ± 0.024 ($n=14$)	0.12 ± 0.047 ($n=14$)	0.13 ± 0.014 ($n=13$)
Random	10095 ± 445	0.019 ± 0.029	0.26 ± 0.047	0.09 ± 0.020
	$P < 0.001$	$P = 0.04$	$P < 0.001$	$P = 0.03$

still evident, however, even 14 years after colonization (Fig. 3[b]). New colonies grew extremely rapidly in the first four years; thereafter, growth declined to 10%–20% per annum and exhibited lower interannual variability (Fig. 3[c]).

Between 1985 and 1996, population gains in 14 new colonies were matched by population declines in old colonies (Fig. 4[a]), suggesting that Chiniak Bay may have harbored a closed metapopulation of kittiwakes. We assessed that possibility by comparing estimated recruitment of immigrants to new colonies with the estimated availability of emigrants from old colonies. The availability of potential emigrants from old colonies was highly variable among years and was characterized by pulses of emigration tied to reduced nest-counts in 1987, 1989, 1997, and 2004 (Fig. 4[b]). Parallel population trends of old and new colonies since 1996 (Fig. 2[a]) suggest that both subpopulations created and then absorbed large numbers of individuals simultaneously (Fig. 4[b]). We suspect that apparent source-sink dynamics after 1996 were an artifact of fluctuations in breeding propensity synchronized between old and new colonies, and not a true reflection of immigration and emigration. Emigrants from old colonies were abundant when new colonies formed during the mid-1980s (Fig. 4[b]), but by the early 1990s could not account for all observed immigration to new colonies. This shortfall of immigrants implies that the growth of new colonies was sustained by individuals from outside Chiniak Bay. Moreover, the period of poor productivity that favored the formation of new colonies between 1983 and 1990 acted to limit the supply of immigrants to these same colonies in the early 1990s (Fig. 2[b,c]).

We assessed whether dispersal of established breeders from old colonies contributed to growth of new colonies by determining whether the declines observed in old colonies exceeded the expected mortality of adults. The collective decline of 9 old colonies exceeded adult mortality in some years (Fig. 5[a]), but the mean rate of decline between 1985 and 1996 (-0.063) did not differ ($t = 0.52$, $P = 0.6$, $n = 12$ years) from the presumed rate of adult mortality (7.5%). Examining the growth rates of old colonies individually, we found that breeding dispersal was likely to have occurred in five colonies and was especially prevalent in four colonies (Chiniak, Utesistoi, Long Outer, and Vesoki) between 1985 and 1996 (Fig. 5[b]). In those colonies, population declines indicative of breeding dispersal occurred in runs of consecutive years, reducing the likelihood that apparent dispersal was an artifact of changes in breeding propensity or nest persistence between years. Old, declining colonies were predominantly located in outer Chiniak Bay, including the colony at Cape Chiniak that at one time comprised approximately 50% of the bay's total population of kittiwakes.

DISCUSSION

We found that habitat quality (defined in the broadest sense) played a greater role in the formation of new kittiwake colonies than did differences in the quality of individuals. New colonies exhibited higher productivity than old colonies despite being colonized, in all likelihood, by inexperienced breeders (Storey & Lein 1985, Tims *et al.* 2004) that are typically less productive than older breeders (Coulson & White 1958). Had we been able to compare productivity of inexperienced breeders in new versus old colonies, we should have found an even greater difference between the two. In addition, new colonies formed during a period of depressed habitat quality within old colonies, as suggested by low productivity, large

colony size, and declining population trends in the latter. Moreover, declines of the old colonies in the mid-to-late 1980s indicate that old colonies were unattractive to prospecting birds at a time when potential recruits were abundant. Overall, our results contradicted three of five predictions of the Individual Quality hypothesis, yet we cannot reject that hypothesis outright—lower-quality individuals may indeed have dispersed to form new colonies. If so, superior habitat in new colonies more than compensated for the effect of individual quality on productivity.

Patterns of formation of new kittiwake colonies in Chiniak Bay mirror those observed by Tims *et al.* (2004) for Common Terns (*Sterna hirundo*) in Massachusetts. New tern colonies exhibited greater productivity and rates of chick growth than did a large, established colony in the same bay. Breeding parameters of terns were negatively correlated with colony size, nest density, and foraging trip duration, suggesting intraspecific competition for food or nest sites had compromised habitat quality in the older colony.

In Chiniak Bay, new kittiwake colonies were founded by variable numbers of pioneers (23 pairs on average) and exhibited immediate, rapid growth through an influx of immigrants. Immigration is the only means by which kittiwake colonies can grow for 4–5 years after colonization because of delayed maturity; however, we found that immigration contributed to the robust growth of new colonies for at least 14 years.

Other researchers observed that new colonies of common terns (Tims *et al.* 2004), Audouin's gull (*Larus audouinii*, Oro & Ruxton 2001), Manx shearwaters (*Puffinus puffinus*, Storey & Lein 1985), and kittiwakes in the Atlantic Ocean (Heubeck *et al.* 1999, Kehoe

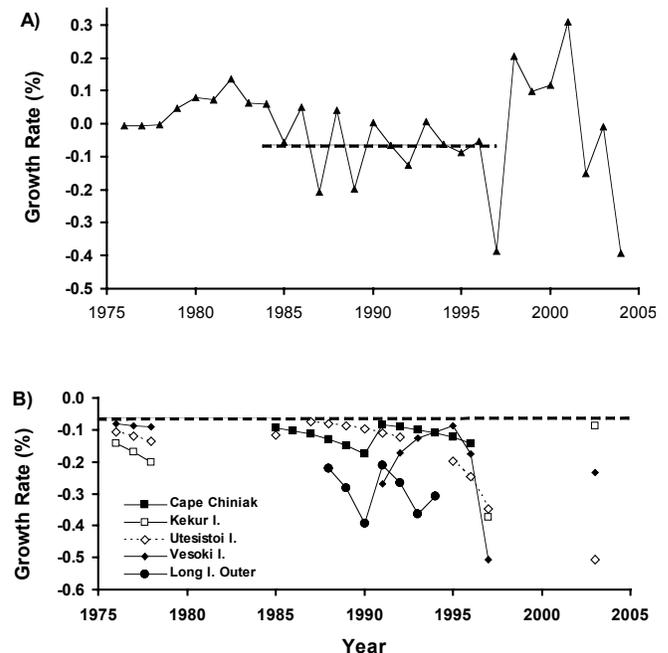


Fig. 5. Observed rates of decline in old colonies in relation to adult mortality. (A) Data for all colonies combined show general agreement between declining numbers and the average rate of adult mortality (7.5%, dashed line) between 1985 and 1996. (B) In five colonies examined individually, the annual rate of decline was consistently greater than 7.5% between 1985 and 1996, suggesting established breeders dispersed from these colonies.

& Diamond 2001) were also founded by moderately sized clusters of nests and grew rapidly by attracting large numbers of immigrants (Danchin & Monnat 1992). In contrast, new seabird colonies grow more slowly when founded by only a few breeding pairs (Nelson 1978, Fleet 1984, Martinez-Abraín *et al.* 2001). Coulson (1983) and Heubeck *et al.* (1987) reported negative correlations between the size and growth rate of kittiwake colonies in Britain, just as we observed decelerating growth of new colonies in Chiniak Bay.

Modeling indicated that some established breeders may have relocated from old to new colonies, despite the fact that most seabirds, including kittiwakes, usually exhibit high site-fidelity (Aebischer & Coulson 1990). Though uncommon, dispersal of established breeders does occur in seabirds (e.g. Oro & Ruxton 2001, Tims *et al.* 2004) and has been documented for kittiwakes experiencing declining habitat quality (Danchin *et al.* 1998, Danchin & Monnat 1992). While we assert that emigration from old colonies within Chiniak Bay supported the initial growth of new colonies, that source was insufficient to account for the rapid growth of these expanding colonies during the early 1990s. Thus, we conclude that Chiniak Bay is not a closed metapopulation of kittiwakes; rather, it exchanges immigrants with colonies beyond its boundaries (see also Coulson & Neve de Mevergnies 1992).

We assert that new colonies formed because of poor habitat quality in old colonies and, although many old colonies declined markedly, new colonies grew rapidly by attracting both first-time and established breeders from established colonies within and outside of Chiniak Bay. The performance-based conspecific-attraction hypothesis (Danchin *et al.* 1998) neatly explains these contrasting population dynamics—highly productive new colonies attract prospecting kittiwakes because productivity reflects habitat quality. According to this model, new colonies will continue to grow rapidly as long as they remain highly productive and attractive to prospectors. The observed moderating pace of new-colony growth within Chiniak Bay can be explained as a per capita decline in the abundance of potential recruits as new colonies made up an increasing proportion of the total population. Although conspecific attraction may be the main proximate mechanism driving metapopulation dynamics in seabirds, it does not explain

why new colonies typically exhibit high levels of productivity in the first place.

In a review of biotic and abiotic factors affecting habitat quality, dispersal patterns and population dynamics in seabirds, Boulinier and Lemel (1996) concluded that the temporal and spatial scales over which a given factor operates are of key importance. Adverse density-dependant effects of interspecific competition for food and nest sites can affect habitat quality in the localized, colony specific manner observed in Chiniak Bay. Ashmole (1963) argued that seabird populations are regulated primarily by competition for food during the breeding season through diminished foraging efficiency and reduced chick production in large colonies, an idea supported by a number of studies (Birkhead 1977, Diamond 1978, Furness & Birkhead 1984, Birt *et al.* 1987, Cairns 1989, Lewis *et al.* 2001). While the availability of nest sites is believed to be only rarely limiting to seabird populations (Birkhead & Furness 1985, Olsthoorn & Nelson 1990), high-quality nest sites can be in short supply (Potts *et al.* 1980) and may limit the size and growth rate of large kittiwake colonies in Britain (Porter & Coulson 1987).

Density-dependant decline in habitat quality may explain why new colonies are highly productive, but it does not explain why prospectors demand such a large premium in habitat quality to colonize new habitat. The “information barrier” hypothesis (Forbes & Kaiser 1994) addressed this issue by implicitly incorporating an “Allee” type of density dependence (Allee 1931)—conspecifics provide valuable information on habitat suitability that is responsible for inverse density dependence (*increasing* habitat quality with increasing density) in small colonies. That effect ultimately is overwhelmed by costs of intraspecific competition as a colony grows. This model explains higher productivity of newly-formed colonies by suggesting that seabirds colonize new habitat only when the penalty of joining an old colony—low habitat quality—exceeds the risk of pioneering.

In a classic work that has become a touchstone of habitat selection theory, Fretwell (1972) developed the concept of the “ideal free” distribution, but also proposed two lesser-known models that better suit the typical seabird example. The “ideal Allee” model (after Allee 1931) proposes that the benefits of group living (including information) generate inverse density-dependence in small groups. The “ideal despotic” model proposes that costs associated with obtaining a breeding territory in the midst of existing territory holders (“despots”) dissuades established breeders from relocating to new colonies. We suggest that by merging Fretwell’s “ideal Allee” and “ideal despotic” models, we can improve upon the “information barrier” hypothesis and explain not only the high productivity and rapid growth of newly formed seabird colonies, but also the reluctance of established breeders to disperse to what is clearly better habitat. Our reasoning is elaborated in Appendix 1.

We assert that while the hybrid “ideal despotic Allee” model may be a useful tool for understanding the formation and growth of new seabird colonies in general, it does not fully explain population dynamics of kittiwakes within Chiniak Bay: new colonies continue to exhibit greater productivity than old colonies even though new and old colonies are currently comparable in size—and presumably density. In addition to operating on a fine spatial scale (highly localized) and independent of density, whatever factor is responsible for depressed habitat quality in old colonies must have come to the fore since the mid-1970s—when kittiwakes pioneered older

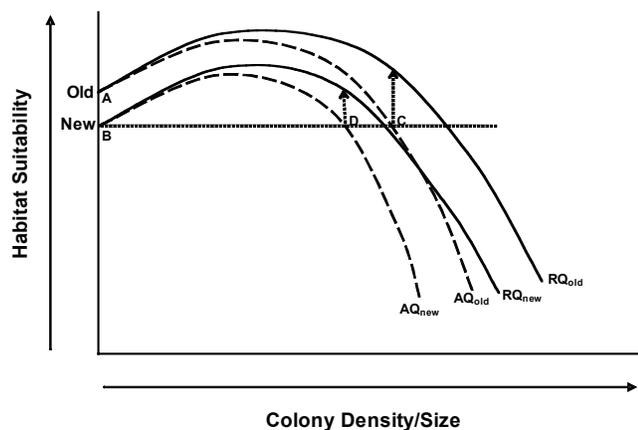


Fig. 6. Graphical representation of the “Ideal Despotic-Allee” model of habitat distribution, combining features of the “Ideal Despotic” and “Ideal Allee” models proposed by Fretwell (1972). The hybrid model predicts patterns of productivity, population trends, and meta population dynamics that are commonly observed when new seabird colonies form (see Appendix 1 for explanation).

colonies (generally tall, sheer cliffs) whose sites were perceived as better habitat than the future sites of new colonies (characterized by shorter cliffs). It must have also acted over a considerable period of time because the productivity differential between old and new colonies has persisted since the mid-1980s.

We have no data quantifying either density-dependant or density-independent factors that might differentially affect kittiwake colonies in Chiniak Bay, but the close proximity of old and new colonies discounts food abundance and abiotic conditions as candidates. With overlapping foraging ranges (Suryan *et al.* 2000), birds from all colonies in principle have equal access to food resources. Ectoparasites such as ticks can have a localized effect on seabird colonies (Duffy 1983, Boulinier & Danchin 1996, Danchin *et al.* 1998), but we found few ticks on kittiwakes from any colony in Chiniak Bay during four years of intensive study (2001–2004). Notably, however, the populations of aerial predators such as Bald Eagles (*Haliaeetus leucocephalus*) and Peregrine Falcons (*Falco peregrinus*) on kittiwake adults, eggs, and nestlings have increased markedly over the past 30 years (Ambrose *et al.* 1988, Zwiefelhofer 1997). Anecdotal evidence suggests eagles and falcons may roost and hunt preferentially from taller cliffs, and thereby exert a localized direct and indirect effects (Paine *et al.* 1990) on older colonies in Chiniak Bay.

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REFERENCES

- AEBISCHER, N.J. & COULSON, J.C. 1988. Survival of the kittiwake in relation to sex, year, breeding experience and position in the colony. *Journal of Animal Ecology* 59: 1063–1071.
- ALLEE, W.C. 1931. Animal aggregations. A study in general sociology. Chicago: University of Chicago Press.
- AMBROSE, R.E., RITCHIE, R.J., WHITE, C.M., SCHEMPF, P.F., SWEM, T. & DITTRICK, R. 1988. Changes in the status of Peregrine Falcon populations in Alaska. In: Cade, T.J., Enderson, J.H., Thelander, C.G. & White, C.M. (Eds). Peregrine Falcon populations, their management and recovery. Boise, ID: The Peregrine Fund. pp. 73–82.
- ASHMOLE, N.P. 1962. The Black Noddy *Anous tenuirostris* on Ascension Island. *Ibis* 103b: 235–273.
- ASHMOLE, N.P. 1963. The regulation of numbers of tropical ocean birds. *Ibis* 103b: 458–473.
- BADUINI, C.L., LOVVORN, J.R. & HUNT, G.L. 2001. Determining the body condition of Short-tailed Shearwaters: implications for migratory flight ranges and starvation events. *Marine Ecology Progress Series* 222: 256–277.
- BIRKHEAD, T.R. 1977. The effect of habitat and density of breeding success in the Common Guillemot (*Uria aalge*). *Journal of Animal Ecology* 46: 751–764.
- BIRKHEAD, T.R. & FURNESS, R.W. 1985. Regulation of seabird populations. In: Sibley, R.M. & Smith, R.H. (Eds). Behavioural Ecology. Oxford: Blackwell Scientific Publishing. pp. 145–167.
- BIRT, V.L., BIRT, T.P., CAIRNS, D.K. & MONTEVECCHI, W.A. 1987. Ashmole's halo: direct evidence for prey depletion by a seabird. *Marine Ecology Progress Series* 40: 205–208.
- BOULINIER, T. & DANCHIN, E. 1996. Population trends in kittiwake *Rissa tridactyla* colonies in relation to tick infestation. *Ibis* 138: 326–334.
- BOULINIER, T. & DANCHIN, E. 1997. The use of conspecific reproductive success for breeding patch selection in terrestrial migratory species. *Evolutionary Ecology* 11: 505–517.
- BOULINIER, T. & LEMEL, J.Y. 1996. Spatial and temporal variations of factors affecting breeding habitat quality in colonial birds: some consequences for dispersal and habitat selection. *Acta Oecologica* 17: 531–552.
- BOULINIER, T., SORCI, G., MONNAT, J.Y. & DANCHIN, E. 1997. Parent-offspring regression suggests heritable susceptibility to ectoparasites in a natural population of kittiwakes *Rissa tridactyla*. *Journal of Evolutionary Biology* 10: 77–85.
- BROWN, C.R. & BROWN, M.B. 1996. Coloniality in the Cliff Swallow: the effect of group size on social behavior. Chicago: University of Chicago Press.
- BROWN, C.R. & BROWN, M.B. 2001. Avian coloniality: progress and problems. In: Nolan, V. & Thompson, C.F. (Eds). Current ornithology. New York: Kluwer Academic/Plenum Publishers. pp. 1–81.
- BROWN, C.R., STUTCHBURY, B.J. & WALSH, P.D. 1990. Choice of colony size in birds. *Trends in Ecology and Evolution* 5: 398–403.
- BUCKLEY, N.J. 1997. Spatial-concentration effects and the importance of local enhancement in the evolution of colonial breeding in seabirds. *American Naturalist* 149: 1091–1112.
- BURGER, A.E. 1997. Arrival and departure behavior of Common Murres at colonies: evidence for an information halo? *Colonial Waterbirds* 20: 55–65.
- BURGER, J. & SHISLER, J. 1980. The process of colony formation among Herring Gulls *Larus argentatus* nesting in New Jersey. *Ibis* 122: 15–26.
- CADIOU, B., MONNAT, J.Y. & DANCHIN, E. 1994. Prospecting in the kittiwake, *Rissa tridactyla*: different behavioral patterns and the role of squatting in recruitment. *Animal Behaviour* 47: 847–856.
- CAIRNS, D.K. 1989. The regulation of seabird colony size: a hinterland model. *American Naturalist* 134: 141–146.
- COULSON, J.C. 1983. The changing status of the kittiwake *Rissa tridactyla* in the British Isles, 1969–1979. *Bird Study* 30: 9–16.
- COULSON, J.C. & NEVE DE MEVERGNIES, G. 1992. Where do young kittiwakes *Rissa tridactyla* breed, philopatry or dispersal?. *Ardea* 80: 187–197.

- COULSON, J.C. & WHITE, E. 1958. The effect of age on the breeding biology of the kittiwake *Rissa tridactyla*. *Ibis* 100: 40–51.
- DANCHIN, E. 1992. Modeling seabird populations and implications for management introduction. *Ardea* 80: 157–160.
- DANCHIN, E., BOULINIER, T. & MASSOT, M. 1998. Conspecific reproductive success and breeding habitat selection: implications for the study of coloniality. *Ecology* 79: 2415–2428.
- DANCHIN, E. & MONNAT, J.Y. 1992. Population dynamics modeling of two neighboring kittiwake *Rissa tridactyla* colonies. *Ardea* 80: 171–180.
- DIAMOND, A.W. 1978. Feeding strategies and population size in tropical seabirds. *American Naturalist* 112: 215–223.
- DUFFY, D.C. 1983. The ecology of tick parasitism on densely nesting Peruvian seabirds. *Ecology* 64: 110–119.
- FLEET, D.M. 1984. Changes in the numbers of breeding kittiwakes in Helgoland. *Ringing and Migration* 5: 32–34.
- FORBES, L.S. & KAISER, G.W. 1994. Habitat choice in breeding seabirds: when to cross the information barrier. *Oikos* 70: 377–384.
- FRETWELL, S.D. 1972. Populations in a seasonal environment. Princeton: Princeton University Press.
- FURNESS, R.W. & BIRKHEAD, T.R. 1984. Seabird colony distributions suggest competition for food supplies during the breeding season. *Nature* 311: 655–656.
- GOLET, G.H., IRONS, D.B. & ESTES, J.A. 1998. Survival costs of chick rearing in Black-legged Kittiwakes. *Journal of Animal Ecology* 67: 827–841.
- GOLET, G.H., SCHMUTZ, J.A., IRONS, D.B. & ESTES, J.A. 2004. Determinants of reproductive costs in the long-lived Black-legged Kittiwake: a multiyear experiment. *Ecological Monographs* 74: 353–372.
- HAMER, K.C. & FURNESS, R.W. 1991. Age-specific breeding performance and reproductive effort in Great Skuas *Catharacta skua*. *Journal of Animal Ecology* 60: 693–704.
- HATCH, S.A. 1987. Did the 1982–9183 El Niño-southern oscillation affect seabirds in Alaska? *Wilson Bulletin* 99: 468–474.
- HATCH, S.A., ROBERTS, B.D. & FADELY, B.S. 1993. Adult survival of Black-legged Kittiwakes *Rissa tridactyla* in a Pacific colony. *Ibis* 135: 247–254.
- HEUBECK, M., MELLOR, R.M., HARVEY, P.V., MAINWOOD, A.R. & RIDDINGTON, R. 1999. Estimating the population size and rate of decline of kittiwakes *Rissa tridactyla* breeding in Shetland, 1981–97. *Bird Study* 46: 48–61.
- HEUBECK, M., RICHARDSON, M.G. & DORE, C.P. 1987. Monitoring numbers of kittiwakes *Rissa tridactyla* in Shetland. *Seabird* 9: 32–42.
- KEHOE, F.P. & DIAMOND, A.W. 2001. Increases and expansion of the New Brunswick breeding population of Black-legged Kittiwakes, *Rissa tridactyla*. *Canadian Field-Naturalist* 115: 349–350.
- KHARITONOV, S.P. & SIEGEL-CAUSEY, D. 1988. Colony formation in seabirds. *Current Ornithology* 5: 223–272.
- KILDAW, S.D. 1999. Competitive displacement? An experimental assessment of nest site preferences of cliff-nesting gulls. *Ecology* 80: 576–586.
- LARNED, A. 2004. Results of seabird monitoring at Chowiet Island in 2004: summary appendices. Homer, Alaska: US Fish and Wildlife Service.
- LEWIS, S., SHERRATT, T.N., HAMER, K.C. & WANLESS, S. 2001. Evidence of intra-specific competition for food in a pelagic seabird. *Nature* 412: 816–819.
- MANUWAL, D.A. 1974. Effects of territoriality on breeding in a population of Cassin's Auklet. *Ecology* 55: 1399–1406.
- MARTINEZ-ABRAIN, A., ORO, D. & JIMENEZ, J. 2001. The dynamics of a colonization event in the European shag: the roles of immigration and demographic stochasticity. *Waterbirds* 24: 97–102.
- MCGRATH, D. & WALSH, P.M. 1996. The breeding population of kittiwakes on the south coast of Ireland, 1985–95. *Irish Birds* 5: 375–380.
- NELSON, B. 1978. The gannet. Berkhamstead: Poyser.
- OLSTHOORN, J.C.M. & NELSON, J.B. 1990. The availability of breeding sites for some British seabirds. *Bird Study* 37: 145–164.
- ORO, D. & RUXTON, G.D. 2001. The formation and growth of seabird colonies: Audouin's Gull as a case study. *Journal of Animal Ecology* 70: 527–535.
- PAINE, R.T., WOOTTON J.T., & BOERSMA P.D. 1990. Direct and indirect effects of peregrine falcon predation on seabird abundance. *Auk* 107: 1–9.
- PODOLSKY, R.H. & KRESS, S.W. 1989. Factors affecting colony formation in Leach's Storm-Petrel. *Auk* 106: 332–336.
- PORTER, J.M. & COULSON, J.C. 1987. Long-term changes in recruitment to the breeding group and the quality of recruits at a kittiwake *Rissa tridactyla* colony. *Journal of Animal Ecology* 56: 675–689.
- POTTS, G.R., COULSON, J.C. & DEANS, I.R. 1980. Population dynamics and breeding success of the shag, *Phalacrocorax aristotelis*, on the Farne Islands, Northumberland. *Journal of Animal Ecology* 49: 465–484.
- ROLLAND, C., DANCHIN, E. & DE FRAIPONT, M. 1998. The evolution of coloniality in birds in relation to food, habitat, predation, and life-history traits: a comparative analysis. *American Naturalist* 151: 514–529.
- STOREY, A.E. & LEIN, J. 1985. Development of the first North American colony of Manx Shearwaters. *Auk* 102: 395–401.
- SURYAN, R.M. & IRONS, D.B. 2001. Colony and population dynamics of Black-legged Kittiwakes in a heterogeneous environment. *Auk* 118: 636–649.
- SURYAN, R.M., IRONS, D.B. & BENSON, J. 2000. Prey switching and variable foraging strategies of Black-legged Kittiwakes and the effect on reproductive success. *Condor* 102: 374–384.
- TIMS, J., NISBET, I.C., FRIAR, M.S., MOSTELLO, C. & HATCH, J.J. 2004. Characteristics and performance of Common Terns in old and newly-established colonies. *Waterbirds* 27: 321–332.
- WITTENBERGER, J.F. & HUNT, G.L. 1985. The adaptive significance of coloniality in birds. In: Farner, D.S., King, J.R. & Parkes, K.C. (Eds). *Avian biology*. Vol. 8. New York: Academic Press. pp. 1–78.
- ZWIEFELHOFER, D. 1997. Kodiak National Wildlife Refuge 1997 Bald Eagle nesting and productivity survey. Kodiak, Alaska: US Fish and Wildlife Service, Kodiak National Wildlife Refuge. pp. 1–17.

APPENDIX 1

Fretwell (1972) assumes that individuals will make “ideal” habitat selection decisions and recruit into the colony of the highest quality when they: i) they have perfect information about the quality of habitat in each colony, and ii) can move between colonies at will. All curves depicted in Fig. 6 adhere to Allee’s (1931) principle in that the “realized quality” (RQ) of habitat within a given colony initially increases with density but ultimately decreases at high densities because of increasing costs of intraspecific competition. Because of the “despotic” nature of established territory holders (Fretwell 1972), the initial cost to a newcomer of establishing a breeding territory (and acquiring locality-specific information on resources, predators, etc.) is reflected by a lower, cost-adjusted “apparent quality” (AQ) curve for each colony (Fig. 6). The hybrid model adheres to Fretwell’s despotic principle in that potential recruits select among breeding colonies on the basis of apparent quality; however, once an individual establishes a breeding territory, it becomes a despot itself and enjoys the greater realized quality of its chosen colony.

The hybrid model functions in the following manner: If two breeding habitats are initially empty, prospective breeders will first occupy the “old” colony at point A, because its habitat quality is higher than that of the “new” colony at point B (Fig. 6). As more recruits are added to the old colony, both its apparent and realized quality initially increase, then decline with increasing density. At point C, the apparent quality of the old colony is depressed to the point where it equals that of the unoccupied new colony at point B (lower horizontal dashed line). Individuals are encouraged to pioneer the new colony. Kittiwakes now recruit exclusively into the new colony, as its apparent quality increases initially. Upon subsequent decline to point D, the apparent quality of old and new colonies is again similar, and recruits are attracted to both in equal numbers. The time required to achieve equilibrium is dictated by a number of factors, including the relative sizes of new and old colonies and the annual supply of potential recruits. Note that in the hybrid model, the realized quality (and productivity) of the two colonies may differ even when their apparent qualities are the same (indicated by vertical arrows). Note also that established breeders should relocate from old to new colonies if at any time the apparent quality of the new colony exceeds the realized quality of the old one. Although the hybrid model is explicitly density driven, density-independent factors can be represented simply by displacing habitat quality curves up or down along the y axis.
