matches that of nonactin) would correspond to increased electrostatic interaction between cation and carbonyl groups. This anomaly is probably not due to hydrogen bonding, which usually reduces the carbonyl stretch frequency; ^{13}C-NMR data (*11*) provide evidence that carbonyl hydrogen bonds are absent. The anomalously low frequency of the Tl^+ complex corresponds to a reduction of the electrostatic interaction between the cation and carbonyl group. This reduction could arise from a transfer of electron charge to the Tl^+ ion from the carbonyl oxygen, which may also contribute to the total interaction energy. The nonactin extraction coefficients for NH_4^+ and Tl^+ are also anomalous (*4, 5*).

The methods described above can also be applied to other parts of the molecule. For example, the frequency of the intense peak in the complex near 525 cm^{-1} [which is apparently associated with the tetrahydrofuran subunits (*9*)] varies with ionic radius (Fig. 3a), suggesting that the tetrahydrofuran rings interact with the cation, perhaps only indirectly through the nonactin backbone [a conclusion inferred from recent ^{13}C-NMR results (*11*)]. The anomalous position of the bulky $(NH_2)_2CNH_2^+$ ion in Fig. 3a may arise from additional steric interactions.

Many Raman frequencies do not depend appreciably on ionic radius or shape, even though their relative intensities change on complexation; an example is the 920-cm^{-1} line (Fig. 3b).

In some models of ionophore specificity, ionic selectivity arises partially from differences in the mechanical energy required to distort the antibiotic cavity to accommodate ions of different radii. If the observed changes in the ester carbonyl stretch frequency arose from this perturbation, they would be expected to depend on the magnitude of the distortion and thus on the ionic radius. For the larger alkali ions and the ammonium derivatives, the ester carbonyl stretch frequency depends on the ion-carbonyl electrostatic interaction energy U rather than on the ionic radius R. For the Na^+ ion, in which steric constraints are known to be important, the ester carbonyl stretch frequency is anomalous, showing that this frequency can respond to steric effects. This finding emphasizes the importance of electrostatic forces in nonactin cation interactions and thus tends to support electrostatic models (*4, 5*) for the ionic selectivity of nonactin.

Note added in proof: Recent x-ray crystallographic data on the NH_4^+-tetranactin complex (*12*) show that the NH_4^+ cation is hydrogen bonded to the four tetrahydrofuran oxygen atoms. For this structure, U is smaller than shown in Fig. 1b, increasing the observed anomaly. The NH_4^+ hydrogen bonds may also account for the great stability of the NH_4^+-nonactin complex. That the stabilities of the NH_3OH^+ and $C(NH_2)_3^+$ complexes are considerably lower (*13*) suggests that these complexes do not contain such hydrogen bonds.

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Adaptive Significance of Synchronized Breeding in a Colonial Bird: A New Hypothesis

Abstract. *Bank swallows nest gregariously in colonies usually ranging from 10 to 300 nests. Different pairs within the same colony are highly synchronized with each other, and 67 percent of the nests fledged their young over a period of only 6 days. This high degree of synchronization is demonstrated to be of adaptive significance. Reproductive fitness increases as a function of the precision of synchrony of the colony. It is proposed that social foraging plays an important role in maximizing the feeding efficiency in this species and that asynchronous breeding decreases the effectiveness of this social foraging, particularly in late nesters and among young, newly fledged birds. An individual that fledges either early or at the peak of synchrony will emerge to find a steady stream of other birds traveling to local, ephemeral, concentrations of food. The late emerger finds itself practically alone and thus is deprived of the potential benefits of the pooled information about locations of food resources available to the full colony.*

Synchronization in the timing of breeding is a common feature of the reproductive biology of many colonial nesting birds (*1*). One question arising is whether such synchronization is of ultimate adaptive importance or whether it is a proximal result of either (i) a high degree of gregariousness or (ii) a common responsiveness to the same environmental trigger for breeding.

Surprisingly, very few quantitative studies have dealt with breeding synchrony or have been directed to a search for any effects of synchronization on reproductive fitness. We now present demographic data that provide one of the first clear instances of a positive selective advantage to breeding in synchrony. We then propose a new hypothesis to partially account for the increased reproductive success noted in highly synchronized colonies.

The bank swallow (*Riparia riparia*) is a gregarious bird that breeds in dense colonies ranging from 10 to 300 pairs (*2*). The birds dig their nests 0.5 to 1.3 m deep into vertical banks along rivers, on cliffs, or in sand and gravel pits.

As part of a large-scale study of the adaptiveness of coloniality in this species (*3*), we gathered detailed behavioral and demographic data from over 400 nests in 15 colonies in the vicinity of Tompkins County, New York, during 1970 and 1971. Nest contents were checked at intervals allowing us to determine the time of laying, clutch size, incubation period, and date of hatch, and to monitor the growth and survival of the nestlings during their development until the age of fledging (*4*).

The bank swallows showed an extremely high degree of within-colony synchronization. Including the peak hatch date for each colony, 67 percent of all nests hatched over a period of only 6 days. Nearby colonies, although highly synchronous within

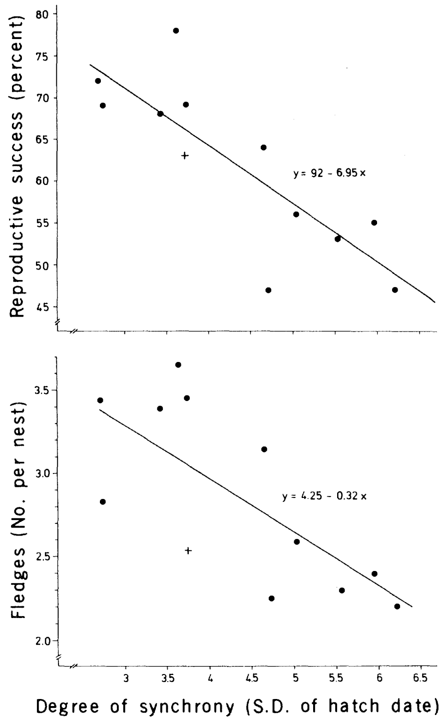

Fig. 1. (Top) Average reproductive success of different colonies of bank swallows plotted relative to their degree of within-colony synchronization (correlation coefficient, $r_1 = -.82$, $P < .001$). (Bottom) Mean number of fledglings produced per pair of swallows plotted relative to colony synchronization (correlation coefficient, $r_2 = -.72$, $P < .001$). Plus sign denotes a renesting colony.

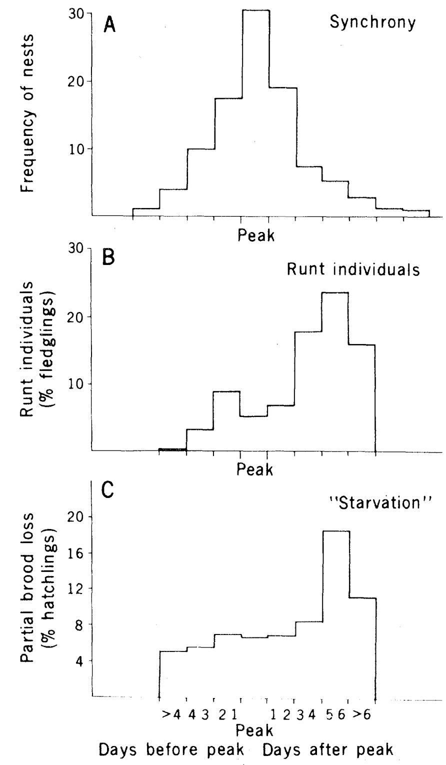

Fig. 2. The frequency of (A) nests, (B) retarded or "runt" nestlings, and (C) presumed starvation losses, each plotted as a function of the temporal position of the nests with regard to within-colony synchronization. Data from ten colonies were pooled.

themselves, were not always in phase with each other (*5*).

We used the standard deviation of the mean of the hatch date as an inverse measure of the degree of synchrony of each colony. The data provided us with two estimates of the average fitness of a pair of swallows in each of the colonies: the average number of young raised per pair to fledging age, and the percentage of eggs laid that produced viable young at fledging (reproductive success). When these measures are plotted as functions of colony synchronization, a clear trend emerges, with the more highly synchronized colonies showing higher average reproductive fitness (Fig. 1). The magnitude of this synchrony effect is great, with 68 percent of the variability in reproductive success (r_1^2), and 52 percent in the number of fledglings (r_2^2) being explainable on this basis (*6*).

We hypothesize that there are at least two advantages of synchronous breeding for bank swallows: (i) it reduces losses to predation by minimizing the time over which colony members are vulnerable and (ii) it maximizes the potential for group localization of food through social foraging. Only the second advantage is discussed in this report.

Bank swallows feed on aerial insects, often covering vast areas of 12 to 20 square miles (1 square mile = 2.56 km^2) during their normal foraging activities. They are generalized and opportunistic feeders, concentrating their foraging efforts wherever local concentrations of flying insects occur. The temporal and spatial distribution of aerial insects is strongly affected by the temperature and winds as well as by the local vegetation and topography. Moderate winds can cause weak-flying insects to pile up and form temporary concentrations where windbreaks occur, commonly along the lee sides of tree lines or hedgerows or along the wooded edges of open fields. As the winds change, so do the locations of the optimal food clumps. Human activity also strongly affects the distributions of aerial insects, especially on calm days. Mobile insects are attracted or are disturbed into flight as farmers fertilize, plow, or cut their fields. Hence a bank swallow is faced with the task of finding concentrations of aerial insects, concentrations that form a patchy, mobile, and highly ephemeral food resource.

Bank swallows were observed to feed socially, following each other out of the colony and traveling in loose streams to areas of localized food abundance. We have hypothesized that this social foraging is a means of maximally exploiting their particular food niche (*3*). In times of food stress (for example, during periods of cold, strong winds, or prolonged rain) it would be advantageous for individuals having difficulty obtaining food and returning from unsuccessful foraging expeditions to take advantage of other colony members returning from favorable feeding areas. Any tendency for an unsuccessful forager to follow other birds as they depart the colony would bring about an increase in foraging efficiency. This idea of colony members "pooling information" (inadvertently or purposefully) about feeding locations is not new (*7*); colonial, aerial feeders such as swallows, in fact, are prime candidates in which to expect such social foraging.

The potential benefits of social foraging should increase as the size and food demands of the nestlings increase. One period during the breeding cycle when these benefits might be particularly great is the time of fledging of the young. Since parents feed juveniles only irregularly after fledging, the young must begin foraging during their first few hours of independence. The first days after fledging thus are a critical period for the survival of young bank swallows. They must obtain sufficient energy to sustain them over the period when they are developing the flight strength, speed, and precision maneuverability that are necessary for efficient capture of insects on the wing. An individual that fledges from a nest that is closely synchronized with the rest of the colony will emerge to find a steady stream of adult birds traveling back and forth to the currently productive feeding areas. Since a fledgling's initial foraging attempts are bound to be somewhat inefficient, it can benefit greatly by "parasitizing" information from other colony members and thus minimizing the time and energy spent in finding and traveling to suitable feeding areas.

A few days after fledging occurs, both young and parents leave the colony location entirely. Groups of fledglings return to the colony sporadically, but most of their time is spent elsewhere. Thus, as the peak time of fledging passes, a colony rapidly becomes deserted with the effect that late nesters are left practically alone. Adult birds must now forage more independently (at the time when food demands are greatest) and late young, when they fledge, do not have the opportunity to follow swarms of parents to the constantly changing clumps of insects. Birds on the tail end of the synchrony curve, in essence, find themselves in a much "smaller" colony without the capacity for group localization of food concentrations.

One prediction of this hypothesis is that food-induced stress (and eventually starvation) will operate more heavily on birds out of phase of synchrony with their fellow colony members, and specifically on those that are late nesters (*8*). To examine this we analyzed nestling growth and mortality as a function of the temporal position of each nest with respect to the peak date of synchrony for each colony. Two possible indicators of food stress were examined: (i) partial brood reduction and (ii) runt individuals. (i) Avian ecologists frequently distinguish between two broad categories of nestling mortality. Predation generally claims an entire brood since most predators, once having gained access to a nest chamber, remove all young. Losses of one or two individuals from a brood are usually the result of other causes, including disease, accidental death, and, most frequently, starvation (*9*). We regarded partial brood losses of swallows as a probable indicator of food stress. (ii) Bank swallows begin incubation with the laying of the next to last egg, with the result that the clutch hatches asynchronously over a period of 2 or 3 days. If food for the young is abundant, the growth curves converge and siblings become indistinguishable. If food is not abundant, the size differential present at hatching of the last egg can continue or increase. Any individual nestling that was significantly retarded in its development relative to its brood mates was designated a "runt" (*10*). Runts are usually the individuals that will starve if the food shortage is severe enough. Even if they do fledge, their postfledging survivorship can be expected to be considerably lower than that of their brood mates. We therefore interpreted the presence of runts just prior to fledging as further evidence of an increased food stress on those nests.

Figure 2A shows the precision of within-colony synchronization, Fig. 2B shows the occurrence of runt individuals, and Fig. 2C shows partial brood losses, each plotted relative to the peak dates of colony synchronization. The data support our hypothesis since retarded individuals and probable starvation losses both occur much more frequently among late nesters than among any other category.

Several other hypotheses (including predator swamping, increased alertness and predator defense, and pooling of "decision-making" information concerning environmental stimuli) could be advanced to explain the increase in reproductive success that we found in highly synchronized colonies. The effects of most of these hypotheses are additive and their relative importance in promoting synchronized breeding should be expected to vary in different species and in different localities as a function of local ecological factors. The most important factors should be the distribution and predictability of the food supply, the types and abundance of potential nest predators, and the degree of difficulty in predicting optimal times for breeding.

For bank swallows nesting in upstate New York, we propose that the benefits derived from social foraging, coupled with the tendency to leave the nesting colony as soon as the young have fledged, produces one strong selective advantage for precise, within-colony synchronization of breeding behavior (*11*).

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5. The average degree of within-colony synchronization (measured as the standard deviation of hatch dates) was 4.3 days. The standard deviation for between-colony synchronization was 11.3 days.
6. These fitness measures are also significantly related to colony size (*3*). The synchrony relationship remains highly significant, however, after colony size effects have been removed (partial correlation coefficient, reproductive success versus synchrony is –0.92, $P = .001$; partial correlation coefficient for the number of fledglings versus synchrony is –0.85, $P = .001$).
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11. We thank D. Goldman and D. Rubin for assistance in the field and R. Buskirk, J. T. Emlen, Jr., H. Horn, I. Patterson, and R. Ricklefs for discussions and comments on the manuscript. This report is dedicated to Dr. John T. Emlen, Jr., whose pioneering studies on the social behavior of many groups, including swallows, have provided a continuing inspiration to both his students and kin.

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Memory Retrieval from Long and Short Lists

Abstract. *Reaction time in Sternberg's memory retrieval task with both short and long lists is a bilinear function of list length, changing slope at the limits of memory span. Separate long-term and short-term retrieval processes are implied. An alternative one-process model expressed by a logarithmic function is also considered.*

When human subjects must decide whether a stimulus item was present in a short list of memory items, mean reaction time (RT) for the decision is usually a linear function of the number of memory items (*1, 2*). Sternberg (*1*) proposed that the linear function reflects a serial span of memory in which a representation of the stimulus item is compared with representations of each memory item.

Most memory scan experiments have used memory lists short enough to fall within the limits of the span of immediate memory (the number of items that can be recalled without error) (*3*). The limits of immediate memory span are often thought to represent a division between short-term and long-term memory. Because short-term and long-term memory may involve different retrieval processes (*4*), a complete theory of memory retrieval must include an understanding of retrieval from long-term memory and the relation between long- and short-term retrieval.

To determine whether the scan model applies when information resides in long-term memory, we tested lists that exceeded the span of immediate memory and compared performance on these lists with performance on subspan lists. The memory lists were composed of two-syllable, common English words. Subjects memorized lists of 2, 4, 6, 8, 10, 12, 16, or 20 words to a criterion of two consecutive perfect recalls of the list members, in any order. Memorization of a list was followed by a series of trials in which a single test word was presented verbally and the subject decided whether the test word was in the list, pushing one of two buttons to indicate his decision. In experiment 1 we presented each word in any list once, along with an equivalent number of words not on the list (negative tests) (*5*). We presented the test words in a random sequence, which was preceded by one dummy negative test and followed by two dummy tests which were positive or negative with equal probability. This type