HABITAT SELECTION IN BIRDS WITH CONSIDERATION OF THE POTENTIAL ESTABLISHMENT OF THE PARAKEET (*MYIOPSITTA MONACHUS*) IN NORTH AMERICA

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Animals depend upon their habitat for all essentials of life, including food and a place to reproduce. Those species able to move from one habitat to another must evolve certain processes whereby they select areas suitable to their biological requirements.

Orians (1971) points out that birds seeking a place to breed must usually make rapid habitat selections because time is often short, particularly at northern latitudes. He also indicates that intraspecific competition may complicate the process.

Habitats do not exist in homogeneous blocs but rather in complex mosaics each having a different intrinsic value to potential inhabitants. It would then follow that natural selection accounts for members of a given species tending to settle in habitats most suitable to themselves (Orians 1971).

HABITAT SELECTION MECHANISMS

Lack (1971) describes how he first came to consider the mechanism of habitat selection. He was impressed with the rapidity with which populations of birds changed as a plantation of Scots pine (*Pinus sylvestris*) grew into mature trees. He reasoned that these birds must relate to some obvious feature of the environment in order to increase and decrease their numbers so rapidly, and termed this the use of psychological factors in habitat selection.

The terms "Proximate Factor" and "Ultimate Factor," as used by Baker (1938), aid us considerably in understanding habitat selection mechanisms. Ultimate factors are those actually having selective or survival value. These include, among other things, availability of food, quality of nesting material and freedom from predators. Proximate factors are environmental cues that evoke the initial settling response in birds searching for habitat. The latter are Lack's psychological factors. Hilden (1965) suggests that such features as landscape, terrain, presence of a nest hole and temperature might be proximate factors.

Although, in most instances, the precise nature of proximate and ultimate factors has not been intensively studied, Bongiorno (1970) provides an excellent example in his study of a laughing gull (*Larus atricilla*) colony in New Jersey. He believes the most important ultimate survival factor to be the chance of the gulls' nests being washed out dur-

ing storms. Laughing gulls traditionally nest on the highest areas of the island which are delineated by taller grasses. They apparently select nesting habitat on the basis of grass length (proximate factor) without consideration of possible flooding. The fact that floods occur two to four years apart reduces the possibility of the birds learning from experience that higher ground is less likely to be flooded. Bongiorno tested his hypothesis by cutting the grass in one nesting area and thereby effectively prevented nesting. Here is a good example of an easily recognizable proximate factor (grass length) serving as a release mechanism for habitat settling, although the comparatively unrecognizable flooding potential is the real limiting factor (ultimate factor). Like Borgiorno, Lack (1971) also believes that proximate factors are simple environmental features.

Another example, where various environmental factors act as proximate factors in habitat selection, is presented by the prairie chicken (*Tympanuchus cupido*) and sharp-tailed grouse (*Pedioecetes phasianellus*), two related species of the North American prairie. Here, the presence or absence of trees is the important factor in determining whether sharp-tailed grouse or prairie chickens will be present in a grassland. The sharp-tails choose the area with trees and bush (Hammerstrom 1963) while the prairie chickens prefer extensive grassland (Briggs 1968). The number or kind of trees present appears to be of lesser importance than the fact that trees are present or absent (Briggs, unpublished observation). The idea that physiognomy, rather than species diversity plays the more important role in habitat selection is also supported by the finding of MacArthur and MacArthur (1961) that the magnitude of plant species diversity has no effect on bird species diversity, but foliage height diversity, a simpler feature, does have a positive correlation with bird species diversity.

Hilden (1965) believes that habitat selection through proximate factors works on the principle of *summation of stimuli*, an ethological theory developed through studies of animal behavior. According to Hilden's theory, an innate force guides birds to the area of their breeding (or feeding or resting) habitat, then perception of certain environmental stimuli accumulate until a threshold is exceeded and a settling response is evoked. The more the stimuli exceed the threshold level, the stronger the response. Not every habitat considered suitable need possess all the characteristics of an optimal environment. It is enough that the combined effect of the individual stimuli exceeds the threshold of the settling response. One would expect, of course, much variation among different species of birds. In some species one key stimulus might outweigh several lesser stimuli, and this key stimulus might be necessary for the threshold to be reached. In some situations this "super-stimulus" might be enough alone to evoke settling. An example might be the presence or absence of a suitable hole for hole-nesting birds.

Hilden also points out that not all birds nest at the first suitable site encountered, but many appear to explore several sites before actually nesting. This may be due to a two-parted settling reaction with certain proximate factors releasing the settling response and other factors releasing the actual nesting response. He also postulates that such " 'exploratory behavior" could represent a conflict between settling and migratory instincts. In a habitat which barely exceeds the settling threshold, the still strong migratory drive may override the initial settling response with the bird moving on until the settling threshold is further exceeded. This would result in the choice of a better habitat – one which releases a stronger settling response than that encountered initially.

Orians (1971) makes the point that a co-evolution should exist between fitness in different environments (ultimate factors) and the capacity of these environments to evoke the proximate settling behavior. This would imply that the proximate factors used to select habitat should be in some way related to the quality of the habitat. This, in fact, is the case with Bongiorno's (1970) laughing gulls where the tall grass used to select breeding habitat is related to the degree of safety from nest flooding.

As mentioned earlier, food is sometimes used as a proximate factor. Lack (1954) discusses two species of birds which nest alongside locust swarms. Probably, however, food is more often an ultimate factor and another stimulus is the proximate one. For instance, some desert birds nest only after a rain (proximate factor), presumably to insure availability of food (ultimate factor) for broods. Hilden (1965) believes that as an ultimate factor, food puts only loose limits on the habitat for most species, but he points out that the positive correlations between bird density and food supply show that the most productive habitats usually constitute optimal environments for birds.

The presence or absence of other birds of the same species can also have a proximate effect on habitat selection. Displaying males usually have a positive effect on females and may have a negative effect on other males. Lack (1971) indicates that juveniles of flock-feeding birds are influenced by the presence of other members of the species which are in the preferred habitat of the species. Such a response may be of considerable importance among colonial nesters. Lack stresses, however, that there must also be other influences, since sometimes new breeding colonies are started by birds breeding for the first time.

EFFECT OF COMPETITION ON HABITAT SELECTION

Hilden (1965) believes that intraspecific competition determines the width of the range of a species within its habitat. When the population is low, only optimal habitats are exploited, but with population increase less favorable areas are also settled. Orians (1971) presents an equation developed by Fretwell and Lucas (1969) to show the effect of popula-

tion density on habitat suitability. First, it must be assumed that birds have a perfect ability to assess habitats. If S_i represents the goodness of the "*i*th" habitat for a given species and S_{iq} is the average success of the "*q*th" individual in the "*i*th" habitat of the same species. Then:

$$S_i = \frac{1}{n_i} \Sigma S_{iq} \qquad \text{or}$$

the goodness of habitat for a given species equals the sum of the average successes of the individuals of that species in that habitat divided by the number of individuals present. This means, ignoring possible unfavorable effects of low densities, that the intrinsic quality of the habitat decreases as population increases.

If birds are permanently removed from a suitable habitat, others will quickly re-invade from neighboring, possibly less favorable, areas as Bump *et. al.* (1947) found with ruffed grouse.

Interspecific competition, according to Hilden (1965) tends to produce specialization to given niches. This implies that where their ranges overlap, ecologically closely related species are more closely bound to their species-specific habitat than if they were geographically isolated. In the latter case, a species has a greater opportunity to expand its range, particularly if it has a wide amplitude of habitat preferences. MacArthur and MacArthur (1961) state that in order to avoid competition, species in a common area can either eat different foods in the same habitat or eat the same foods in different habitats. These are the extreme adaptations. There are numerous gradations between.

LEARNING IN HABITAT SELECTION

Hilden 1965) indicates that instincts or innate factors play a much greater role in habitat selection than learning. Welty (1962) points out that the corpus striatum, the seat of instinctive behavior, is highly developed in the bird's brain, while the cerebral cortex, an area more important in learning, is relatively small, especially when compared to mammals.

Learning can, however, modify the innate habitat selection patterns. In a classic demonstration, Klopfer (1963) took ten newly hatched chipping sparrows (*Spizella passerina*) from their pine forest nests and raised them in the laboratory. They were later given a choice between pine or oak branches in an aviary. The majority clearly spent most of their time in the pine, for which they evidently had a hereditary preference. Klopfer then took other newly hatched young and raised them in an aviary containing only oak branches. They were then given a choice between oak and pine. While they still preferred pine, these sparrows utilized the oak to a much greater extent than birds with no natal exposure.

Learning as described above, is commonly attributed to imprinting on the natal environment, and Hilden (1965) cities much supporting evidence. Lack (1971) cites an interesting study on reed buntings (*Emberiza schoenichus*). Although reed buntings generally prefer to nest in marshes, they will (perhaps in response to intraspecific competition) also nest on dry ground. Six out of seven females that were hatched in marshes returned to marhses to nest, but only nine out of 22 females hatched on dry ground switched to the more preferred marsh habitat to breed. While these figures are probably too low to be statistically significant, they give some indication that natal habitat can alter innate habitat selection patterns.

In addition to natal habitat imprinting, Hilden (1965) lists site tenacity as a learned response in habitat selection. For example, older individuals of *Sterna hirundo* and *S. paradisaea* will faithfully return year after year to their original breeding areas even when plant succession has advanced to a stage that repels younger members of the same species.

Hilden (1965) also indicates that learning may influence habitat selection. He cites the example of a pair of carrion crows (*Corvus carone*) nesting in a garden, an atypical habitat for this species, after being fed there all winter.

It is generally agreed that corvids are among the most intelligent of all birds. In general, species depending more on intelligence depend less on instinct. Since instinct can be changed only slowly, through natural selection over many generations, abandonment of instinctive attachments to old habitats and occupation of new (foreign) habitats would be expected to be a slow process where learning ability is limited. In contrast, animals depending more on intelligence are at a distinct advantage, for they can override instinct and are capable of learning new ways. Therefore, successful adaptations to new habitats are more likely.

SIGNIFICANCE OF HABITAT SELECTION IN ESTABLISHMENT OF A NEW POPULATION

The Monk Parakeet (*Myiopsitta monachus*) has recently been introduced into the New York City region of the United States. A native of South America, the bird occurs throughout Uruguay, most of Paraguay, southern Bolivia, southern Brazil, and Argentina (Schmidt, 1948), For several years they have been imported into New York as pets, but the origin of the wild population is not entirely clear. There is reason to believe an unknown number escaped when a crate broke open while being unloaded (Bull, 1971). A second source for the breeding nucleus may have been from liberated birds. Owners are frequently disap-

pointed in this parakeet because of its raucity and failure to develop expected mimicry. The Monk Parakeet has been regularly sighted in the New York City region for the last four or five years (Bull, 1971). More recently, birds have appeared at numerous other locations, including Watertown, Waterloo, Owego and Binghamton, New York, and Seaford, Virginia (Bump, 1971), as well as Bradford Co., Pennsylvania (Rockwell, 1971).

In its native South America, the Monk Parakeet inhabits a wide range of vegetative types. These include Patagonian semi-desert scrub, desert grass savanna, pampas, thorn, forest, broad-leaved tree savanna and tropical semi-evergreen forest (Eyre, 1963). Since it is evident that the Monk Parakeet tolerates a wide range of habitats, it is likely, as far as habitat is concerned, that North America can provide many of the proximate factors required for settling and breeding, and probably many or all of the ultimate factors necessary for survival. Moreover, since it is generally agreed that the Psittacidae (parrot family) are among the more intelligent of the birds, learned behavioral adaptations may also enhance the Monk Parakeet's chance of success in North America. The remarkable adaptability of the parakeet to new feeding and nesting situations in the New York City region has already been established (See below).

It is perhaps desirable at this point to consider some of the physical and biological factors which might influence the abundance and distribution of the Monk Parakeet in its new found home. Climate as well as general nature of habitat can impart serious limitations to the ultimate survival of a species in a new region. Welty (1962) states that climate is the greatest determining physical factor for species survival in a given region. In order to compare the climate of the bird's native home with areas in North America where it is a potential resident, we have constructed climographs (fig. 1) showing the general monthly temperature and rainfall patterns for Buenos Aires, Argentina; Brooklyn, New York, and Binghamton, New York.

The winter in Binghamton averages about 30 degrees colder than the Buenos Aires winter, and the Brooklyn winter is approximately 20 degrees less. Rainfall patterns are rather similar for Buenos Aires and Binghamton, although Brooklyn is slightly wetter. Further examination of the climograph will show the breeding season temperatures for Buenos Aires and Brooklyn to be similar, while May in Binghamton is only about ten degrees F. colder than the Buenos Aires equivalent breeding month of November.

Although the climograph does not show the whole picture, it does indicate that if the Monk Parakeet can tolerate the colder winter temperatures and if nonclimatic factors are suitable, this parrot has a chance to survive in North America. It should be emphasized, however, that

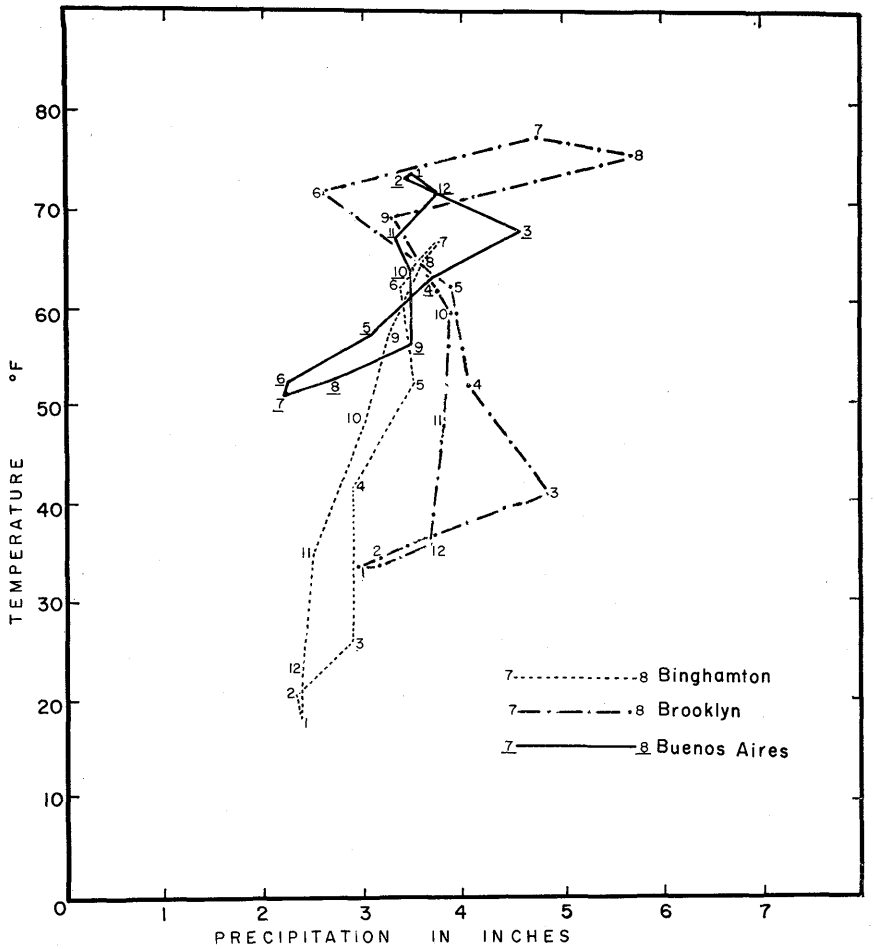

Figure 1. Superimposed climographs showing mean monthly temperature and precipitation for Buenos Aires, Argentina and Brooklyn and Binghamton, New York. The data for constructing this figure was obtained from Wernstedt, 1972.

the Monk Parakeet is not restricted to the Buenos Aires area and therefore experiences a greater variety of climatic conditions in South America than is indicated by the climograph for Buenos Aires.

It was pointed out in the first part of this paper that food can be both a proximate and ultimate factor in habitat selection. When acting as an ultimate factor food does not put strict limits on initial habitat selection. With the Monk Parakeet, however, food may be acting as an important proximate factor. In many areas these parakeets have settled

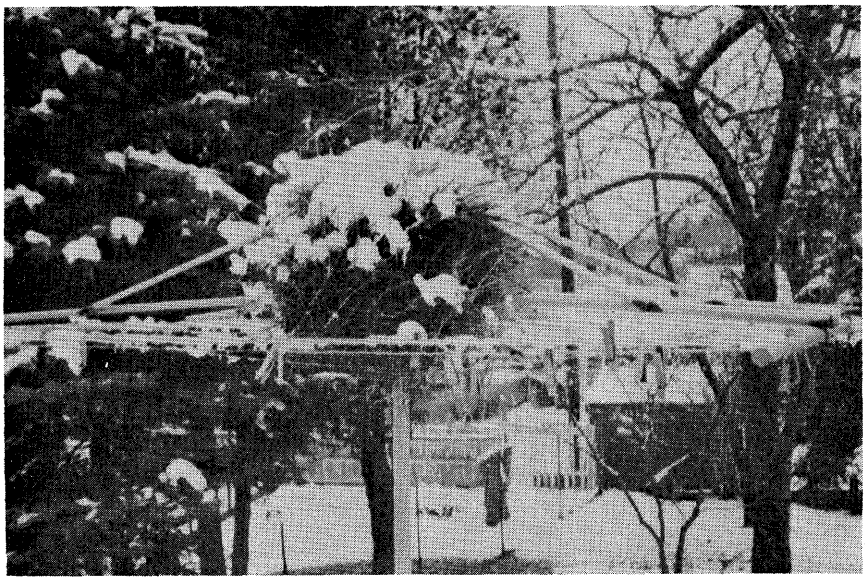

Figure 2. Photograph of a nest constructed by a Monk Parakeet at Binghamton, New York. The bird was still working on the nest when this photograph was taken in November 1972.

and built nests at or near feeding stations, and this is true with the bird we presently have under observation at Binghamton, New York. If a species is an unspecialized feeder and adaptable to new food sources, exploitation of food resources in a new habitat would be expected to be a fairly simple process. Bull (1971) provides evidence that the Monk Parakeet in the New York City region *CAN* effectively utilize the available food resources. He has found that they eat fruit, pine seeds, acorns, grain and will take a variety of offerings from bird feeders. We, therefore, think it unlikely that food will be a factor limiting the spread of the parakeet in the area under consideration, but we would expect birds to be more common (and large colonies to be formed) where food is more readily available, such as in agricultural areas and near well-maintained feeding stations.

Another possible factor discussed in the first part of this paper was the availability of suitable nesting sites. As a proximate factor this does not seem to pose a problem for the Monk Parakeet. Traditionally the birds nest in trees in South America, and since proximate factors are simple, trees in North America should be sufficient to elicit a nesting response. Moreover, Bull has found that the parakeets in New York will nest on man-made structures if suitable trees are absent, and the Monk Parakeet

in Binghamton is presently constructing a nest on an outdoor aluminum clothes tree (fig. 2). The *ultimate* effects of nest site selection on the production of the bird will require further study. The protection provided by the enclosed nest, however, combined with the bird's aggressive nature, suggest that the Monk Parakeet may be able to fledge young successfully in a variety of nesting situations.

Another habitat selection factor we considered was competition, both interspecific and intraspecific. The interspecific problems this parrot could encounter will not be known until more research is done on the bird in its new habitat. Because of its diverse food preferences, we expect it to compete with several endemic species, but how detrimental this will be to native birds remains to be seen. The aggressive nature of the parakeet may also lead to competition and exclusion of some native species from nesting areas, but again further observations are needed. On the other hand, perhaps the stick nests will provide additional nesting sites for native birds as they do in South America (Conway, 1965). The possibility of competition with native species limiting the spread of the Monk Parakeet, itself, is another problem about which we cannot speculate with confidence at this time.

The Monk Parakeet is a gregarious bird (Conway, 1965), so intraspecific competition may not put serious limits on the settling density in a given area. As in many colonial birds, the fact that they are gregarious may necessitate the presence of other members of the species before habitat settling and subsequent reproduction are successfully undertaken. Darling (1938) has noted that gregarious birds often fail to reproduce successfully when colony size is small. While the psychological effects of gregariousness go beyond the scope of this paper, this may be a factor of major importance in determining whether or not the parakeet becomes successfully established in some areas where individuals, or small isolated populations, are presently found.

SUMMARY

1. Birds have the ability to search for good habitat.
2. The intrinsic quality of a given habitat decreases as the population increases.
3. Birds use various features of the habitat as stimuli for settling (proximate). These may have co-evolved with the factors having actual survival value (ultimate).
4. Proximate factors are generally considered to be simple and to work on the principle of summation of stimuli.
5. Food may be both a proximate and ultimate factor.
6. Intraspecific competition influences settling density and determines the limits or range within suitable habitat.

7. Interspecific competition can force greater habitat specialization.
8. The innate habitat selection mechanisms can be altered slightly by learning. This is mainly by imprinting on natal habitat, but experience and conditioning also can have an effect.
9. Some species are versatile in their habitat requirements, while others are rather narrow.
10. The Monk Parakeet has been introduced into North America at locations climatologically similar to parts of the species native range. Its food and nesting habits are quite diverse, and the fact that the species has lived in North America for an undetermined number of years suggests that it might have a chance of becoming established as a permanent resident. Factors, other than habitat, will need to be examined, however, before a reasonable survival assessment can be made.

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THE 1972 SPRING MIGRATION AT DERBY HILL WITH REMARKS ON THE PERIOD 1963-1971

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I. INTRODUCTION

During the last ten years a considerable amount of data on the spring migration occurring at the Derby Hill hawk lookout on the southeastern corner of Lake Ontario has been assembled. Beginning with the observations of J. R. Haugh and T. J. Cede during the early and mid-nineteen sixties, observations have been made on a regular basis. Some new data, particularly regarding the length of the period of migration of some hawks and seasonal counts of some species, have been obtained. It is the purpose of this paper to review the 1972 spring migration at Derby hill with special emphasis upon the hawk movements. Also, where pertinent, comments regarding new data obtained since 1965 will be included.

II. THE 1972 HAWK MIGRATION

A. GENERAL COMMENTS

The 1972 hawking season was one of distinct contrasts. The opinion of any observer on how good a year it was depended mainly upon how lucky or persistent he was. There were many days when observers would leave Syracuse, only forty miles to the south, with southerly winds prevailing, only to reach Derby and find the winds coming from the north. Consequently, they saw only a poor flight when these conditions prevailed. On the other hand, when the correct conditions occurred, the flights were often quite spectacular. This combination of events produced several interesting occurrences. Among these were record single day totals for four species, and record late departure dates for five species.