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A POPULATION STUDY OF THE BURROWING OWL NEAR TAMPA, FLORIDA

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A POPULATION STUDY OF THE BURROWING OWL
NEAR TAMPA, FLORIDA

by

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A thesis submitted in partial fulfillment of the requirements for the degree of Master of Arts in the Department of Biology in

The University of South Florida

June, 1976

Thesis supervisor: Andrew J. Meyerriecks

Certificate of Approval - Master's Thesis

Graduate Council
University of South Florida
Tampa, Florida

CERTIFICATE OF APPROVAL

MASTER'S THESIS

This is to certify that the Master's Thesis of

William D. Courser
Name of Student

with a major in Biology
has been approved by the Examining Committee as satisfactory for the thesis requirement for the Master of Arts degree at the convocation of June, 1976
date

Thesis committee:

Thesis Supervisor: Andrew J. Meyerriecks

Member: John M. Lawrence

Member: Glen E. Woolfenden

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INTRODUCTION

The Burrowing Owl (Speotyto cunicularia) nests in open, prairie-like habitat which renders it easily accessible for behavioral and ecological studies. In suitable locations in Florida, they nest in close proximity to each other with many pairs available for observation. Its relative tameness compared to larger raptors coupled with the conspicuously littered area around its burrows allows easy determination of nesting sites. In addition, the owls will carry on their activities even though an observer is stationed in a car or hidden within 100 feet of a burrow.

The literature on Burrowing Owls in Florida is small and not detailed. Although several studies, cited below, have been made on the species in the western United States no detailed studies have been undertaken on the only breeding population in the eastern United States. No intensive studies of longer than two years have been conducted with the Burrowing Owl. Long term ecological studies are important to the understanding of a species' biology. From knowledge gained by such studies, the Burrowing Owl can be managed to ensure its continuance as a part of the fauna of Florida.

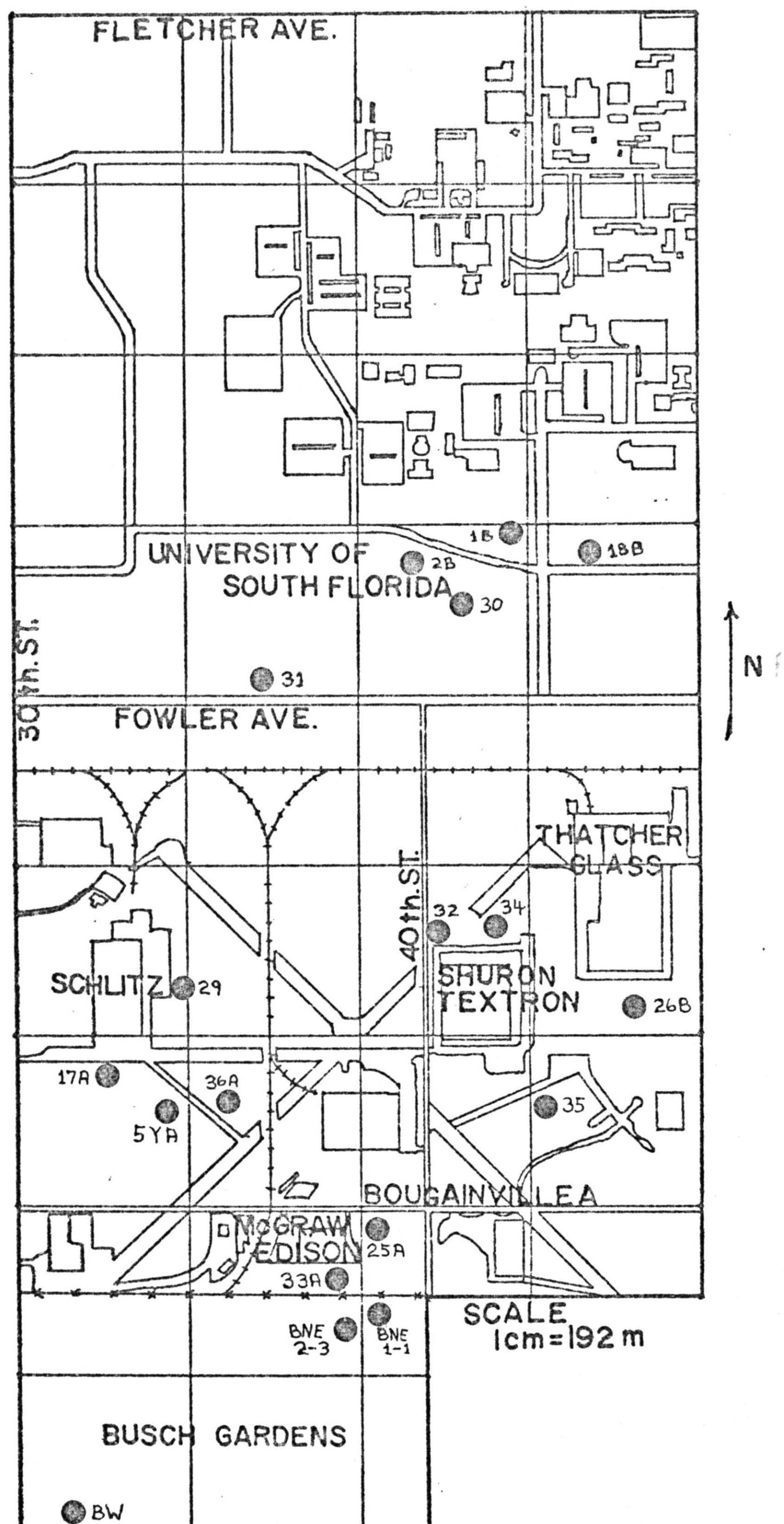
The objectives of this investigation have been to study the population ecology of the species. Reported here is an analysis of the population distribution of the species in the study area, the number of individuals in the population from year to year and the breeding phenology.

DESCRIPTION OF THE STUDY AREA

The study area was located in the northeast section of Tampa, Hillsborough County, Florida on the University of South Florida campus and the adjoining industrial park, formerly an airport. The locale is underlaid by Tampa Limestone Formation covered by sandy soil (Lakela and Long, 1970). The study area was about 600 hectares. Area boundaries were the midlines of the streets outlined in Figures 1-4. This area was selected because it is surrounded on all sides by urban and wooded habitat unsuitable for Burrowing Owls. Thus, the distribution of a population within a well defined, restricted area was easily studied.

The area was formerly a sandhill vegetation type (Lakela and Long, 1970), but partial clearing and irregular mowing has maintained a subclimax of secondary growth. Only naturally occurring plants were identified although planted ornamentals were present, mostly around buildings. Oaks, mainly live oak (Quercus virginiana var.) and turkey oak (Q. laevis) were the dominant trees. Other trees included pines (Pinus elliottii and P. palustris), persimmon (Diospyros virginiana) and Baccharis halimifolia. Spanish moss (Tillandsia usneoides) hung abundantly from the oaks and persimmons. In the industrial park, trees were few, small and irregular in occurrence, while on the campus the oaks were more closely spaced (30-60 meters apart with many open areas) especially towards the north end of the university grounds (8-15 meters apart). Clumps of saw palmettos (Serenoa repens) were scattered amongst

Figure 1. Distribution of a population of Burrowing Owls near Tampa in 1970.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N
THATCHER
GLASS
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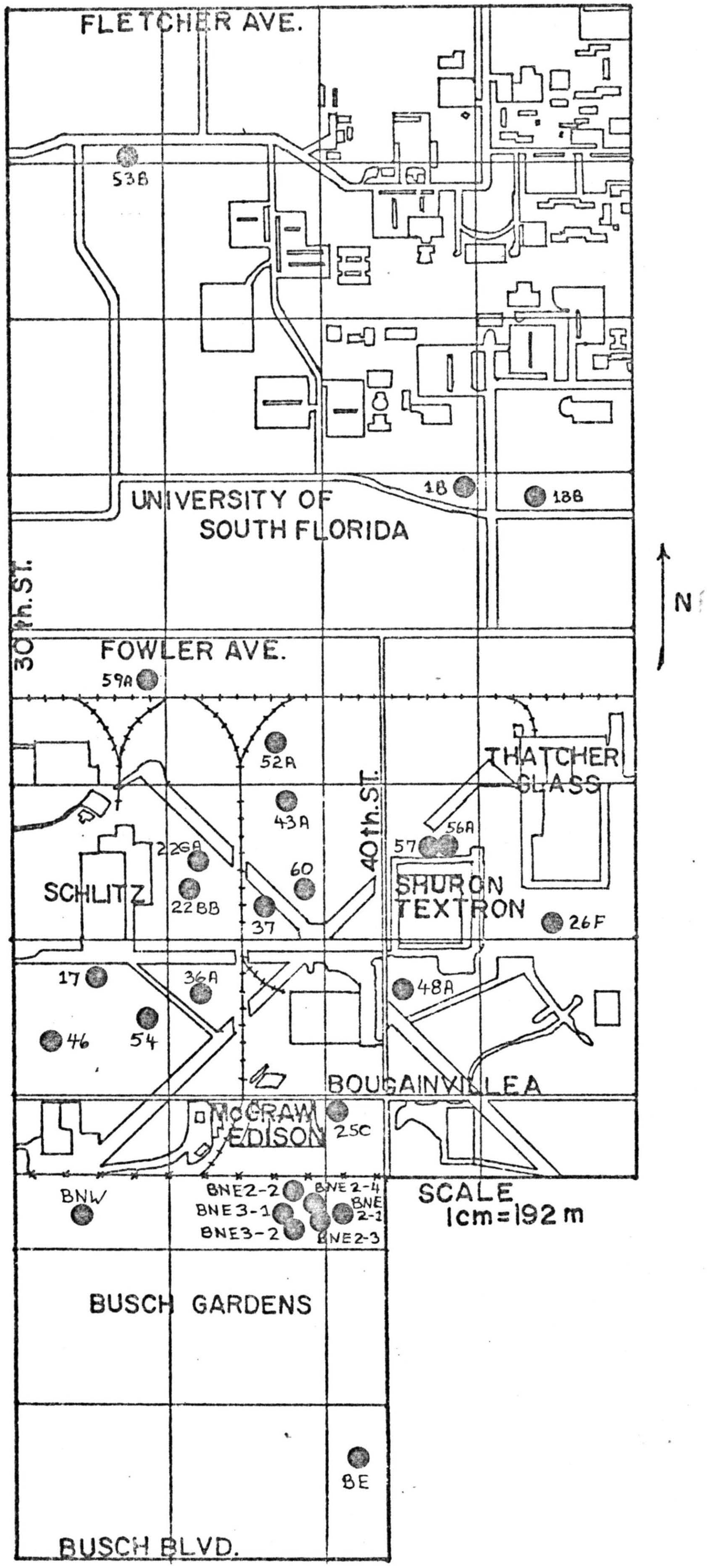
32
34
SHURON
TEXTRON
SCHLITZ
29
26B
17A
36A
5YA
35
BOUGAINVILLEA
McGRAW
EDISON
25A
33A
BNE
2-3
BNE
1-1
SCALE
1cm=192 m
BUSCH GARDENS
BW
BE
BUSCH BLVD.

Figure 2. Distribution of a population of Burrowing Owls near Tampa in 1971.



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SOUTH FLORIDA
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FOWLER AVE.
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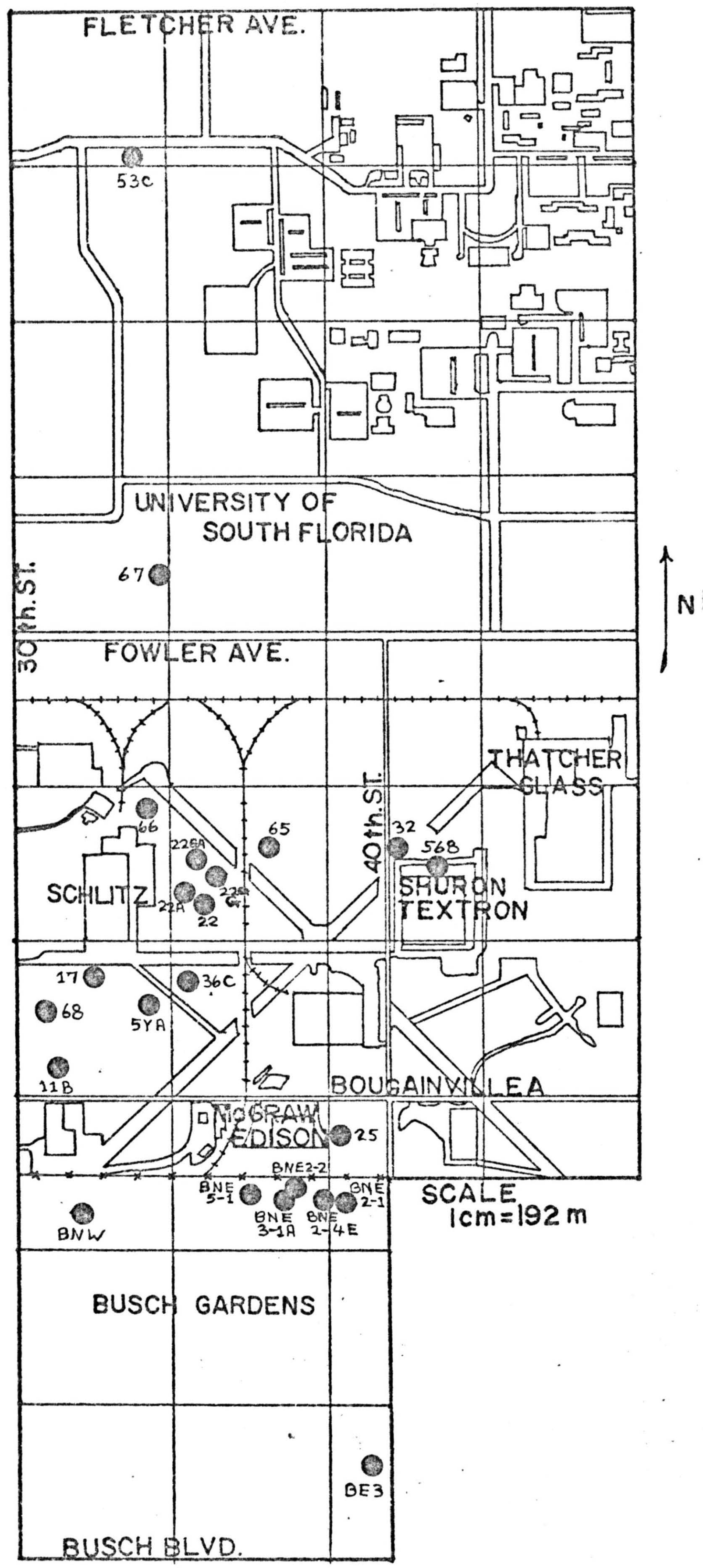
43A
40th. ST.
THATCHER
GLASS
56A
57
226A
60
SCHLITZ
22BB
37
SHURON
TEXTRON
26F
17
36A
48A
46
54
BOUGAINVILLEA
McGRAW
EDISON
25C
BNW
BNE2-2
BNE 2-4
BNE
2-1
BNE3-1
BNE3-2
BNE2-3
SCALE
1cm=192 m
BUSCH GARDENS
8E
BUSCH BLVD.

Figure 3. Distribution of a population of Burrowing Owls near Tampa in 1972.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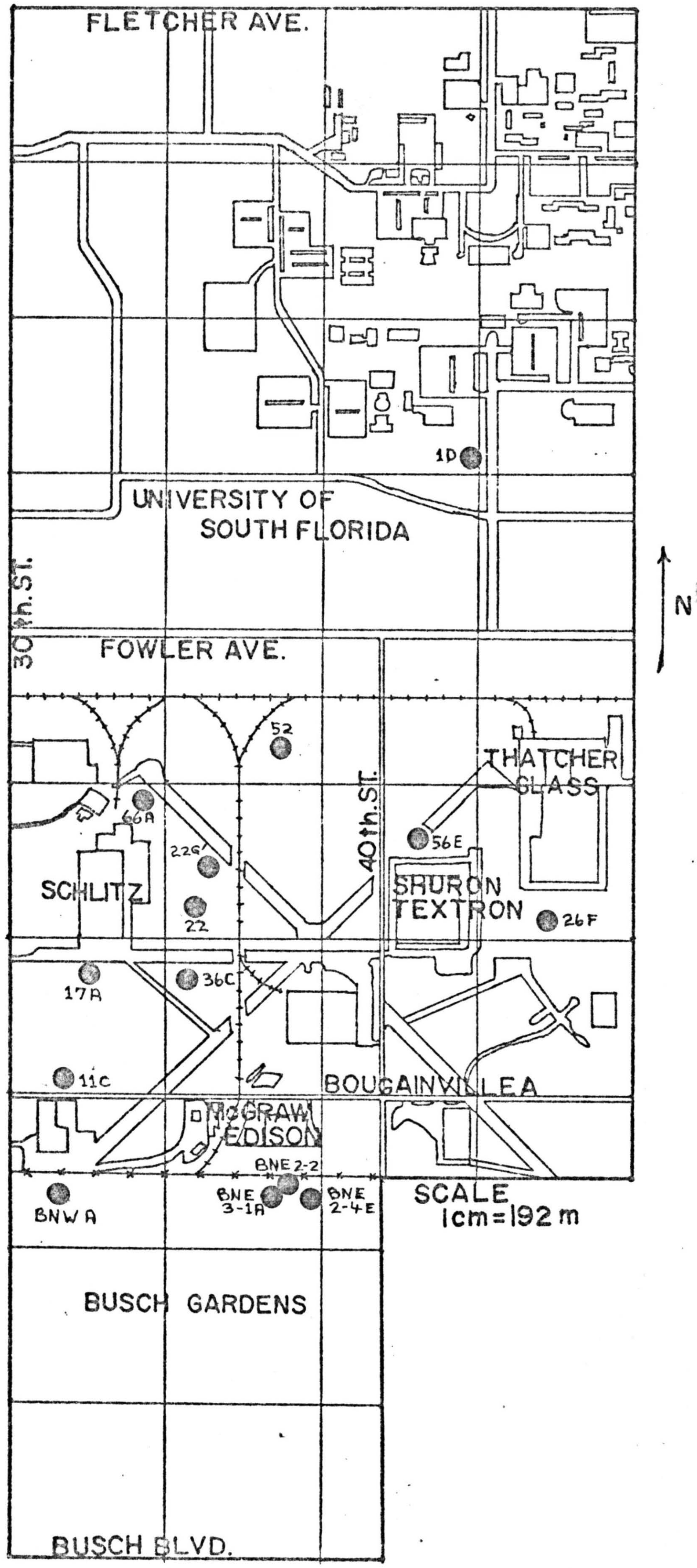
40th. ST.
SCHLITZ
22A
22
SHURON
TEXTRON
17
36C
68
5YA
11B
BOUGAINVILLEA
McGRAW
EDISON
25
BNE2-2
BNE 5-1
BNE 2-1
BNE 3-1A
BNE 2-4E
SCALE
1cm=192 m
BNW
BUSCH GARDENS
BE3
BUSCH BLVD.

Figure 4. Distribution of a population of Burrowing Owls near Tampa in 1973.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THATCHER
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22G
56E
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SCHLITZ
SHURON
TEXTRON
22
26F
17A
36C
11C
BOUGAINVILLEA
McGRAW
EDISON
BNE 2-2
BNE
3-1A
BNE
2-4E
BNW A
SCALE
1cm=192 m
BUSCH GARDENS
BUSCH BLVD.

the oaks at the University of South Florida. The dominant ground cover included sandspurs (Cenchrus sp.), bahia grass (Paspalum notam), natal grass (Rhynchelytrm rosem), cottonweed (Froelichia floridana), Cassia fasciculata, Liatris tenuifolia and dog fennel (Eupatorium sp.). Other plants present included Chloris grasses, Polycarpaea nebulosa, Crotalaria sp., tread-softly (Cnidoscolus stimulosus), cactus (Opuntia bentonii), milkweeds (Asclepias sp.), begger ticks (Bidens pilosa), Chrysopsis nervosa, Heterotheca subaxillaris and roserush (Lygodesmia aphylla).

Fauna characteristic of the area included the following breeding birds: Bobwhite (Colinus virginianus), Killdeer (Charadrius vociferus), Rock Dove (Columba livia), Mourning Dove (Zenaida macroura), Common Nighthawk (Chordeiles minor), Common Flicker (Colaptes auratus), Blue Jay (Cyanocitta cristata), Mockingbird (Mimus polyglottos), Brown Thrasher (Toxostoma rufum), Loggerhead Shrike (Lanius ludovicianus), House Sparrow (Passer domesticus) and Eastern Meadowlark (Sturnella magna). Nonbreeding foragers included the following: Turkey Vulture (Cathartes aura), Black Vulture (Coragyps atratus), Red-tailed Hawk (Buteo jamaicensis), Cattle Egret (Bubulcus ibis), Laughing Gull (Larus atricilla), Purple Martin (Progne subis), Fish Crow (Corvus ossifragus), Red-winged Blackbird (Agelaius phoeniceus), Boat-tailed Grackle (Cassidix major), and Common Grackle (Quiscalus quiscula). Overwintering and migratory birds included: American Kestrel (Falco sparverius), Upland Sandpiper (Bartramia longicauda), Ring-billed Gull (Larus delawarensis), American Robin (Turdus migratorius), Starling (Sturnus vulgaris), Palm Warbler (Dendroica palmarus), Brown-headed Cowbird (Molothrus ater), American Goldfinch (Spinus tristis), Savannah Sparrow (Passerculus sandwichensis), Grasshopper Sparrow (Ammodramus savannarum) and Vesper Sparrow (Pooecetes gramineus).

Mammals present were: opossum (Didelphis marsupialis), striped skunk (Mephitis mephitis), red fox (Vulpes fulva), gray fox (Urocyon cinereoargenteus), southeastern pocket gopher (Geomys pinetis), eastern gray squirrel (Sciurus carolinensis), eastern cottontail (Sylvilagus floridanus) and various mice and rats. Reptiles included: gopher turtle (Gopherus polyphemus), corn snake (Elaphe guttata) and five-lined skink (Eumeces fasciatus).

MATERIALS AND METHODS

The investigations were carried out from October 1969 to April 1974. Over 1,000 hours of field observations were made using 8 x 40 binoculars, 20X spotting scope and infra-red sniperscope. The birds were observed from tree blinds, parked automobiles and underground blinds dug near the nest chamber.

One hundred forty six owls were banded with U. S. Fish and Wildlife Service aluminum bands and plastic color bands. Outside of Busch Zoological Gardens, all young of 35 broods were banded in 1970 through 1973, and 85 per cent of the adults were banded by the 1971 breeding season. No owls were banded within Busch Gardens. Most owls were weighed, measured, inspected for ectoparasites and feather condition and released directly into the burrow after banding. Weighing followed immediately after capture.

The study area was censused by 15 meter transects in late winter and early summer. Known nests were checked on the average of twice a week, more often during the breeding season. Sections within the study area that were not occupied were spot checked occasionally between censuses. Many nests were marked with 30-45 centimeter stakes. The owls used these stakes as perches which made reading color bands easier. Each year, a few nests were chosen for detailed observation. Pellets were collected from October 1969 to October 1970 at four nests.

In addition, several nests each year were carefully excavated to facilitate study of the owl's breeding biology. At such nests, the nest chamber at the end of the burrow was carefully located. An observational access roughly one-half meter square and dug to the depth of the burrow floor was placed beside the nest chamber. A very short passage leading from the access to the nest chamber was excavated. A removable artificial wall fitted into the passage to retain the integrity of the burrow. At ground surface the observational access was covered by plywood. The plywood cover was camouflaged by a thin layer of dirt and sod. The cover was recessed so that the plywood and its camouflage would be roughly equal to the ground surface. These nests were checked at least every other day until the young started to fledge or disperse to other burrows within the territory. Close approach was avoided except when pellet collection, banding and breeding data collection were done.

In order to pinpoint the nesting burrows exactly for statistical calculations, the distance to a burrow was measured by steel tape from large geographical features (fence gates, building corners, large trees, etc.) in at least two different compass directions. The information recorded was plotted to scale on a recent aerial photograph (scale 1" = 400') and then transferred to an overlying semi-transparent paper. The distances between burrows were measured by an engraved, tempered-steel ruler and recorded to the nearest foot (after correction for scale) for statistical calculations (see Appendix). Straight line distances between close neighboring burrows were used as a check on the burrow plotting procedures.

The boundaries of the study area were also marked on the aerial photograph and transferred to the semi-transparent paper. The area was gridded on the paper for the purpose of calculating the Poisson and negative binomial distribution statistics.

The nearest neighbor statistics are taken from Clark and Evans (1954), while the Poisson distribution is from Steel and Torrie (1960) and the negative binominal is from Anscombe (1950) and Southwood (1966). The statistic λ is referenced in Southwood (1966). By using such methods, the population distribution of the Burrowing Owls at any given time can be evaluated and later compated with the pattern of the same area at different years or with those of other populations. The significance of differences between statistically described distributional patterns should be more suitable to evaluation than comparison by simple inspection.

The population of Burrowing Owls in the study area is distributed through a rather homogeneous habitat. Although minor differences exist in such factors as number of trees, mowing, and lighting, the study area differs markedly from the suburbs to the south, southeast and southwest and the more heavily wooded areas of the northwest, north and northeast. Areas in the northwest and north were commercially developed during the course of the study. In order to test statistically the Burrowing Owls' spacial relationships the nearest neighbor technique (Clark and Evans, 1954) was used. This statistic "is a measure of the manner and degree to which the distribution of individuals in a population on a given area departs from a random distribution." Details of the statistical calculations are presented in the Appendix.

The nearest neighbor statistic can determine the type of distribution a population fits. The statistic is applicable to the study population because the area under investigation was the only habit in which Burrowing Owls breed. A few hectares of marginal habitat suitable for

Burrowing Owls adjoined the study area, but the owls did not breed in these locations. Only once during the four year study period was an owl observed in these locations. A single young of the year established a burrow but left after about four months. As the sample size was the entire population rather than a sample from a larger population, the problem of the distribution of a set of points in a specific area versus distribution with respect to a larger area, the problem of utilizing a point outside the specific area as a center of measurement, and the problem of subsampling were avoided. The direct sampling or counting of the burrows, facilitated by the behavior of the species, also avoids the biases of indirect sampling procedures.

The occupied burrow of paired or single owls was used as the point of measurement. Even though the species has spacial requirements beyond the burrow itself, the burrow is the center of mating and nesting activity. Burrowing Owls do not defend foraging areas (Butts, 1973; Coulombe, 1971; Martin, 1973 and Thomsen, 1971). The data for calculation of the statistic were taken from the distribution of the owls on 1 May of each year (see Appendix for details).

One precautionary statement should be made: the comparison of nearest neighbor data from this study to other studies can be made in detail only if the other study population employed the same sampling unit size and sampling unit number. But even with this restriction comparisons can be useful to measure the degree of aggregation of a species under varying habitat conditions and developmental stages (Southwood, 1966).

As an additional check on the nearest neighbor calculations, the study area was gridded into equal-sized squares. Two grid sizes were tested, one of approximately 16 hectares / square and one of approximately

4 hectares / square. The number of burrows per square was recorded as the observed frequency of burrows per square and the data from both grid sizes tested as to the goodness of fit into Poisson or negative binomial distribution (see Appendix for details). If the population fit a Poisson distribution, the distribution of Burrowing Owls would be considered to be random on the study area. By contrast, if the population fitted a negative binomial distribution, clumping of some degree would be indicated (Southwood, 1966).

For calculation of the negative binomial test, an estimate of the value of "k", a parameter of dispersion, must be made. The value k can be estimated by three methods (Southwood, 1966). For both grid sizes, k values were derived by each of the three methods. Upon examination of the estimation results (Appendix), k values derived by the solution of an iterative equation using logarithms to the base 10 gave the best estimate of k. This method is most reliable when the mean is small, which is the case with this study data. Additionally, k values calculated by this method fell within 90-98% efficiency range desirable for a reliable estimation of k (Southwood, 1966).

Estimation of k by the simple method of dividing the mean squared by the difference of the variance minus the mean proved not to be an efficient estimate and hence not reliable for use in the study. The third method, solution of an iterative equation using natural logarithms, did not give k values as closely reproducible from year to year and between both grid sizes as did the method using logarithms to the base 10.

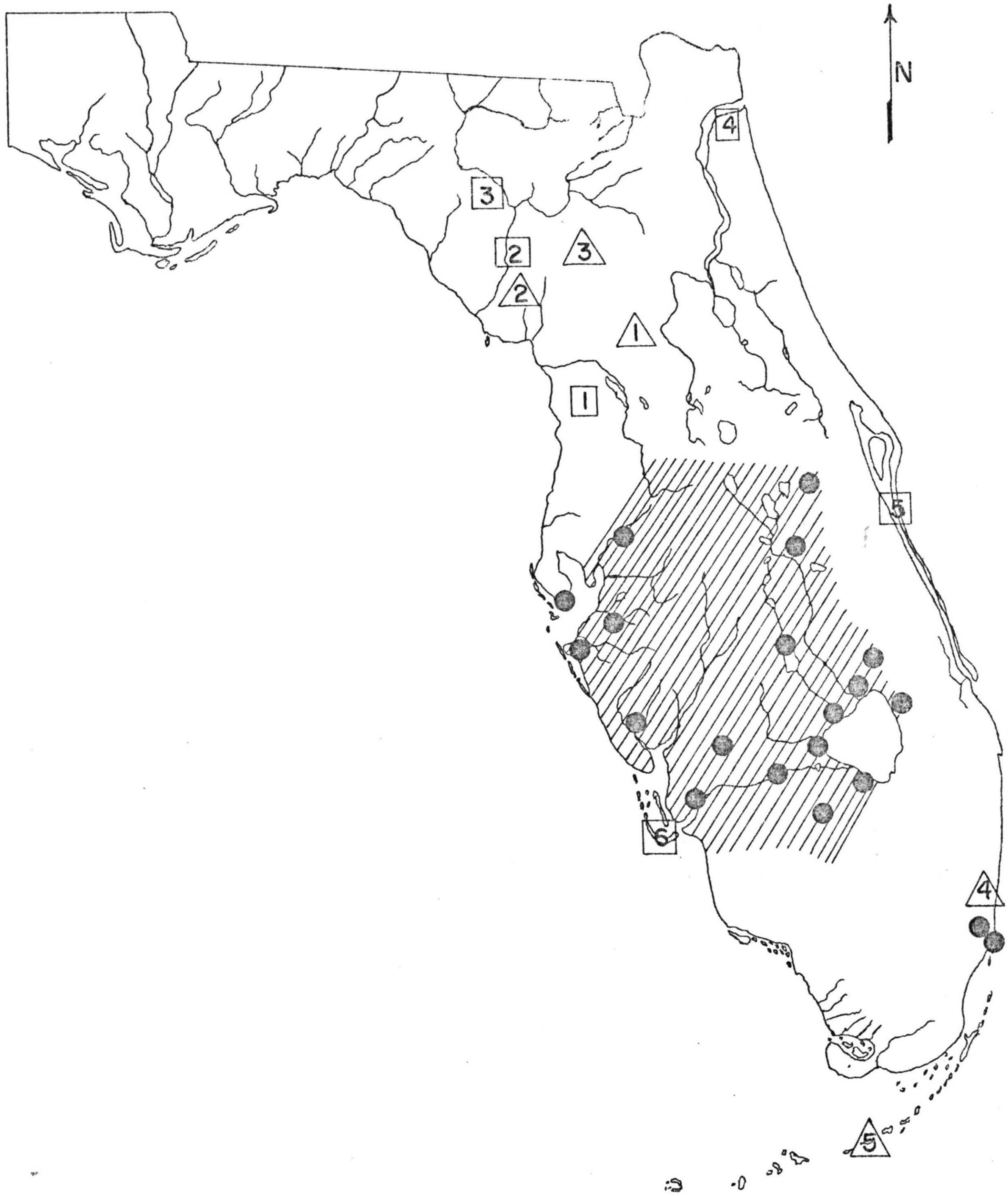
RESULTS AND DISCUSSION

Distribution and Migration

The Burrowing Owl is found only in the New World. In North America, the western subspecies, Speotyto cunicularia hypugaea, breeds west of the Mississippi River from southern Canada into Mexico (American Ornithologist Union Checklist 1957: 283). The Florida subspecies, S. c. floridana, first recorded in Florida by N. B. Moore near Sarasota Bay in 1874 (Ridgway, 1874), generally breeds in the central and southern parts of the peninsula (Sprunt, 1954). With the advent of large scale clearing of formerly forested areas in north-central Florida, Burrowing Owls expanded their breeding range northward. Neill (1954) reported the extension of the owl's range north to Ocala and northwest into Hernando County. Ligon (1963) reported a further breeding range expansion north to Gainesville and Chiefland and south into the Keys. Recent reports (Ogden, 1974; Kale, 1975) have documented the presence of adults with juveniles in Lafeyette and Duval Counties. In 1973 I observed several pairs in Citrus County. Several recent observations (Ogden, 1974; Stevenson, 1972) indicate that the number of Burrowing Owls has been increasing in Gilchrist and Alachua Counties, areas in and near which Ligon (1963) reported the range expansion. Figure 5 documents the present breeding range of the Burrowing Owl in Florida.

In addition to the first breeding record in the Keys, Burrowing Owls are reported to have nested on Passage Key, Manatee County (Sprunt, 1954), Hog Island, Pinellas County (Betz, 1932), Satellite Beach

Figure 5. Breeding range of the Burrowing Owl in Florida. Dark circles are breeding localities already given by Sprunt (1954). Numbered triangles indicate expansion of breeding range, 1 - Ocala, 2 - Chiefland, 3 - Gainesville, 4 - Davie, 5 - Marathon Key as given by Ligon (1963). Numbered squares indicate records since 1963, 1 - Citrus County, 2 - Gilchrist County, 3 - Lafayette County, 4 - Duval County, 5 - Brevard County, 6 - Lee County. Figure modified from Ligon.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(Matchett, 1973) and on an islet northwest of Sanibel Island (A.J. Meyerriecks, pers. comm.). The owls nesting near Sanibel were within a few meters of the Gulf waters. Coupled with the several records of Burrowing Owls from islands off the coast of California, the above observations establish that nesting owls have been recorded near the sea.

Burrowing Owls are generally migratory over the northern parts of their western range (Bent, 1938). With reference to Florida, Bendire (1892) stated that Burrowing Owls "disappear for a time" after the completion of the breeding season. Neill (1954) observed that the birds left the Ocala vicinity after the advent of cold weather. Nicholson (1954) reported that owls in the Kissimmee Prairie are rare in winter but reappear at last year's burrow in February and March. No change has ever been suggested for the northern winter range limit of S. c floridana given by Bent (1938) as Miakka Lake, Istokpoga and Fort Drum, although Sprunt (1954) lists the species as being "resident locally" to Plant City and Kissimmee. Further support for migration in Florida is found in Sprunt's (1938, 1939) observations of owls in the Keys during January and December. Additional observations have been recorded in the Dry Tortugas and Florida Keys (Sprunt, 1954 addendum); and more recently in the Tortugas by B. Harrington (pers. comm.). No specimens were collected from the recent observations to verify subspecific identification. There are also scattered reports of Florida Burrowing Owls outside their normal range in the eastern United States (Bent, 1938; Sykes, 1974), off southeast Florida in October, 1952 (Castenholtz, 1954) and out to sea (Ridgway, 1875; Sykes, 1974). All of the above observations suggest that some type of movement is occurring to and from certain breeding grounds.

No banding results have yet been obtained to demonstrate migration in the Florida subspecies of the Burrowing Owl.

Population Distribution

The results (Appendix and Table 1) of both the nearest neighbor test and the distributional tests show that the distribution of Burrowing Owl nest burrows in the study area is not random. The nearest neighbor statistic "R" has a range of 0 to 2.1491. R is the ratio "...used as the measure of the degree to which the observed distribution approaches or departs from random." An "R" value of 0 would indicate conditions of maximum aggregation. A value of 2.1491 is indicative of uniform spacing while R=1 would be the value for a randomly distributed population (Clark and Evans, 1954). The R values obtained (Table 1) for the study population reveals that the Burrowing Owl nest burrows are less than R=1. The α_3 test of significance of the departure from random of the R values obtained indicate that a greater departure from random distribution might occur between 13% and 19% of the time by chance. The results indicated that the distribution shows some clumping yet is not a great departure from random expectation.

The percentage of reflexive pairs (Table 1) for 1970 and 1971 is extremely close to the 62.15% value expected if the distribution was random while the values for 1972 and 1973 are almost 20% lower than the expected value. The reflexive pair values obtained parallel the R values calculated and further support the observation that the owl's distribution shows clumping but does not greatly deviate from random.

The results of the distributional tests, Poisson and negative binomial, provide additional support for the interpretation and meaning

Table 1

COMPARISON OF PUPULATION DISTRIBUTION STATISTICS
FOR BURROWING OWLS NEAR TAMPA, FLORIDA

Statistic	1970	1971	1972	1973
R	.8229	.8331	.7774	.7893
% Reflexive Pairs	63.16	59.26	43.48	42.86
α 3	.1448	.1924	.1316	.1686
Grid size 16 hectares / square				
Poisson χ^2	4.2238	13.3171	12.1017	4.1542
Negative Binomial χ^2	0.5724	2.8112	3.7045	0.5343
Tab χ^2	7.81	9.49	7.81	7.81
λ	.5662	.4839	.6627	.4143
Grid size 4 hectares / square				
Poisson χ^2	1.1917	9.2402	2.3075	4.6829
Negative Binomial χ^2	0.1052	1.0576	0.9181	1.6417
Tab χ^2	5.99	7.81	5.99	5.99
λ	.0826	.1186	.1698	.1036

of the results of the nearest neighbor test. As seen in Table 1, the population in all four years and using both grid sizes best fits a negative binomial distribution, which is indicative of a non-randomly distributed population (Southwood, 1966). As a check, all estimates of k were used in the calculation of the negative binomial for both grid sizes. In all cases the population fit a negative binomial distribution based on minimal χ^2. The negative binomial test detects clumping in the owl's population distribution. The clumping could be caused by heterogeneity of the habitat, behavior or a combination (Southwood, 1966).

Analyzing both the results of the nearest neighbor test (R indicative of some clumping but the departure from random is not great) and the distributional tests with the observed pattern of the distribution (Figures 1-4) leads to the conclusion that the population does show clumping, yet the clumps appear to be distributed at random. Another way of expressing the pattern would be that the relationship of the nesting birds to each other is clumped in terms of each other but the clumps are randomly distributed in terms of the study area.

Two questions come to mind: What does the distribution mean; and, what causes this distribution? The negative binomial statistic indicates aggregation. The clumping can be caused by active aggregation by the species (behavioral) or by heterogeneity of the habitat (environmental parameters). The statistic λ (Southwood, 1966), a measure of the mean number of individuals in an aggregate, allows one to distinguish between behavioral and environmental clumping. A value for λ of less than 2 indicates that the environment causes the aggregation while a value greater than 2 is indicative of behavioral clumping (the animals are attracted to each other).

As recorded in Table 1, the statistic for all years was well under 2, thus indicating the distribution of Burrowing Owls on the study area is probably controlled by environmental factors. From this, we can now examine what environmental factors in the area could be controlling the distribution.

Discussion of Environmental Parameters affecting Distribution

The environmental parameters that appear to be most important in the Tampa population are 1) frequency of mowing; 2) location of lights; and 3) amount of disturbance. The availability of vacant burrows was not a factor in the owl's distribution because in Florida a large number of burrows are dug by the owls themselves (Bent, 1938; Neil, 1954; Nicholson, 1954; Sprunt, 1954 and Courser, unpublished field notes). The remainder usually are modified burrows of the gopher tortise (Gopherus polyphemus). Perch availability also did not appear to be a factor affecting distribution in the population, as many were available throughout the study area. Perches to survey the surroundings are improtant for survival in open habitats. Perch availability may be a factor in nest site selection in short grass and prairie habitats (Butts, 1973). Sites in Minnesota and the Dakotas always included observation posts of some type (Grant, 1965).

Burrowing Owls almost always are observed in open areas. They expanded their range in Florida as a result of the creation of open habitats (pastures) in formerly wooded areas (Ligon, 1963). Even in open areas they will use the nest mound, posts, trees, brush, fences, wires, etc., to observe their immediate surroundings. It would seem reasonable to conclude that a burrow-nesting bird lacking powerful defensive mechanisms or an elaborate burrow system, and dependent on flight for survival and defense would prefer low ground cover. Detection of potential enemies and efforts to drive or lead them away before the burrow is discovered would be facilitated.

The part of the study area bounded approximately by Fowler Avenue on the north, 40th Street on the east, Bougainville Avenue on the south and railroad tracks to the west (the location of nest sites 43, 52, 59, 60 and 65) was mowed only three times since the fall of 1969: in January 1971; June 1972; and November 1973. The vegetation in the infrequently mowed field was a ruderal community of dog fennel (Eupatorium), various grasses and weedy species. Dog fennel rapidly grows to heights of three feet or more.

The nest sites in the remainder of the study area, with isolated exceptions, were clumped on the property that was mowed at least once per year, but more importantly, the height of the vegetation in these areas was maintained such that it was generally low at the onset of the breeding season. In March 1974, adults wintering at a burrow located in a weedy overgrown area moved back to and nested at the burrow (17A) in an open, mowed area at which they nested in 1973.

It is noteworthy that the greatest use of the infrequently mowed field was made in the 1971 nesting season, following the January mowing. The owls that nested in this part of the study area were young of 1970, new migrants into the area and one male who was observed in the field in 1969, later nested at site 31 in 1970 and returned to the field in the summer of 1970.

Increased owl use in the area of nest sites 48, 56 and 57 occurred in 1971 after the location was cleared and a new factory constructed during 1970. This area was formerly a field similar to that described above.

Only one pair of owls nested in the field in both 1972 and 1973, whereas the new factory grounds continued to be attractive to the nesting owls.

The height of vegetation thus plays a part in the location of nest burrows. The availability of artificial lighting also might be important to the observed distribution of nests. During hundreds of hours of observations studying their behavior, the owls were regularly observed to perch on top of light poles in the many parking lots at the university and industrial park or on fences near the lights, where the owls caught insects attracted to the light that fell to the ground. Some owls used the lights within a few feet of their burrows, while others were observed at lights near parking lots hundreds of feet from their nests. It has already been noted that Burrowing Owls defend only a mating and nesting territory and will forage outside of the immediate burrow area. With the exception of the old field (nest sites 43, 52, 59 and 60), most nests are clustered near lights. A few burrows (site 26 for example), although isolated, are close to light sources.

Disturbance by humans is another factor that may influence the location of a Burrowing Owl's burrow. However, the subject is difficult to evaluate. With one exception, Burrowing Owls accepted access holes and underground observation blinds that disturbed the ground near the burrow and changed the wall of the nest chamber. In the one exception, workmen disturbed a camouflaged underground blind and caused the owls to desert their eggs by exposure of the nest chamber. It was noted that excavation of burrows much before egg laying did tend to cause the owls to shift to auxillary or new burrows within the territory.

At site 1, heavy equipment was used within 25 feet of the nest. The owls continued to work on the nest chamber, then moved only 70-100 meters south in late March to continue their breeding activities. Many nests were exposed to humans at the University of South Florida, to motor bikes, model airplanes and cars at sites near Schlitz Brewery, and to large African quadrupeds at Busch Gardens. Many burrows (areas 1, 17, 18, 36, 48, 56, 57 and others) were within 50 meters of roads and parking lots used by students and factory employees daily, and yet they were used repeatedly by the same or different individuals for nesting.

The decline of the population (discussed elsewhere) starting in 1972 might be indicative of the effects of disturbance. Even though human disturbance does not cause the owls to leave a nesting area immediately, increasing disturbance as a result of human population growth in and around the study area increasing vibrations in the ground coupled with low reproductive success might cause some owls to leave the area for a less disturbed habitat after the breeding season. Even so, disturbance would not be a cause of clumping unless the owls were better able to defend their territories from predators by clumping.

Clumping would tend to draw more human attention to the nesting owls. The owls do, however, join with neighboring pairs in sounding the alarm call against predators such as skunks, foxes and dogs. They will also come into another owl's territory and give the alarm call when a neighboring pair is defending its nest from humans. For example, on 13 May 1970, while I was excavating a burrow in order to band young, the adult from another nest came into the territory I was working in, sat on a fence (about 10-20' from the burrow) and gave the alarm scream while facing me. A similar observation was made on 20 May 1972.

Thus clumping might serve as a better means of defense against predators. However, as this is a behavioral action it is probably a beneficial result of the clumping rather than a reason for clumping.

Locally rich sources of food (other than that caused by the lights) were ruled out as a factor in distribution because no obviously large sources were observed and because observation of the food habits on the Schlitz Brewery property indicated individual variation in the food preferences of pairs. Further studies on prey populations and the effect of mowing on prey populations would be needed to provide more evidence on this aspect of the owl's biology.

Only two construction projects had an impact on the owl's distribution. One nesting area, BW, was destroyed by construction in 1971. The young were captured and held in the Busch Gardens aviaries. Site BW was an isloated nest and so did not influence clumping of the owls to a great degree. When the Shuron-Continental factory was built in 1970 in the area of sites 32, 48, 56 and 57 (Figures 1-4), the effect was to bring 2-3 pairs of owls in closer proximity. Although no data exist from 1969, the area was an old field crossed by an abandoned airport runway prior to the construction of the factory. In the fall of 1969, only one pair of owls was found in this area. With the onset of construction, that pair of owls moved from the field north of the factory onto the cleared grounds, and two other pairs moved into the cleared area. The owls could have been attracted to this area initially by the cleared land. Attraction to the buildings themselves has been ruled out because nesting close to a structure would allow a predator opportunity for undetected approach to the nest. Additionally, the cleared grounds and lighting near buildings have more importance to the biology of the owl than the building itself.

In review, the clumped distribution shown by the Burrowing Owls on the study area is caused by environmental factors, open habitat (created by mowing and lights.

Population Numbers

The population of Burrowing Owls on the study area during each year and over the four-year period April 1970 to April 1974, is graphed in Figure 6. Young recruited into the population are added to the graph in the final third of each December. The percentage of young remaining in the adult population each year is presented in Figure 7.

In the winter of 1970, the study area north of Busch Gardens was occupied by 24 owls. Five birds moved into the area in March and one arrived in April. One unpaired male left in February and a female unable to find a mate departed in April. Thus twenty owls (14 pairs) remained to the end of the breeding season north of the Gardens. Within Busch Gardens, 10 individuals were present in April 1970. Of the 38 birds on the study area, only 30 remained to be counted in the next winter census. Two, a mated pair, were known fatalities while 6 birds disappeared. One owl in Busch Gardens left prior to 15 June. One female left in May after her burrow, built in freshly excavated sand, was caved in by high winds shifting the sand. Another left in July, while one pair that successfully fledged 4 young was gone by October. A third female departed in November.

By January 1971, 49 owls were in the study area, thirty from the original breeding population plus young and incoming adults added to the population. Fourteen young of 1970 remained on territories in the study area making up 29% of the January population. One stayed in marginal habitat adjacent to the study area for just over two months. Five adults were added to the population: a female in late August 1970; a male joining her in early September; another two males in late December and a second female in late January 1971, probably an early migrant moving into

Figure 6. Numbers of Burrowing Owls in a population near Tampa, Florida 1970-1974. Young of the year are added to the adults in the last third of each December.

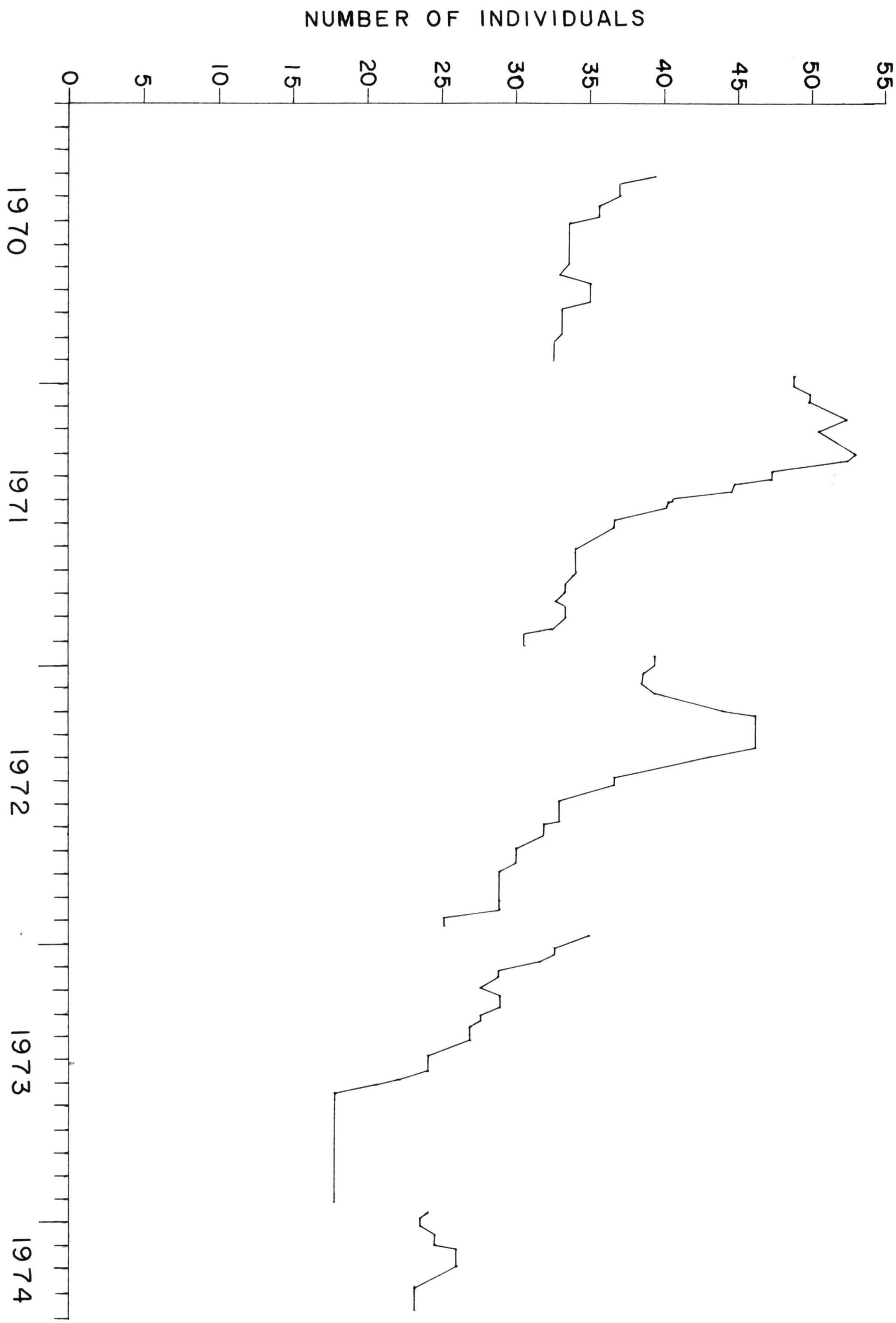
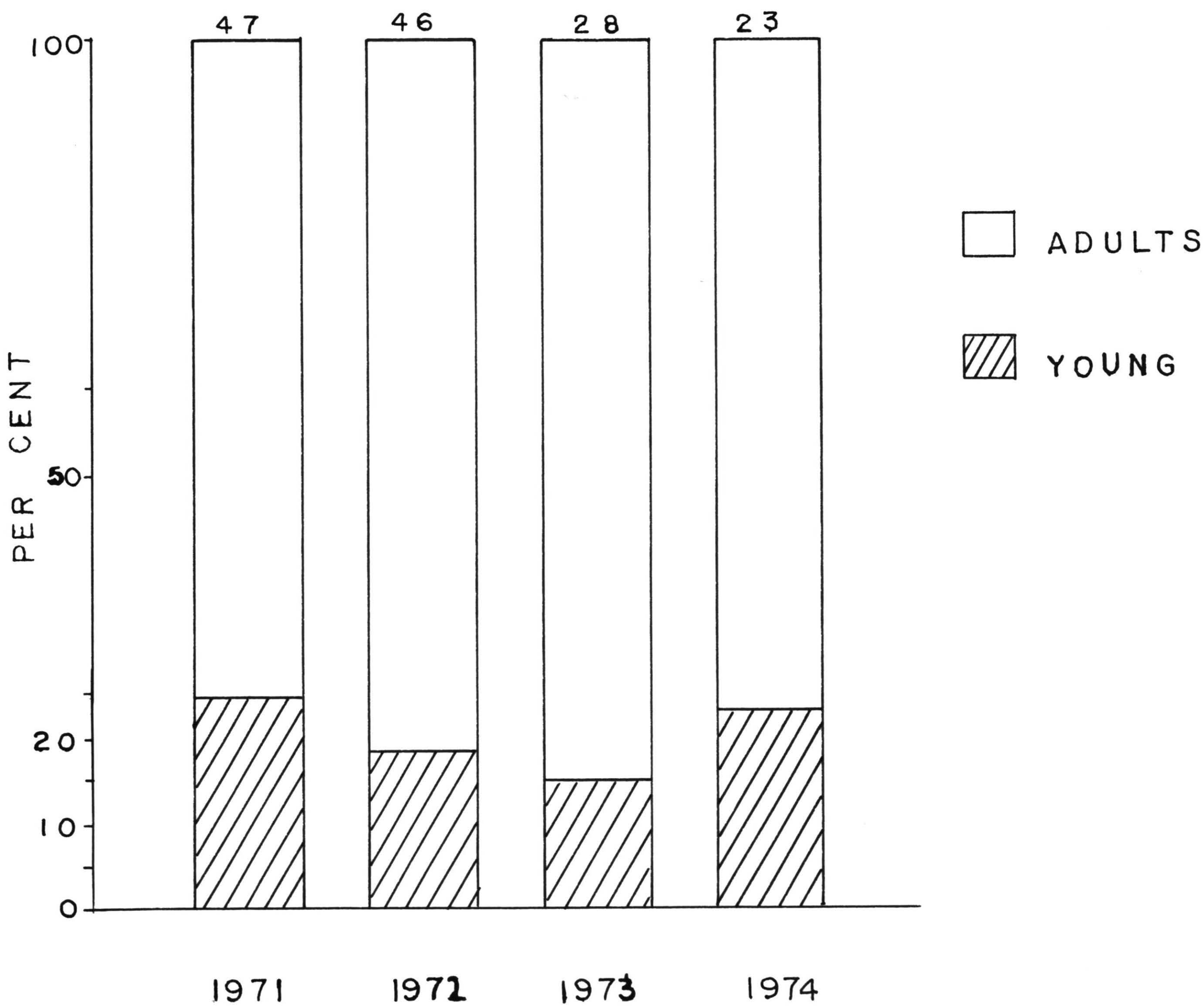

NUMBER OF INDIVIDUALS
0
5
10
15
20
25
30
35
40
45
50
55
1970
1971
1972
1973
1974

Figure 7. Percentage of young Burrowing Owls from the previous breeding season remaining in the adult population each year 1971-1974.


47
46
28
23
100
50
20
10
0
PER CENT
1971
1972
1973
1974
ADULTS
YOUNG

the area.

During February, March and early April 1971, nine additional owls were observed in the study area. Four new individuals arrived in the period 19-25 February. Two of these, a mated pair, were not seen after 23 February. In March, 4 owls arrived on the study area and one left after about two weeks in the area. One additional owl arrived in early April.

Of the ten owls that arrived in the area from 30 January to 10 April, three did not stay. These individuals might not have been able to successfully establish a territory in the area for a variety of reasons or could have only stopped for rest in a flight having a destination farther north. It is possible, but unlikely, that one of the early February immigrants might have moved to a nest site not discovered until April. The population numbers would then be more stable during March and April (Figure 6) and only nine owls would have then moved into the population. In either case, owls from outside moved into the study area from January to early April 1971 and established territories or mated with birds already present in the area.

Departures or deaths in the period February-April 1971 among the resident owls included one male that left in February and a female in March. Another female died in April while one pair in Busch Gardens left after construction destroyed their nest in mid April. Their flying young, advanced compared to the young in the remainder of the population, were placed in captivity at the zoological park. Three young of 1970 also left the population, one in March and two in April.

Forty-seven owls were present at the height of the breeding season in 1971. Of these, only thirty remained on the study area until January

1972. One female left in May and by June three males and two more females were no longer present. During June, two males left and three more females were gone. One female left in both July and August while one male left in each month September through November. One male was found dead in November. Of the 1970 young present in January 1971, eight remained in the study area through January 1972.

In January 1972, thirty-nine Burrowing Owls were on the study area. Thirty of these were adults present during the 1971 breeding season. One young of 1970, not seen since banding, appeared in the study area in late October 1971 and left before mid January 1972. The remaining eight owls (21% of the population) were young of 1971 that were recruited into the population. None of these young left the area until May 1972.

During February and March of 1972, nine owls, two males and seven females appeared in the study area. A third male, a young of 1970 that left the area in June 1971, returned in March of 1972. An eighth female was first seen in April at a Busch Gardens site but could have been present earlier and missed as a result of brooding behavior. Of these eleven immigrants, none left until well into the breeding cycle when one male died in late April and two females were found dead of unknown causes in mid and late May. One female left in early May.

In the period January-April 1972, the 1970 young that came back to the study area in October 1971 left the population in January. One female left the area in both February and April while a male left in March. From May until December 1972, 20 owls (12 males and 8 females) left the area, 12 of these left during May and June. Two males moved into the area, one in late May, the other a young of 1970 not seen since 1970, in June 1972.

At the start of 1973, 33 owls were present in the area; twenty-two owls remaining from the previous breeding season, one male added in June of 1972 and 10 young of 1972. Only half of the 1972 young remained through the breeding season. Even one of these was not seen after mid April 1972.

Only three immigrants, one in late February and two in March came into the study area in 1973. The owl arriving in late February was not seen after the end of March. The small influx of immigrants in 1973 is masked on Figure 6 by the departure of the young of the year (noted above) and two other adults, a male and a female, that left the area in January and February.

From May to December 1973, no new adults entered the study area. 10 owls, 4 males and 6 females left or died, 3 in May, 1 in June and 5 in July and one in early January 1974.

At the start of the 1974 calendar year 22 owls were on the study area. Five of these were young of 1973 and the remainder were owls from the 1973 breeding population. Six owls immigrated into the study area. Two in late January, two in February and two in late April. The two in late April could have been overlooked for a few days. Additionally, the two owls arriving in February left by the first week in April and could have been the same two owls observed at a different site in April. Whichever is the case, owls entered the study area during the 1974 migratory season. Four adults from the 1973 breeding population departed from the area during March and April of 1974.

Reviewing all the data on population fluctuation, three trends are apparent. One, the study area did receive an influx of owls each year into the overwintering population from late January through early April.

In each year the bulk of immigrants arrived over a three to four week span with several owls arriving on the same day or within one or two days (Table 2). In one year, 1973, movement into the area was light but it did occur. The loss of birds from the existing population masked an influx peak on Figure 6 in early 1973.

Further banding studies are required to better define the details of Burrowing Owl movements in Florida and to determine whether early spring immigration into the population is representative of migration or more localized movements between breeding populations. Information is needed on where owls are moving to and from, how far owls will move and what conditions dictate whether owls move or overwinter.

Secondly, dispersion of adults from the breeding population occurred primarily from May through August. The adult population tends to level out by August with only loss or addition of a few adults before the next immigration. It is possible, but as yet undocumented, that birds entering the population in the fall and early winter are migrants or young dispersing from north Florida populations.

The third trend observed from Figure 6 is a downward trend in population on the study area over the period 1973-1974. Three reasons for this drop are apparent. Movement into the 1973 population was very low compared to 1971 and 1972 (Table 3). Only two immigrants established territories in the area in 1973 compared to 7 in 1971 and 11 in 1972. Recruitment of young in 1973 was initially higher than 1972 but less than half of the young actually remained to breed (Table 4). Nine fewer immigrants and three fewer young were responsible for almost two-thirds of the difference in the 1972 and 1973 April population levels. Recruitment and immigration also remained low in 1974.

Table 2

ARRIVAL DATES OF IMMIGRANTS INTO A BURROWING OWL POPULATION NEAR TAMPA, FLORIDA

		1971	1972	1973	1974
January	26				2(♀-?)
	30	1(♀)			
February	12		1(♀)		
	16				2(♂-♀)
	19	2(♂-♀)			
	23	1(♀)			
	24			1(♀)	
	25	1(♀)			
	26		3(♀)		
March	3			1(♀)	
	4		2(♂-♀)		
	7	1(♀)			
	11		2(♂-♀)		
	16		2(♂-♀)		
	17			1(♀)	
	21	1(♀)			
	27	1(♀)			
April	10	1(♂)[b]			
	15		1(♀)[b]		
	19				1(♂)[b]
	27				1(♀)[b]
		9(10)[a]	11	3	6

(a) An unbanded female mated to a banded male was discovered with flying young in June 1971. It is assumed she entered the population by at least mid-March.

(b) Possibly present earlier than date indicated.

Table 3

IMMIGRATION OF ADULT BIRDS INTO A BURROWING OWL POPULATION NEAR TAMPA, FLORIDA

	Migration Year			
	1971	1972	1973	1974
Number of immigrants:				
entering population	10	11	3	6
establishing territories	7	11	2	4
remaining for succeeding breeding year:				
1972	4	-	-	
1973	3	3	-	
1974	1[a]	1	1	

[a] Departed or died in March 1974.

Table 4

RECRUITMENT OF YOUNG INTO A POPULATION
OF BURROWING OWLS NEAR TAMPA, FLORIDA

	Year Class			
	1970	1971	1972	1973
Number of young:				
entering population in January of year following hatching	14	8	10	5
establishing territories and remaining for breeding year				
1971	11	N/A	N/A	N/A
1972	8[a]	8	N/A	N/A
1973	4(5)[b]	4	4	N/A
1974	1	3	3	5

[a] One young left after the end of May 1971 but returned in early March 1972.

[b] One young never seen since 1970, returned in June 1972 and mated with an established female.

The remainder of the difference between population levels of 1972 and 1973, was in the percentage of adults staying or surviving from 1972 to 1973. Eight adults fewer than in previous years (Table 5) remained in the population from 1972-1973. A decrease in the number of remaining adults continued in 1974.

Changes in immigration, recruitment of young and number of adults staying in the population are the reasons for the downward trend in the Burrowing Owl population on the study area. The causes behind the drop in population could be the result of a number of factors. Some building on the study area took place but not in any of the usual nesting sites. One major building opened up habitat and actually "attracted" owls to its cleared grounds. One factor which did increase during the study was human disturbance. The population was always exposed to human disturbance but with the increase in the university student population, the growth in the environs surrounding the study area and increase in pressure to use the open spaces of the study area for motorbikes, kites, rockets, golf practice, etc.; the owls could have been forced elsewhere. One pair of owls in nest site 56-57 area, had several nests caved in by humans. Although prey population levels were not studied, perhaps loss of native habitat not used directly by the owls surrounding the study area may have also contributed indirectly to the population decline.

Breeding Phenology

In order to learn more about the breeding biology of the Burrowing Owl, several nest sites were excavated each year to record dates of egg laying, hatching, growth and development of the young. The number of nests selected each year was small, about 1/5 of the total population but 1/4 of the accessible nests. The number observed was deliberately

Table 5

SURVIVAL OF ADULTS IN A POPULATION OF BURROWING OWLS NEAR TAMPA, FLORIDA

	1970	1971	1972	1973	1974
Adult birds present in April	39	47	46	28	23
Owls present in March of succeeding years					
1971	28(72)	-	-	-	-
1972	15(38)	28(60)	-	-	-
1973	5(13)	13(28)	20(43)	-	-
1974	4(10)	8(17)	12(26)	16(57)	-

( ) Survival per cent.

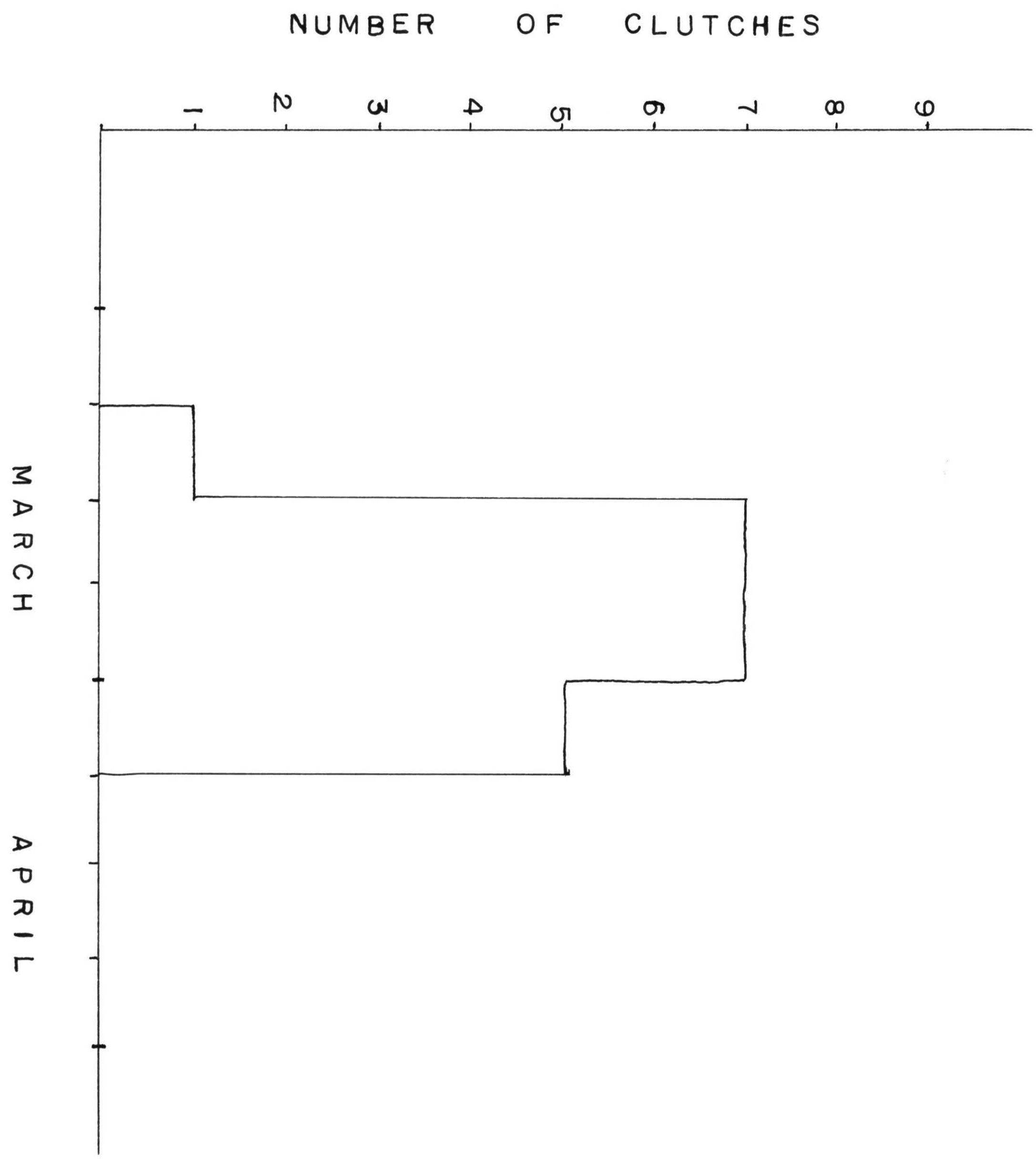
few to minimize possible disturbance of the population. Those nests chosen were found to be a representative sample when the state of development of young banded at other burrows was compared to the burrows whose contents were investigated by an observational access.

The mean date for the laying of the first eggs over five years was 5 April (1970), 2 April (1971), 24 March (1972), 20 March (1973) and 24 March (1974). The number of sample clutches in each year were 3, 6, 4, 4 and 3 for 1970-1974 respectively. The range of the time span for laying first clutches for the five years was 12 March through 8 April (Figure 8). Most pairs bred within 7-10 days of each other with one major exception noted below. A correlation with weather was noted. Weather data was obtained from the long-term records of the Tampa Weather Bureau Station at the Tampa International Airport. December-March of 1970 was cold with both maximum and minimum monthly temperatures below the long-term average. Minimum temperatures in the winter of 1971 were 1-2^{o} C. below average but higher than 1970's minimums except March. Maximum temperatures in 1971 were equal to or slightly above average with March just slightly below average. Winter 1971 was overall warmer than 1970.

In 1972, maximum temperatures were above average with the exception of February. Minimum temperatures were far above average in December and January, slightly below average in February and near average in March. Therefore, 1972 was warmer than both 1970 and 1971.

Temperatures in 1973 were above average except for February and above those of 1971 except for February. December and January 1973 temperatures were about three degrees cooler than 1972 but March temperatures were the warmest in the four years 1970-1973.

Figure 8. Dates of laying of first egg for Burrowing Owls near Tampa 1970-1974. Number of clutches = 20.


NUMBER OF CLUTCHES
1
2
3
4
5
6
7
8
9
MARCH
APRIL

Winter 1974 was colder than average in both December and February but warmer in January and March. The warmest January and March temperatures of the five year period occurred in 1974. One of the earliest laying of first eggs, 12 March, occurred in 1974 although the mean was 24 March.

Rainfall in winter 1970 was above average at 48 centimeters (cm.) and the highest for the five-year period. The same period, December-March of 1971 had dry conditions, with winter rainfall the lowest, at 22.1 cm, of the five years. Rainfall was also sparse at 23.3 cm in 1972. In 1973 precipitation was again above average while 1974 rainfall was slightly above that of 1972. Winter rainfall seemed to have no effect on the start of the breeding schedule as both the latest (1970) and the earliest (1973) mean date for the laying of the first egg were in periods of above average rainfall. The next latest date for laying (1971) occurred in the driest winter. Both rainfall and temperature seemed to have little effect on immigration into the study area.

To summarize, weather conditions prior to breeding were cold and wet in 1970, cool and very dry in 1971, warm and dry in 1972, warm and dry in 1973 and warm and wet in 1974. Egg laying dates showed a correlation with temperature. Two females demonstrated a variability of 9 days and 11 days between dates of first egg in two different years. One female differed 11 days between 1971, a cool winter, and 1973, a warm winter.

Egg dates in Bent (1938) are listed as 22 March to 21 May with the height of the season being 4 April to 23 April. Howell (1932) notes that the eggs are laid from about mid-March to the last of May. The owls in Tampa would seem to be close to what has previously been documented. However, the type of documentation is unknown. Confusion about incubation period, egg laying rates (generally one about every 2 days) and renesting could affect the historic record.

One pair of owls, site BW, consistently fledged young in advance of other pairs in the population. In 1970, their young were developing adult breast feathers in mid-June, while the other juveniles were not at this state of development until a month later. In 1971, three flying young were present on 8 April while the rest of the population was not even finished with egg laying!

Successful renesting also was documented during the study. Site 53B owls, a 1970 sibling pair, experienced flooding of their nest on 15 May 1971. A clutch of five eggs (originally six but one disappeared) was lost. A new burrow, 53C, was excavated adjacent to the old burrow and a second clutch was laid. The new burrow was not excavated but two young were raised. One was first seen on the burrow nest mound on 20 July 1971. The measurements and degree of feather sheathing on 20 July were typical of owls four weeks old. Thomsen (1971) and Butts (1973) also note the occurrence of renesting after loss of eggs or nesting in their study populations. Renesting was also noted in Florida by Rhoads (1892).

SUMMARY

A population study of the Burrowing Owl in Tampa, Florida, was conducted from February 1970 - April 1974. The population nested on the grounds of the University of South Florida and the adjoining industrial park.

The distribution of owls on the study area was in clumps or groups which were randomly dispersed throughout the 600 hectare area. The primary factors influencing distribution were environmental, with probably the two most important being vegetation height and location of lights.

The population was largely permanent with losses offset by immigration of new birds and recruitment of young of the previous year into the population. Immigration occurred from late January through April, with a peak in February and March. Most dispersing adults left the area from May through August.

During the last two years of the study period, the population declined. Reasons for the decline included less immigration into the population, a lower recruitment rate of young and a decrease in the number of adults remaining or surviving until the next breeding season.

A correlation of weather with average date of laying of first eggs was noted. Successively warmer years in 1971, 1972 and 1973 produced earlier mean laying dates. Successful renesting in the population was observed.

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APPENDIX

POPULATION DISTRIBUTION STATISTICAL CALCULATIONS

Calculations

The size of the study area is 64,390,392 square feet or 3.71 square kilometers.

1970

Nearest Neighbor

Burrow	Nearest Neighbor	r^2(feet)	r^2(feet^2)
18B	1B	619	383,161
1B	18B	619	383,161
2B	30	463	214,369
30	2B	463	214,369
31	2B	1438	2,067,844
32	34	400	160,000
34	32	400	160,000
26B	35	1025	1,050,625
35	26B	1025	1,050,625
29	36A	900	810,000
36A	5YA	325	105,625
5YA	36A	325	105,625
17A	5YA	569	323,761
25A	33A	413	170,569
BW	BE	2594	6,728,836
BE	BNE 2-3	2000	4,000,000
BNE 1-1	BNE 2-3	219	47,961
BNE 2-3	BNE 1-1	219	47,961
33A	BNE 1-1	375	140,625

Statistic	Value
N	19
ρ	0.0000002951
$\sqrt{\rho}$	0.0005432311
Σr	14,391
Σr^2	18,165,117
$\bar{r}_A$	757.42105
$\bar{R}_E$	920.47128
R	0.8228622
$\sigma_{\bar{r}_E}$	110.3767769
c	-1.477216
α_3	0.1447613

Poisson Distribution

Statistic	16 hectares/square	4 hectares/square
x	19	19
n	40	160
$\bar{x}$	0.475	0.1188
s^2	0.6147	0.1305

Number of burrows/square	Observed Frequency	Number of burrows/square	Observed Frequency
0	27	0	143
1	8	1	15
2	4	2	2
3	1		

Negative Binomial

Statistic	16 hectares/squre	4 hectares/square
k	0.99	1.0
p	0.4798	0.1188
q	1.4798	1.1188
R	0.3242	0.1062
qk	1.474	1.1188

1971

Nearest Neighbor

Burrow	Nearest Neighbor	r(feet)	r^2(feet^2)
53B	1B	3888	15,116,544
1B	18B	619	383,161
18B	1B	619	383,161
59A	52A	1219	1,485,961
52A	43A	388	150,544
43A	52A	388	150,544
22BB	22GA	231	53,361
22GA	22BB	231	53,361
37	60	519	269,361
60	37	519	269,361
57	56A	100	10,000
56A	57	100	10,000
26F	56A	1019	1,038,361
48A	25C	1113	1,238,769
36A	54	363	131,769
54	36A	363	131,769
17	54	613	375,769
46	17	631	398,161
25C	BNE 2-2	431	185,761
BNE 2-2	BNE 2-4	94	8,836
BNE 2-4	BNE 2-3	88	7,744
BNE 2-3	BNE 2-4	88	7,744
BNE 2-1	BNE 2-3	94	8,836
BNE 3-2	BNE 3-1	119	14,161
BNE 3-1	BNE 3-2	119	14,161
BNW	46	1413	1,996,569
BE	BNE 3-2	2000	4,000,000

Statistic	Value
N	27
ρ	.0000004193
$\sqrt{\rho}$	.0006475
Σr	17,369
Σr^2	27,893,769
$\bar{r}_A$	643.2963
$\bar{r}_E$	772.1411
R	.8331
$\sigma_{\bar{r}_E}$	297.1768
c	-.433563
α_3	.192448

Poisson Distribution

Statistic	16 hectares/square	4 hectares/square
x	27	27
n	40	160
$\bar{x}$	0.675	0.1688
s^2	1.5071	0.2544

Number of burrows/square	Observed Frequency	Number of burrows/square	Observed Frequency
0	25	0	139
1	10	1	17
2	2	2	3
3	1	3	0
4	0	4	1
5	2		

Negative Binomial

Statistic	16 hectares/square	4 hectares/square
k	1.018	1.088
p	0.1658	0.6204
q	1.1658	1.6204
R	0.1422	0.3829
q^k	1.169	1.6907

1972

Nearest Neighbor

Burrow	Nearest Neighbor	r(feet)	r^2(feet^2)
53C	67	3506	12,292,036
67	66	1969	3,876,961
66	22GA	713	568,369
22GA	22G	213	45,369
22G	22	200	40,000
22	22A	106	11,236
22A	22	106	11,236
32	56B	356	126,736
56B	32	356	126,736
65	22G	644	414,736
36C	5YA	344	118,336
5YA	36C	344	118,336
11B	68	519	269,361
17	68	438	191,844
68	17	438	191,844
25	BNE 2-2	463	214,369
BNE 2-2	BNE 2-4E	131	17,161
BNE 2-4E	BNE 2-1	113	12,769
BNE 2-1	BNE 2-4E	113	12,769
BNE 3-1A	BNE 2-2	200	40,000
BNE 5-1	BNE 3-1A	387	149,769
BE-3	BNE 2-1	2131	4,541,161
BNW	11B	1169	1,366,561

Statistic	Value
N	23
p	.0000003572
$\sqrt{p}$	.0005976621
Σr	14,959
Σr^2	24,697,695
$\bar{r}_A$	650.3913043
$\bar{r}_E$	836.5931184
R	.7774284655
$\sigma_{\bar{r}_E}$	91.18417599
c	-2.04204087
α_3	.131572595

Poisson Distribution

Statistic	16 hectares/square	4 hectares/square
x	23	23
n	40	160
$\bar{x}$	0.575	0.1438
s^2	1.4814	0.2496

Number of burrows/square	Observed Frequency	Number of burrows/square	Observed Frequency
0	29	0	143
1	6	1	14
2	2	2	1
3	0	3	1
4	2	4	1
5	1		

Negative Binomial

Statistic	16 hectares/square	4 hectares/square
k	1.206	1.025
p	0.4768	0.1403
q	1.4768	1.1403
R	0.3228	0.123
q^k	1.6003	1.144

1973

Nearest Neighbor

Burrow	Nearest Neighbor	r(feet)	r^2(feet^2)
1D	52	2963	8,779,369
52	66A	1219	1,485,961
26F	56E	1200	1,440,000
56E	26F	1200	1,440,000
66A	22G'	919	844,561
22G'	22	231	53,361
22	22G'	231	53,361
36C	22	700	490,000
17A	36C	750	562,500
11C	17A	881	776,161
BNW-A	11C	1094	1,196,836
BNE 2-2	BNE 2-4E	131	17,161
BNE 2-4E	BNE 2-2	131	17,161
BNE 3-1A	BNE 2-2	200	40,000

Statistic	Value
N	14
p	.0000002174
$\sqrt{p}$	.0004662617
Σr	11,850
Σr^2	17,196,432
$\bar{r}_A$	846.4285714
$\bar{r}_E$	1072.359149
R	.789313
$\sigma_{\bar{r}_E}$	85871.99369
c	-.0026310159
α_3	0.1686

Poisson Distribution

Statistic	16 hectares/square	4 hectares/square
x	14	14
n	40	160
$\bar{x}$	0.35	0.0875
s^2	0.4897	0.1307

Number of burrows/square	Observed Frequency	Number of burrows/square	Observed Frequency
0	30	0	149
1	7	1	9
2	2	2	1
3	1	3	1

Negative Binomial

Statistic	16 hectares/square	4 hectares/square
k	1.018	1.014
p	0.3438	0.0863
q	1.3438	1.0863
R_k	0.2559	0.0794
q	1.351	1.0876