Experimental Zoogeography of Islands

A thesis presented

by

Daniel Solomon Simberloff

to

The Department of Biology

in partial fulfillment of the requirements

for the degree of

Doctor of Philosophy

in the subject of

Biology

Harvard University

Cambridge, Massachusetts

August, 1968

Copyright reserved by the author

TABLE OF CONTENTS

Introduction 1

Acknowledgments 3

Part I. Defaunation and Monitoring Techniques 5

Abstract 6

Introduction 7

The Islands 19

Defaunation 32

Monitoring Technique 56

Acknowledgments 63

References 64

Part II. The Colonization of Empty Islands 67

Abstract 68

Species Counts 70

Seasonality 78

Patterns of Colonization 87

Colonization Curves 95

Dispersal 105

Immigration and Extinction Rates 110

Acknowledgments 116

References 117

Part III. A Model for Insular Colonization 118

Abstract 119

Symbols Used in Text 121

The Independent Variable in Rate Curves 126

A Model for Colonization of the Small Islands in the Keys 132

The Simulation 181

Acknowledgments 198

References 199

INTRODUCTION

This thesis is unusual in that it consists partly of a joint contribution by Professor E. O. Wilson and myself. It falls naturally into three parts, to be published and referred to throughout this thesis as follows:

I: Background and experimental design -
Wilson and Simberloff, 1968

II: Results and preliminary conclusions -
Simberloff and Wilson, 1968

III: Implications of this experiment for zoogeography in general, including a discussion of previous models and presentation of a new model -
Simberloff, 1968

Both Professor Wilson and myself participated fully in all aspects of the experiment proper; the seniority of authorship for parts I and II reflects as accurately as possible the division of labor on the various sections of the work. The reason for the collaboration was that the project was simply too complex and time-consuming to be performed by a single investigator.

Part III, the longest section, is wholly my own production. Although I received criticism and counsel from

Professors Wilson and W. H. Bossert, my reliance on their advice was no greater than seems normal for doctoral candidates. All faults are entirely my own.

ACKNOWLEDGMENTS

My debt to Prof. Edward O. Wilson, my thesis advisor, will be obvious upon the most casual reading of this work. Throughout my entire graduate career he has provided both intellectual inspiration and sound advice on surmounting the bureaucracies of the Graduate School of Arts and Sciences and the Biological Laboratories. In particular, this experiment could not, of course, have been performed without his collaboration.

In my thesis research as in several other projects, Prof. William H. Bossert has generously devoted time and thought to many aspects of the work. His patient assistance in mathematical matters is greatly appreciated.

The many persons who have aided this experiment in various ways are acknowledged within the text. Without all their contributions the work would have been immeasurably more difficult, if not impossible. I am grateful to Mrs. Linda Regnier for carefully typing a manuscript richly endowed with mathematical expressions and taxonomic names.

My graduate existence was eased by generous support, first through a United States Public Health Service Traineeship, then by an I.B.M. Fellowship of the Harvard Computing Center, and finally through a Richmond Fellowship. The Committee on Evolutionary Biology aided my summer research.

My wife Martha provided spiritual encouragement during the traumatic moments which occurred frequently throughout this work and material aid in both clerical and field work.

I. Defaunation and Monitoring Techniques

ABSTRACT

A technique for insular defaunation utilizing methyl bromide fumigation was evolved.

Seven islands in Florida Bay, of varying distance and direction from potential zoogeographic source areas, were censused exhaustively. The small size (45 ft. diameter) and ecological simplicity of these islands, which consist solely of red mangrove (Rhizophora mangle) trees with no supratidal ground, allowed the determination of all resident species. The completeness of the censuses was corroborated by chloropicrin fumigation.

The breeding land fauna of these islands is composed almost exclusively of terrestrial arthropods, with 20-50 species usually present. Surveys of these taxa in the Florida Keys, with emphasis on mangrove inhabitants, were made during 1967.

The seven experimental islands were defaunated in early 1967, and were then monitored for colonists for 17-20 man-hours every 18 days. Precautions were taken to prevent contamination by investigators and to insure recording of crepuscular and nocturnal forms.

INTRODUCTION

The first attempt to formulate a quantitative theory which would unite an ever-increasing mass of insular biogeographic data was made by MacArthur and Wilson (1963), who postulated an equilibrium number of species on an island determined by the intersection of unique immigration and extinction curves drawn against the number of species already present. In addition to speculation on the forms of these curves and effects of varying the parameters island area and distance from source area, they derived the equation

$$(1) \quad t_{0.90} = 1.1515 \frac{\text{mean } \hat{S}}{X}$$

where

$\hat{S}$ ≡ the hypothetical equilibrium number of species on an island

mean $\hat{S}$ ≡ the mean of $\hat{S}_i$ for a number of identical islands

X ≡ the extinction rate (or turnover rate, since an equilibrium requires that extinction = immigration) in number species per time at equilibrium

$t_{0.90}$ ≡ time required for number of species present to increase from 0 to 90% of $\hat{S}$.

Later the same authors elaborated upon the general shapes of immigration and extinction curves, discussed

colonization rates and curves, and predicted the distribution of survival times of species colonizing an island (MacArthur and Wilson, 1967).

Data to test these hypotheses are scarce. Most biogeographic information consists of distributions of numerous taxa which, when combined with information furnished by the fossil record (scant or non-existent for numerous taxa in many instances) and geology, can lead to descriptions of static situations (broad patterns of distribution, zoogeographic regions, etc.) and hypotheses about the essentially long-term processes responsible for them (e.g., Darlington, 1957).

Such theories, though occasionally suggestive for specific groups, fail to explain the existing taxonomic distributions and the underlying colonization mechanisms for most of the myriad islands of all sizes dotting the globe. Dealing mainly in geologic time, they neglect the short-range (even daily) events which largely determine the parameters of colonization on many islands and which become increasingly more important than evolution as distance of island from source area decreases. In particular, they do not provide a test for the existence of an equilibrium number of species or for the accuracy of equation 1.

The literature on biotic dispersal, both anecdotal and systematic, provides information on the relative importance

in immigration of active and passive transport and a wealth of data on agents of the latter (e.g., Wolfenbarger, 1946). Migrations involving overwater dispersal can even be traced to specific meteorological events (French, 1964). For no island, however, is the time course of colonization by even a large fraction of the inhabitants known. The sheer number of records of long distance overwater dispersal implies that immigration rates are probably high--especially for organisms capable of anemochorous transport. But the shape and determinants of the immigration curve cannot be deduced; at best a lower limit might be given.

More complete and illuminating information is given by experiments involving colonization of artificial "islands." Maguire (1963) investigated the colonization of sterile bottles of fresh water placed at distances up to 400 yards from the source area (a pond). When his data from bottles at different distances are summed and a correction is made for putrefaction the colonization curve of species visible at 45X magnification versus time is monotonically increasing and concave downward, approaching an equilibrium asympotically--in accord with the rough shape predicted by MacArthur and Wilson (equation 2):

$$(2) \quad S(t) = \hat{S}(1-e^{-Gt}) \quad ,$$

where S(t) is the number of species on the island at time t and G is a constant.

The colonization of glass slides by fresh water diatoms was studied by Patrick (1967). Sterile slides were suspended in a spring. "Island" area was varied through use of slides of different surface area, while increasing "island" distance was simulated by decreasing the amount of water flowing over the slides. The latter procedure, while decreasing immigration rate, is not strictly analogous to the decrease in immigration rate on distant islands envisioned by MacArthur and Wilson (1967), for they postulate that the proportion of various species among the propagules would be different on far and near islands, in addition to fewer propagules of all species landing on a distant island. Patrick's decreased water flow causes fewer propagules, but in the same proportions as previously.

Patrick's results confirm certain aspects of the MacArthur-Wilson theory, in particular the effects of island area on colonization and extinction rates and the broad dependence of extinction rate on species density. Most of her islands were colonized quickly at first and then much more slowly and irregularly (partly in accord with equation 2), but the experiment did not provide good evidence on the existence and characteristics of an equilibrium $\hat{S}$.

A number of artificial and more or less permanent constructs more closely approximate true oceanic islands. For some, surveys of certain taxa at given points in time

were detailed but in no instance were a sufficient number of good surveys at proper intervals made to draw accurate colonization curves and to give reliable data on turnover rate and a possible equilibrium number of species. Notable are the Dutch polders; the Wieringermeer Polder in particular was closely studied faunistically and especially floristically by Feekes (1936) and Schaank (1935-38). Because of the quickly increasing land mass and subsequent cultivation an equilibrium or even meaningful colonization curves were precluded, but interesting data were collected on the order of colonizing taxa and the pattern of replacements and extinctions.

"Spoil areas"--islands formed by material dredged from channels--are common in many areas and, as with polders, their dates of inception are known. All are temporary, eventually washing into the sea, but they often exist long enough for colonization with breeding to occur. We have examined four such islands of rock, crushed coral, and coral sand between Key West and the Dry Tortugas and found them colonized by a very small subset of the total Florida Keys flora and ant fauna. The repeated appearance of the same species may provide information on the distribution of dispersal (and hence immigration) capabilities, but because of the small total number of species and physical instability of the islands they have limited value in a study of the

time course of colonization and existence and mechanisms of maintaining an equilibrium $\hat{S}$.

The same limitations apply to nunataks--newly ice-free areas in the midst of glaciers--and in addition there may for some taxa be contamination from organisms surviving glaciation. These considerations notwithstanding, Einarsson (1967) has described colonization of several "new" nunataks by plants. His data for Braedrasker nunatak do not indicate extinctions, but in both mosses and vascular plants the colonization curve apparently shows an initial lag, then increases linearly and eventually becomes mildly concave downward. An equilibrium had not been reached by 1966, 5 years after the land first became ice-free.

Evidence from naturally formed oceanic islands is scarce and no single study is sufficiently complete to examine immigration, extinction, and colonization simultaneously.

Botanical maps of the Dry Tortugas made in 1904 (Millspaugh, 1907) and 1916 (Bowman, 1918) give information on extinction rate and its relation to area (MacArthur and Wilson, 1967). Although the surveys were not of comparable thoroughness, the latter was fortunately the more complete; lower limits for extinction can therefore be derived. The curve of extinction rate versus number of species present on islands of similar area supports roughly the MacArthur-

Wilson prediction of a monotonically increasing, upward concave shape. Nevertheless, only 4 points are available and all are rough estimates. Furthermore, the fitted curve deviates widely from the intermediate points. Although these data tell nothing about the existence of an equilibrium, most of the islands involved are considerably older and more stable than the artificial ones described earlier and the floras discussed can therefore be interpreted as having arisen from prolonged colonization and species interaction.

The island of Krakatau exploded in 1883 with the probable extinction of all fauna and most or all flora. Knowledge of the pre-catastrophe fauna is limited to a sketchy description of molluscs (von Martens, 1867). In the 25 years after eruption, few zoologists visited the island. Their records which tend to be anecdotal and incomplete, are summarized by Dammerman (1948). Jacobson (1909) in 1908 briefly monitored all but the microfauna of Krakatau. After this initial effort, various specialists examined a few taxa, more or less casually and at odd intervals. Then, in 1919-21 and 1932-34, Dammerman made extended and more comprehensive surveys. The Krakatau information can be summarized as follows:

1) For no taxon were more than three surveys made, and what information is available is of uneven completeness and reliability.

2) No points are available on a colonization curve until at least 25 years after defaunation, and certainly not enough points for any taxon to interpolate a curve convincingly.

3) A wealth of data, largely unexploited, exists about colonization and extinction of individual species which might profitably be compared to similar evidence from other islands.

4) It is particularly regrettable that the mass of information on insects and spiders is too unsystematic to have quantitative significance.

Observations of birds are probably the most reliable zoogeographic legacy of Krakatau, and MacArthur and Wilson (1967) have used the results of three monitorings (1908, 1919-21, 1932-34) together with the hypothesis of the existence of an equilibrium to make several calculations. Their most important result was that if the avifauna after 30 years was between 67% and 100% of the hypothetical $\hat{S}$ (which seems reasonable from a consideration of species-area relationships), equations (1) and (2) imply a turnover (extinction) rate at equilibrium of 0.77-1.15 species/year. No inference can be made about the shapes of extinction and immigration curves versus either time or number of species.

The floral colonization of Krakatau, described by Docters van Leeuwen (1936), showed in general an approximately linear increase in number of species present between 1883 and 1934. MacArthur and Wilson (1967) note that this

linearity implies parallel immigration and extinction curves and ascribe the effect either to the immense species pool on Java and Sumatra or to succession.

Islands newly risen by any means from the sea are sterile so far as terrestrial biota is concerned, and several of these supply interesting but quantitatively insufficient data. The North Sea island of Memmert, near the mouth of the Ems River, arose from an intertidal sand bank between 1890 and 1895, forming in the end a supratidal area of at least 5 sq. km. with dunes 8 m. high. After 1907 the area was artificially increased. Data on colonization by birds were gathered by Leege (1938) and on insects by Alfken (1924). The birds apparently have high immigration and extinction rates; unfortunately surveys were too intermittent and not designed so as to yield good numerical data. The evidence on insects is even more frustrating, consisting of frequent, very sketchy early monitorings that yielded useful information only on the taxonomic affinities of some early colonists, followed by a single exhaustive survey in 1917-18.

The volcanic island of Anak Krakatau, which first appeared near Krakatau in 1928, is another example of newly emerged, sterile land. Although its shape was altered by several eruptions (even in this decade) the area remains about 1 sq. km. and the highest point approximately 100 m. Dammerman emphasized the remarkable biological opportunity

which the birth of Anak Krakatau presented, but a sufficient research program was not organized. Although colonization and its study were complicated by eruptions which occasionally sterilized the island, it is unfortunate that more frequent monitorings were not performed and that more attention was not given to the time course of invasion. A list of the birds, insects, and arachnids on Anak Krakatau is given by Dammerman (1948). No quantitative conclusions can be drawn, however. The botanical surveys suffer from similar shortcomings.

Surtsey, a volcanic island south of Iceland, first appeared in 1963 and has grown to a present area of about 2.5 sq. km. and height of about 200 m. From its birth it has been studied intensively, investigations being performed even amidst falling lava bombs. The Surtsey Research Society was formed at an early date and its focus has shifted progressively toward biology as volcanic events cease (Hermannsson, 1967). All aspects of the flora and fauna of Surtsey and its surrounding area are being studied actively, with results to date published in the Surtsey Research Progress Report III (1967) and Proceedings of the Surtsey Research Conference (1967). Colonization by all organisms has been hindered by eruptions on Surtsey and on two adjacent temporary islands, but for several taxa the beginnings of colonization and perhaps extinction curves can be drawn.

Our definition of colonization and a discussion of this and other biogeographic terms is deferred until Part II of this series. It will be seen that the nearness of Surtsey to source areas makes a precise mathematical interpretation of the early information for birds and terrestrial arthropods difficult. Tentative graphs of the data on the latter gathered by Lindroth et al. (1967 and pers. comm.) show an upward concave beginning for the plot of number of species versus time.

In marked contrast to all previous opportunities, the biogeographic potential of Surtsey is being fully exploited. The principle difficulty with Surtsey is that its presumed source areas--Iceland and the Westman Islands--are species-poor in both flora and fauna, especially so compared to the Indonesian neighborhood of Krakatau. This implies that, if there is an equilibrium, $\hat{S}$ will be very low and certain mathematical characteristics of associated curves may be artifacts of the low number of species involved. Fridriksson (1967) predicts that colonization will proceed with exceptional slowness on Surtsey and extinction rates will be high compared to those on Anak Krakatau because of the harsh climate and poor growth conditions on the former. It would seem, however, that the species pool of Iceland will contain a much larger proportion of species preadapted to survival under arctic conditions than is so for Indonesia. Furthermore,

one would expect succession on Surtsey to be simpler than on the Krakatau islands. If the MacArthur-Wilson theory is essentially correct, $\hat{S}$ on Surtsey will be low but $t_{0.90}$, from equation (1), may well be no larger than on a tropical island of comparable size and distance from the source area. The lower $\hat{S}$ would tend to decrease $t_{0.90}$, as would a high extinction rate.

With the single exception of Surtsey, then, there has been a notable failure to capitalize upon the development of new (or sterilized) islands. The infrequent natural occurrence of such events tends to render quantitative biogeographic theory the increasingly more intricate and esoteric product of abstract speculation and of enlargement and sophistication of untestable hypotheses. What is needed, clearly, is a means of producing islands similar to natural ones or of sterilizing pre-existing islands. Such a method must initially allow replication as well as variation in such parameters as distance from source area and size of island. Later, it could be developed to study such problems as the effects of stepping stones and archipelagos on colonization or the importance of size of species pool. A first experiment would not even have to treat the entire biota of the islands concerned, if the total number of species involved were large enough to avoid complications associated with small numbers, and if colonization by entire large taxa

could be studied in order to ensure against considering only those species whose peculiar biology makes them prominent in some way in a colonization experiment.

THE ISLANDS

As one travels through the Florida Keys toward Key West on the Overseas Highway (U.S. Route 1) he sees numerous small, approximately circular islands, particularly on the Gulf of Mexico side in Florida Bay. These occur in such large numbers and widely varying configurations, and furthermore are so readily accessible, as to constitute a potential natural "laboratory" for experimental biogeography.

A closer examination of the islands with diameter 35-65 feet (e.g., Figure 1) shows that they are almost always completely composed of red mangrove (Rhizophora mangle) trees, with very rarely a small black mangrove (Avicennia nitida) bush included. There is only occasionally supratidal land, and this usually in areas of weak tide. Such land is only intermittently supratidal, since during prolonged winds of 10 knots or more it is completely flooded for days on end. The islands are between 15 and 30 feet high and consist of one to a few mangrove trees. Although individual islands may differ in several minor respects such as number of large trunks and amount of dead bark they are on the whole remarkably similar physically, so much so that were an investigator

Figure 1: Island E3



not thoroughly familiar with small mangrove islands he might have trouble telling certain of them apart but for their respective locations.

A fruitful defaunation experiment with these islands would require:

i) that there be enough accessible islands to permit replication and to allow us to vary the parameter distance from nearest source area.

ii) that the animal diversity be sufficient to allow mathematically meaningful results.

iii) that the extremely small size of these islands compensate for their relative nearness to source areas to produce a distance effect.

In June 1966 we first set out to see whether these requirements were met. Using maps (the U. S. Coast and Geodetic Survey series and the U. S. Geological Survey series) and aerial photographs we located promising areas for exploration. Possible experimental islands were then examined by boat.

We found that accessible islands of the proper size were numerous at all distances up to 200 yards from the nearest source area. Beyond 200 yards small islands were rare, although larger islands (diameter 150 feet and greater) were plentiful. Persistent exploration yielded a very few small islands at distances from one quarter of a mile to

one mile from nearest source area.

The questions of animal diversity and distance effect were approached from two directions. First, we made careful faunistic surveys of islands chosen for possible defaunation. Secondly, since the breeding fauna of islands this size consists almost entirely of insects and spiders, we assembled a reference collection of terrestrial arthropods of the Florida Keys. This collection, made with the assistance of Mr. Robert Silberglied, served two main functions. It enabled us to identify colonists on the experimental islands, and it provided a measure of the size of the species pool of the presumed source area, the entire Florida Keys.

Animal diversity on the small mangrove islands was certainly adequate for statistical purposes. About 75 insect species (of an estimated 500 that inhabit the mangroves and an estimated total of 4000 that inhabit all the Keys) commonly colonize these small islands. There are also 15 species of spiders (of a total Keys complement of perhaps 125 species) and a few scorpions, pseudoscorpions, centipedes, millipedes, and terrestrial isopods. Single islands contain at any given moment 20-40 species of insects and 2-10 species of spiders.

Many birds visit the islands, some for extended periods, either to roost or to forage. However, very few build their nests on islands this small. The only bird species observed

to breed on our experimental islands were the green heron, white-crowned pigeon, and gray kingbird. These have not been included in the censuses to be presented later. Snakes occasionally swim to small mangrove islands to slough their skins, especially water snakes of the genus Natrix. Finally, when islands are located on shallow mud banks raccoons may wade or swim to them, presumably to forage for crabs.

On the basis of their distance and direction from nearest source area, their size, and their accessibility, the islands listed in Table 1 were chosen for the defaunation attempt. As a control one island was chosen in the vicinity of each series and was censused with the experimental islands. At the time of the final monitoring of the experimental islands the controls were censused again to ascertain whether any long-range change in the fauna of small mangrove islands in Florida Bay had occurred during the course of the experiment. An explanation of the census method and rules for determining the number of species present will be given in Part II of this series.

The two series of islands form natural groups. Each consists of islands of similar size, structure, and location. Series 1 lies within the Great White Heron National Wildlife Refuge, in a region north of Sugarloaf Key (Map 1). Series 2 is in the Everglades National Park near the Calusa Keys north of Islamorada (Map 2). E7 was chosen to test a method

TABLE 1. Parameters of experimental islands

	Island Name	Diameter (feet)	Distance From Nearest Source (yards)	Initial Number Arthropod Species	Location
Series 1	E1	35	583	25	Off Squirrel Key
	E3	40	188	31	In Rattlesnake Lumps
	ST2	35	167	29	Off Saddlebunch Key
	E2	40	2	43	Off Snipe Keys
	E6†	50†	80†	30†	In Johnston Key Mangroves
	E7	25	15	29	Nr. Manatee Creek
Series 2	E8	60	1300*	29	Between Calusa Keys and Bob Allen Keys
	E9	60	415	41	Between Calusa Keys and Bob Allen Keys
	E10†	35†	40†	20†	Nr. Bottle Key

* "Stepping Stone" 51 620 yds. away

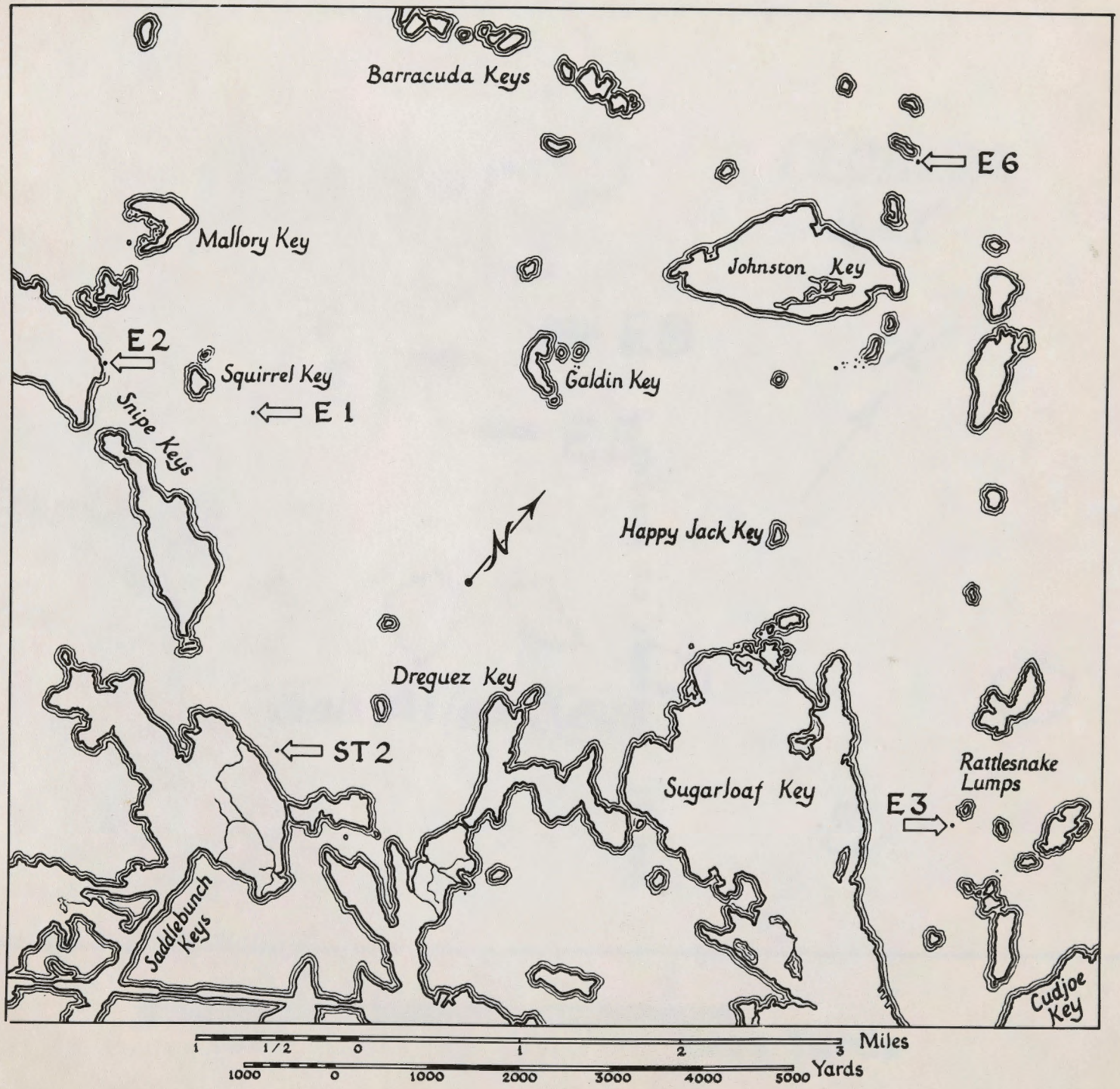
† Control island; all parameters approximate and uncorrected

of defaunation and is in Barnes Sound south of the Glades Canal (Map 3).

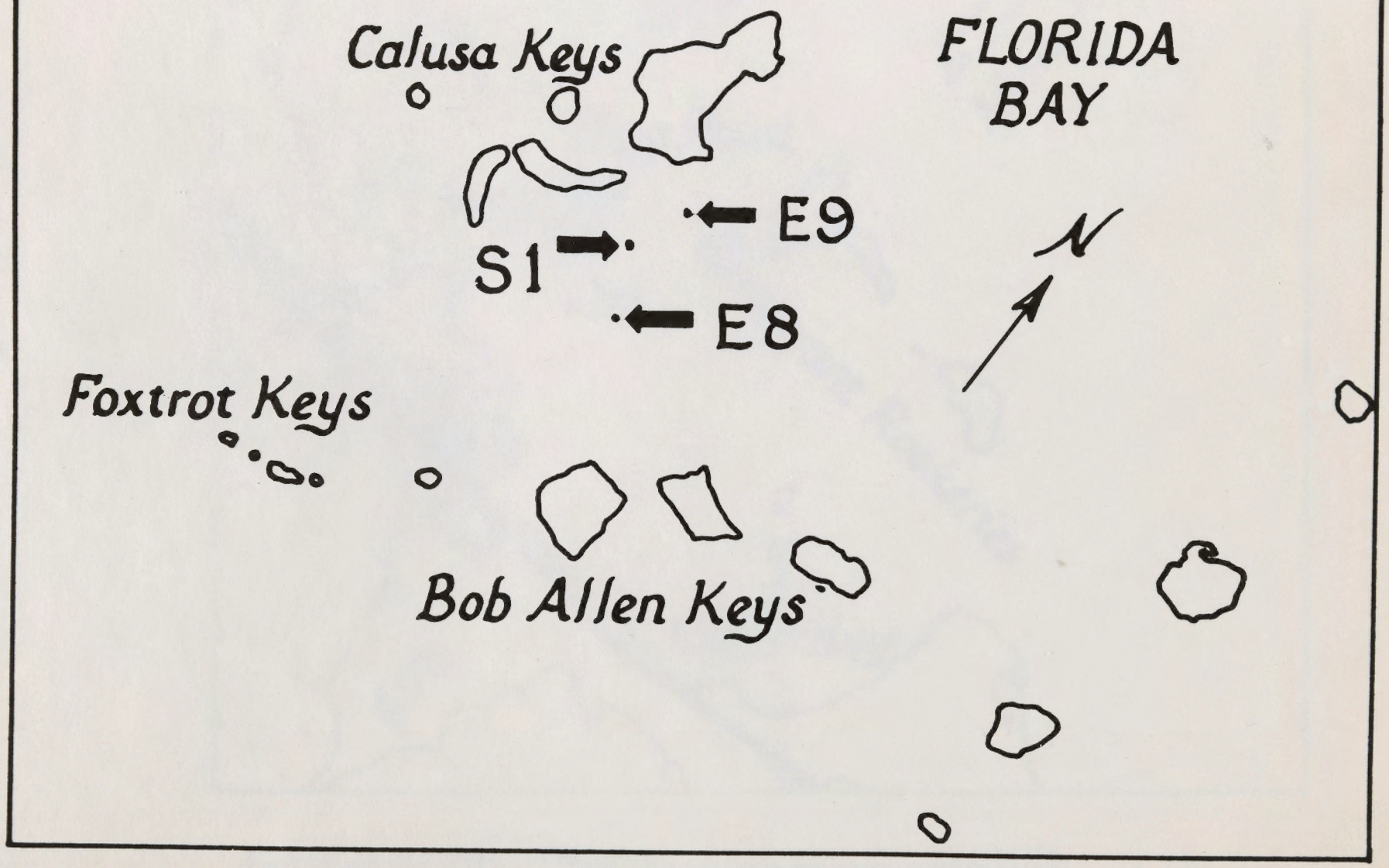
The coefficient of correlation for island series 1 between "distance from nearest source" and "number of arthropod species" is -.83, and this strong indication of a distance effect is obviously corroborated in the E8-E9 series. Qualitative differences in faunas of increasingly distant islands were even more striking than quantitative ones. For many groups--especially ants and spiders--the decrease in number of species with increasing distance is accomplished so regularly that one can guess accurately not only how many species will be on an island but also which species. Some notably poor dispersers, for example centipedes and pseudoscorpions, were found almost exclusively on near islands.

Islands of this size can be remarkably long-lived. All Rhizophora mangle trees, and particularly those on low, small islands, have numerous aerial roots--both brace roots growing out from the main stem and prop roots growing down from branches. The latter can emerge from as high as 4 m. above the water (LaRue and Muzik, 1954) and in time can become as thick as the main stem. These prop roots may eventually develop "brace" roots of their own and frequently it becomes impossible among a group of "trunks" to distinguish the main stem.

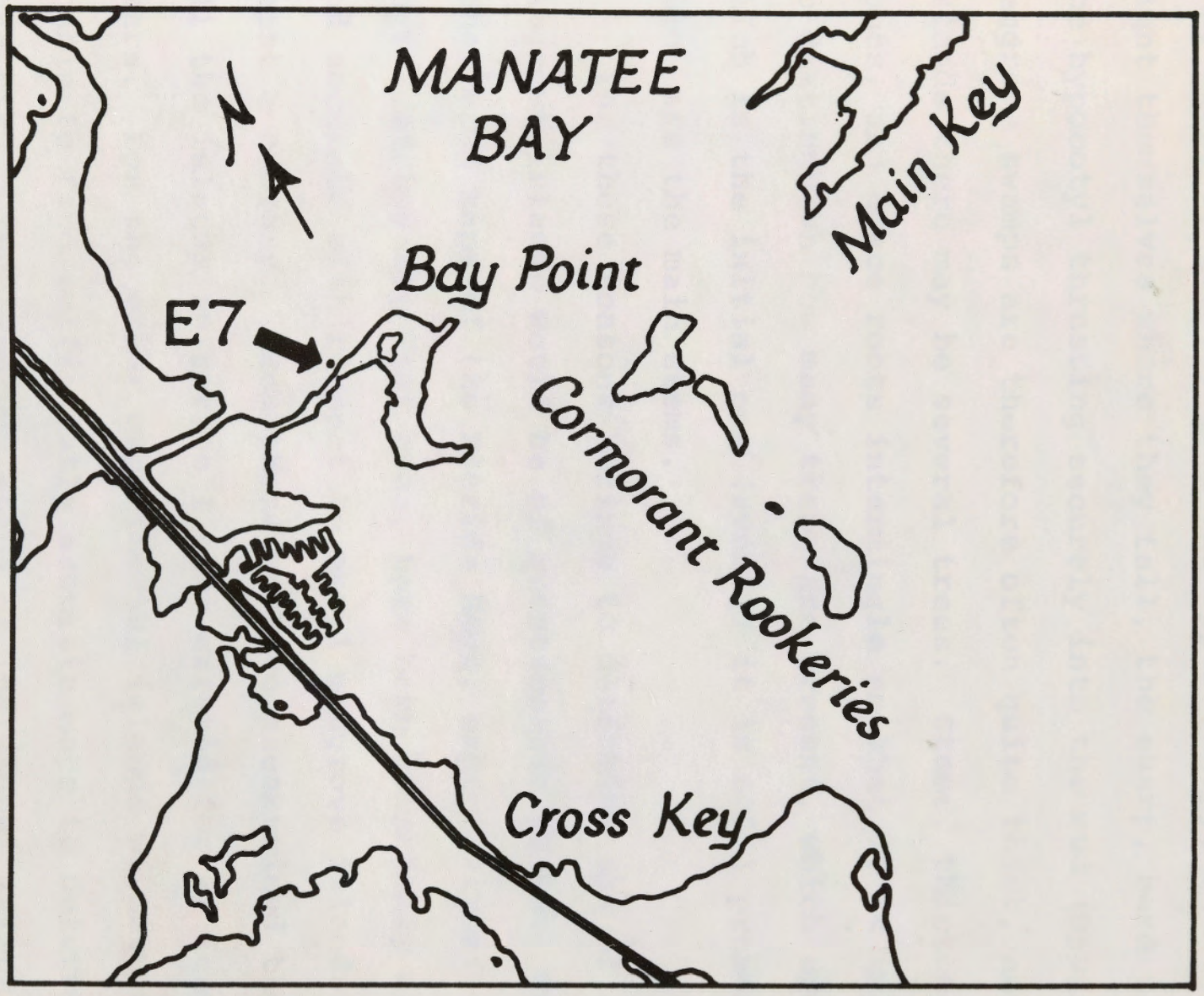
Map 1: Islands of series 1


Barracuda Keys
E6
Mallory Key
Johnston Key
E2
Squirrel Key
Galdin Key
E1
Snipe Keys
Happy Jack Key
N
Dreguez Key
ST2
Sugarloaf Key
Rattlesnake Lumps
E3
Saddlebunch Keys
Cudjoe Key
1 1/2 0 1 2 3 Miles
1000 0 1000 2000 3000 4000 5000 Yards

Map 2: Islands of series 2


Calusa Keys
FLORIDA BAY
E9
S1
E8
N
Foxtrot Keys
Bob Allen Keys
1000
5000 Yards

Map 3: Island E7

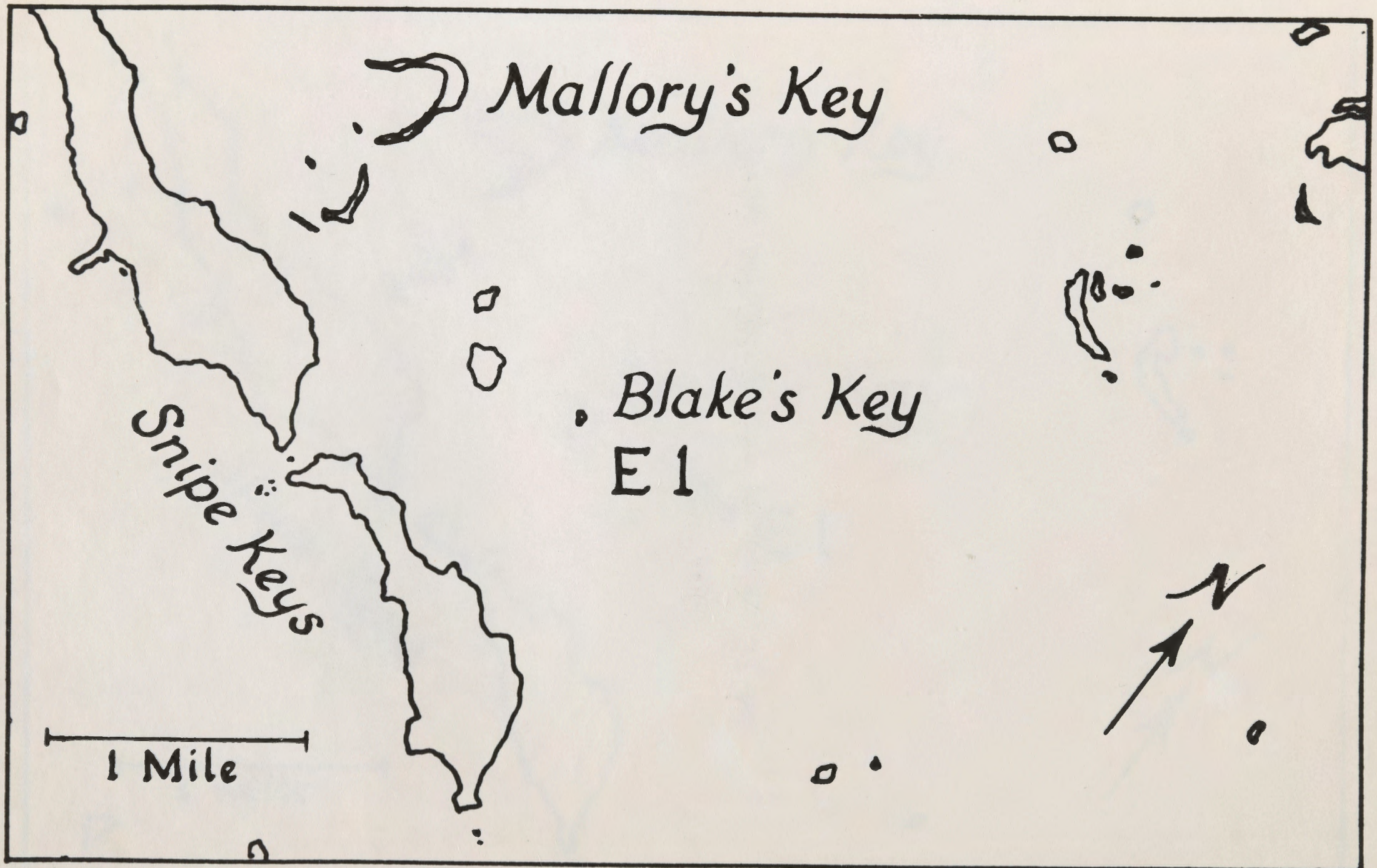

MANATEE
BAY
N
Main Key
Bay Point
E7
Cormorant Rookeries
Cross Key
0
1/2
1
2 Miles
0
1000
2000 Yards

Rhizophora produces viviparous fruits that grow on the tree until they become large, long, pointed seedlings. When they drop, frequently from the upper canopy, some evidently plant themselves where they fall, the sharp, hard point of the hypocotyl thrusting securely into the mud (Davis, 1940). Mangrove swamps are therefore often quite thick, and on small islands there may be several trees. Stems, thickened prop roots, and brace roots intermingle so that it is impossible to distinguish how many trees are present, which are which, which is the initial one (even if it is still present), and which are the main stems.

For these reasons borings to determine age of small mangrove islands would be of questionable value. On the other hand maps of the Florida Keys, especially of the Sugarloaf Key-Key West area, have been remarkably detailed and accurate with respect to small mangrove islands for at least a century. From these we have ascertained that E7 and all the islands in series 1 have existed for at least 25 years. For the other experimental islands we have been unable to find sufficiently accurate maps to determine longevity. The size and shape of individual islands may change, even drastically, but in general the islands survive the climatic catastrophes to which they are repeatedly subjected. For example, Map 4 shows our experimental island E1 (Blake's Key) and surrounding area as it appears on a

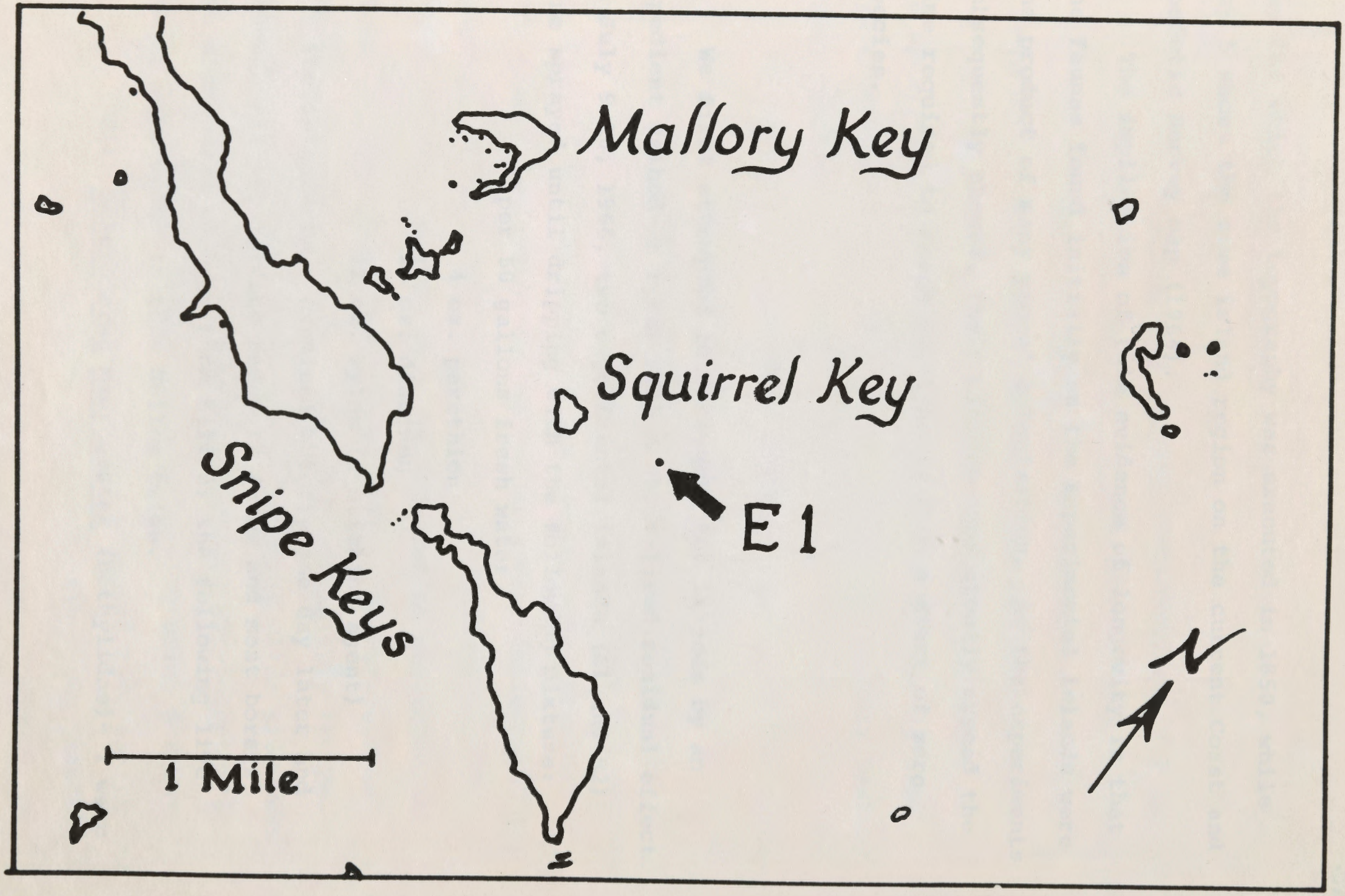
Map 4: Island El and surrounding region

1851


Mallory's Key
Blake's Key
E 1
Snipe Keys
1 Mile
N

Map 5: Island El and surrounding region

1964


Mallory Key
Squirrel Key
Snipe Keys
E1
1 Mile
N

map for which the topography was executed in 1850, while Map 5 shows the same island region on the current Coast and Geodetic Survey map (1964).

The implication of this evidence of longevity is that the faunas found initially on the experimental islands were the product of many years' colonization. As the experiments subsequently showed, their minimum ages greatly exceed the time required to reach equilibrium from a start of zero species.

DEFAUNATION

We first attempted to defaunate the islands by an expedient method--a spray with a short-lived residual effect. On July 9-10, 1966, two experimental islands (E1 and E2) were sprayed until dripping with the following mixture:

per 50 gallons fresh water,

4 oz. parathion

16 oz. diazinon

12 oz. Pylac (a sticking agent)

The islands were examined briefly one day later and although all the surface and bark fauna and most borers were discovered to have been killed, the following live animals were found in thin hollow twigs.

E1: Scleroderma macrogaster (Bethylidae)- 1 wasp

E1: Crematogaster ashmeadi (Formicidae) - worker, larvae

E2: ?Styloleptus biustus (Cerambycidae) - 2 larvae

Paracryptocerus varians (Formicidae) - 2 colonies

Tapinoma littorale (Formicidae) - 1 colony

To ensure that these survivors were not killed, either by a delayed effect of the insecticide or by a residue of the spray, the islands were examined more thoroughly nine days after spraying. The following live, apparently healthy animals were found at that time:

E1: ?Styloleptus biustus (Cerambycidae) - 2 larvae

E2: ?Styloleptus biustus (Cerambycidae) - 1 larva

Caterpillar (Lepidoptera)

Xenomyrmex floridanus (Formicidae) - 2 colonies

The sizes of the ant colonies and beetle larvae preclude their having immigrated during the nine days following spraying.

In short, a spray cannot be expected to penetrate all the hollow twigs of a Rhizophora island. Therefore some twig-dwellers will probably survive, particularly if they inhabit narrow twigs (Tapinoma and Xenomyrmex) or else pack their tunnels tightly with powdery excreta (Styloleptus). Had we attempted to kill these survivors by using a spray with a long-lived, powerful residue, we would have sacrificed the beginning of the colonization curve, since immigrants

may be killed by the residue. Because we had to be certain that all colonists, or at least all but those belonging to a small number of known taxa, would be destroyed, we reluctantly abandoned the spray technique.

We next turned to the much more difficult alternative technique of fumigation. Since a fumigant is by definition a gas the residual effect is negligible. Furthermore, since we were now dealing with gas molecules rather than liquid droplets, presumably even the inhabitants of hollow twigs would be contacted. The gas would enter crevices accessible to air, provided the exposure were long enough and dosage sufficiently high. This is of course the basis of the standard method used by professional exterminators on termites and other wood-boring insect pests.

Fumigation of living plants is a relatively uncharted area. The effect on the plant seems almost always harmful, but experiments by past investigators have generally been unsystematic and details of treatment are rarely given precisely. The biochemical effects of fumigants on plants are poorly known, damage usually being described in terms of the physical appearance of the plant shortly after fumigation (Page and Lubatti, 1963). To our knowledge, the only prior fumigation of mangrove was by B. P. Stewart (pers. comm.), who used methyl bromide on small plants. With 2 lbs./1000 cu. ft. for 2 hours at 90° F. and 2.5 lbs./1000 cu. ft. for

2 hours at 80° F he found that all insects apparently were killed, although some did not die until 48 hours after fumigation. Also no data were taken on mortality in roach eggs. Damage to the plant was limited primarily to young leaves and twigs. The latter effect accords with the general finding of Page and Lubatti (1963) that growing stages of both plants and insects are more susceptible to fumigation than are resting stages.

Our problem was exacerbated by the fact that the Rhizophora tree springs directly from water. This eliminated otherwise promising fumigants that are highly soluble in water such as hydrogen cyanide; these substances would either dissipate out under the fumigation tent through the water base or concentrate to an unknown extent in the water under the tree instead of the air around it. Either effect would greatly complicate the maintenance and measurement of gas concentration.

Consequently, the following four, relatively insoluble fumigants were selected for field testing:

Pestmaster Soil Fumigant-1 (methyl bromide 98% wt.; chloropicrin 2% wt.)

Acritet 34-66 (acrylonitrile 34% vol.; carbon tetrachloride 66% vol.)

Dow Ethylene Oxide (ethylene oxide 100%)

Vikane (sulfuryl fluoride 95% wt.; inert ingredients 5% wt.)

All field tests were performed on small Rhizophora trees in Matheson Hammock Park, Coral Gables, by National Exterminators of Miami, Florida, under the direction of Mr. Steve Tendrich in consultation with the authors. Additional tests on the mortality of mangrove colonists were performed at National Exterminators' laboratory in Miami.

The problem consisted of determining for each fumigant the intersection of two sets of points in a two-dimensional space, one axis being duration of fumigation and the other concentration of fumigant. The third obvious dimension, temperature, remained at 75°-85° F. outside the tent. The first point set was that of all duration-concentration pairs causing no more than bearable damage to the tree. The second set was that of pairs lethal to all mangrove colonists.

We soon discovered that any measurable concentration of either Acritet or Vikane caused extensive, apparently irreversible damage to red mangrove. Ethylene oxide, too, had to be discarded because of intolerable tree damage at low dosages.

Continued work with methyl bromide showed that at 22 oz./1000 cu. ft. for 2 hours damage to the tree consisted only of about 10% browned leaves after one week with no later worsening. This duration and concentration killed all

mangrove colonists (including such resistant forms as roach eggs and lepidopteran cocoons) with one possible exception: our experimental technique did not allow us to ascertain whether all cerambycid and curculionid beetle larvae were killed. When data from all tests at this duration-concentration are lumped together, over 95% of cerambycids and 80% of weevils when dug out of their burrows 1-10 days after fumigation were dead. The remainder all died within 2 days of removal. Monro and Delisle (1943) report that many insects are active soon after exposure to methyl bromide but succumb in time (some lepidopterous larvae persisting for two months), and that this delayed effect is especially common in fumigations at the low concentrations used in our own field tests. This peculiarity is confirmed by Chisholm (1952) for Japanese beetle larvae and other insects.

It would thus be tempting to ascribe the death of these few larvae to a delayed effect of the fumigant, and indeed the results from our experimental islands (given in Part II of this series) suggest that the cerambycids were eliminated. In a control experiment, however, consisting of the removal of five unfumigated cerambycid larvae (Styloleptus biustus) from their respective burrows, all died within 5 days without any additional treatment. Thus it is uncertain whether the subsequent death of the few larvae removed alive from the test trees was due to delayed action of the fumigant or simply

to desiccation or some other effect of removal from their excavations.

The essential physical damage to the trees was a browning of leaves and shoots and occasionally heavy oozing of sap. At 60 oz./1000 cu. ft. the leaf browning was manifest upon tent removal, but at 35 oz./1000 cu. ft. and less there was little or no immediate browning. The effect typically became evident at about 24 hrs. and worsened in terms of fraction of leaves browned through 72 hrs., by which time up to 90% of the leaves were brown and after which no further browning occurred. Browning did not occur randomly throughout the leaves. Instead, whole sections of the tree became completely brown while others remained almost unscathed. The upper canopy was always more severely browned, but there seemed no other pattern to which sections were damaged.

Abscission of browned leaves began within a week and, often aided by wind, was usually complete within 8 weeks. At this time damaged trees looked superficially dead except for those green sections (if any) that remained unaffected. Closer examination showed that the damaged trees could be conveniently divided into three classes, as follows.

For those trees where browning of leaves and shoots appeared complete by 72 hrs. the damage was irreversible. Within a few months bark began to peel and twigs with green wood could not be found. A year later there was no evidence

of revivification. Island E8 unfortunately falls in this class.

On other trees, including island E7, a large majority of the leaves and shoots were browned but a small continuous section remained unaffected. Here the damaged part apparently died, while the small healthy section continued to produce shoots and green leaves. It should be noted that the numerous prop roots of Rhizophora ensure that any section of a tree containing at least one major branch will be rooted directly to the substrate.

Trees less severely damaged (60% or fewer browned leaves) showed the following pattern of recovery. Unaffected sections remained unchanged, while leaf abscission in most of the damaged sections was accompanied by the sprouting of new shoots directly from almost all branches. New green leaves appeared on a few of the branches from which brown leaves had fallen. Within two months the trees appeared normal except for occasional patches in the extreme upper canopy that remained bare. Island E1, which 2 days after fumigation appeared to have about 50% brown leaves, recovered as just described so that after one month it did not appear to have incurred more damage than similar trees do during heavy storms, and two months after defaunation seemed quite normal except for a small bare patch in the upper canopy. At no time did bark crack or peel.

In most damaged trees of the first two classes--where either the whole tree or all but a small section was irreversibly destroyed--there was copious oozing of sap for up to a week after fumigation. Such oozing was never observed in untreated trees, nor in those fumigated trees which showed good recovery.

The action of methyl bromide on living plants has probably been studied more thoroughly than that of any other fumigant, but as with all such work the majority of publications deal largely in purely physical and visual terms. Mainwaring (1961) has examined the physiological responses of several plants to methyl bromide and his numerous observations imply that its major effect is auxin inhibition. This hypothesis seems consistent with all previously reported effects of methyl bromide fumigation (Page and Lubatti, 1963). The damage which we describe seems too drastic and certainly too immediate to be attributed solely to auxin inhibition, although the presence of such a biochemical action cannot be ruled out.

Whatever the biochemical effect of methyl bromide on Rhizophora mangle, it apparently had the expected Q_{10} of 2-3. Our initial tests in Matheson Hammock were conducted on small plants in a swamp dominated by large trees. Consequently they were well shaded and the temperature inside the fumigation tent remained within 5° F. of the air temperature (75°-85° F.).

The experimental islands obviously could not be shaded, and even on overcast days the temperature inside the tent (undoubtedly increased considerably by heat absorption through its dark outer surface) was at least 90° F. On sunny days the inner temperature was so high that the covering alone, without fumigant, caused burning of leaves, especially those touching the tent and in the upper canopy. Indeed, it seems probable that the generally more severe damage to the upper canopy throughout this experiment was caused by higher temperature, especially since methyl bromide gas has a density (3.974 g./l. at 20° C.) considerably greater than that of air. Its concentration would consequently be expected to decrease toward the upper canopy.

Air humidity is much less important than temperature in its effect on fumigation damage to plants (Page and Lubatti, 1963); our experiments were almost all conducted within a narrow humidity range (65%-90%) and the effects of varying this parameter were not studied.

Two experimental islands fumigated during daytime were both damaged--E7 severely and E1 less so (see above). Massive use of dry ice was impractical because of transportation problems, and increased circulation inside the tent had no effect. To reduce damage associated with heat we therefore fumigated all other islands at night. Concentration was increased to 28-30 oz./1000 cu. ft. with no observable additional damage.

The chemical means for defaunation having been chosen and tested preliminarily, we were left with an overwhelming physical problem--how to fumigate an entire island?

Assuming that we could somehow get the fumigation tent, an 80' x 80' piece of plastic-impregnated canvas with additional side pieces for larger islands, onto an island, the tree could not support the weight without major limb breakage, since even our special half-weight tent weighed 600 lbs. It was evident that some sort of superstructure was needed, one which would surround and rise over the island to remove most or all of the tent weight from the tree.

Perhaps the most obvious idea, that of constructing a permanent framework and lowering it over the islands by transport helicopter, was discarded because the expense of building such a framework was not justified by our small number of islands.

We next considered a temporary framework to be assembled in the field, presumably a rectangular solid which would cover an entire island. One such method for which the frame was built and tested--in Miami and then over small mangrove islands near Key Largo--employed the structure in Figure 2. The steel center support of this framework, the remainder of which was constructed of lightweight aluminum expressway sign supports, was anchored on the tree or in the substrate near the center of the island. This method proved to have

Figure 2: Partial framework of expressway sign supports


NATIONAL
EXTERMINATORS

several drawbacks on islands with muddy substrates, the most important being the difficulty of keeping the four legs from sinking to different depths in the mud.

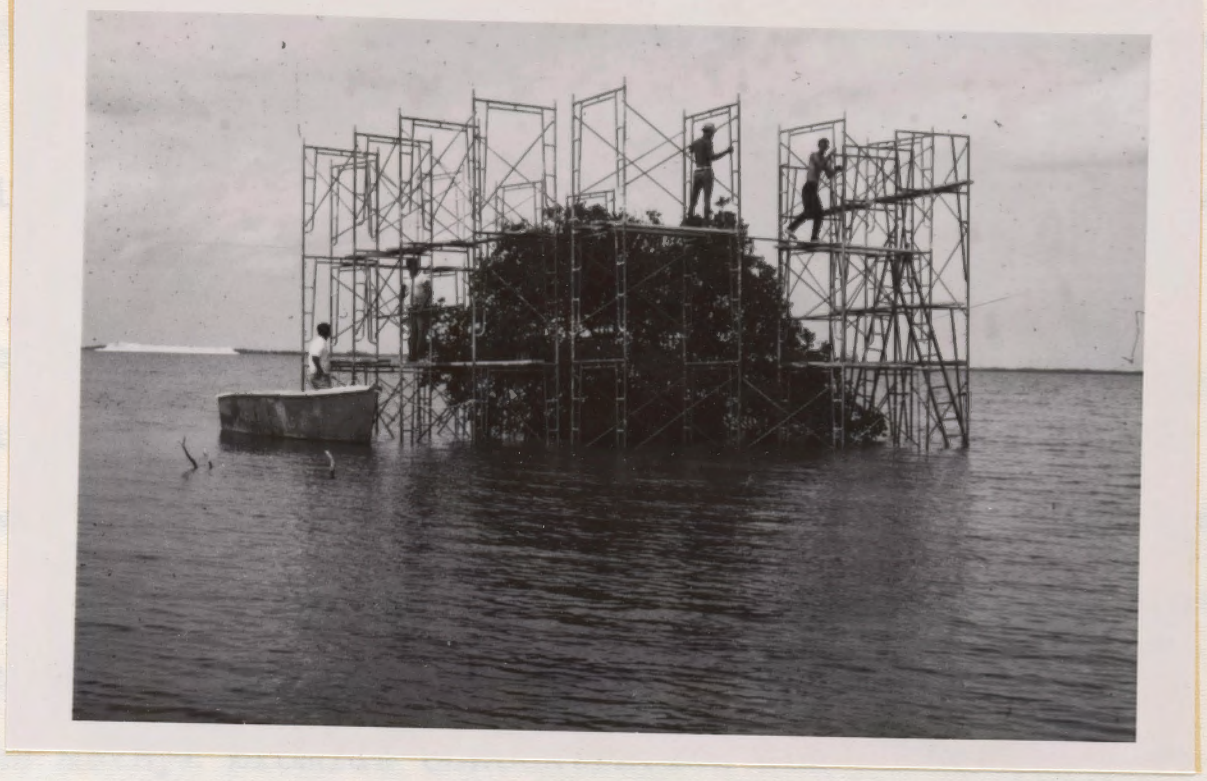
A second, more promising method utilized a temporary full framework (shown nearly complete in Figure 3) of construction scaffolding set on planks. Preliminary work with this method justified a full-scale test and on October 10, 1966, island E7 (Map 3) was defaunated to test both the scaffolding framework and previously determined fumigation specifications.

All work was done in the daytime, at a temperature of about 80° F. Planks to prevent the framework from sinking into the mud were placed underwater in a square around the island and held manually until the first tier of scaffolding (which was sufficiently heavy to keep them from floating) was placed on them. The remaining tiers were added, one side at a time, until the island was surrounded by a cube of scaffolding. Figure 3 shows the framework complete except for the upper tier of scaffolding in the right rear corner and the square walkway of planks around the very top of the structure.

The tent was then raised by block and tackle to the top of the framework and lowered over the island (Figure 4). Methyl bromide was introduced from 100 lb. cylinders through two shooting stations at opposite sides of the island 8 ft.

Figure 3: Scaffolding over Island E7; complete except for top walkway

Figure 4: Fumigation tent over Island E7





above the water. Each station emptied into a metal tub mounted with a fan to disperse the gas. The chloropicrin (added to the odorless methyl bromide as a safety measure) precipitated and dripped into burlap sheets at the bottom of the tubs. Concentration was measured frequently by a Gow-Mac thermal conductivity meter with a self-contained pump attached to a testing station 8 ft. above the water and well away from the two shooting stations. The fans and meter were powered by a 12 1/4 hp. portable gasoline-run AC generator located on a nearby workboat.

The methyl bromide concentration was increased from 0 to 22 oz./1000 cu. ft. over 30 min., then kept at 22-25 oz./1000 cu. ft. for 2 hours. The gas was released through seam openings for 45 min. and the tent was then removed.

E7 was monitored by the method to be described shortly (but with considerably more twig breakage) for 2 hours immediately after defaunation and for the complete next day. The results generally confirmed the evidence from the Matheson Hammock tests. Of the original 23 observed colonists, 11 were recovered all dead, frequently in large numbers and all life stages. The details are given in Table 2. The only live animals found were larvae of two deep-boring beetles, and these formed only a small fraction of the original population, as shown by the following recovery data.

	live	dead
Styloleptus biustus (Cerambycidae)	2	57
Pseudoacalles sp. (Curculionidae)	2	8

One of the two live cerambycids was extremely sluggish and died an hour after removal. The other cerambycid and the two weevils seemed healthy, though one of the weevils became torpid and died 9 hours after removal.

The tree was severely damaged as described on p. 39. Within two months 85% of the foliage was dead, although the single living section has remained unchanged to the time of publication.

In sum, the gas worked essentially as expected and this aspect of the fumigation was left unchanged in subsequent defaunations, except that the work was henceforth done at night in all but one instance. The scaffolding framework had disadvantages, chief among them being the large crew necessary to erect it (at least five men) and the number of pieces and weight of the equipment. This necessitated numerous boat trips between E7 and our staging area near Manatee Creek. Moreover, the shallow water along the route precluded the use of large craft. This problem turned out to be greatly aggravated on the other experimental islands, most of which were considerably further from a convenient staging area.

TABLE 2. Colonists on E7 during defaunation

INSECTS	
Embioptera:	gen. sp.*
Orthoptera:	Latiblattella n. sp.
	Cycloptilum sp.
	Tafalisca lurida*
Coleoptera:	Pseudoacalles sp.'
	Leptostylus sp.
	Styloleptus biustus'
	Tricorynus sp.
Psocoptera:	Archipsocus panama
Hemiptera:	Pseudococcus sp.
Lepidoptera:	Nemapogon sp.*
Hymenoptera:	Casinaria texana
	Camponotus floridanus*
	Camponotus planatus*
	Paracryptocerus varians*
	Pseudomyrmex elongatus*
	Xenomyrmex floridanus*
ARACHNIDS	
Araneae:	Ariadna arthuri
	Eustala sp.
	Leucauge venusta*
Acarina:	Galumna sp.
OTHER	
Chilopoda:	Orphnaeus brasilianus*
Isopoda:	Rhyscotus sp.*

*discovered dead after fumigation

'discovered mostly dead after fumigation (see text)

Consideration was therefore given to sacrificing the complete framework for a partial one, possibly a single tower rising far enough over an island so that most of the tent weight would rest on the tower instead of the tree. Such a method would not afford the protection against wind given by a complete framework, but would require much less equipment and, hopefully, a smaller work crew.

Again there were several alternatives, and a number of permanent towers (such as broadcasting towers and various construction booms) were studied. They seemed in general to be much larger and heavier than we needed, and would require a sizable barge for transport--but the shallow water and travelling distances involved made this unattractive. Furthermore, it soon became apparent that a tower method would entail considerably more aerial and acrobatic skill than we possessed.

National Exterminators therefore contracted a steeplejack full time to devise and to implement a tower method for fumigation of islands. After a month of experimenting on islands near Key Largo, the following procedure was adopted.

A collapsible 30-ft. triangular steel tower was erected in the center of the island, either propped on a large root or forced deep into the ground. The steeplejack then climbed to the top and threw out three guide wires which were fastened down with mudscrews or stakes, depending on the

substrate. Using a block and tackle, one man on the tower and one on the island lifted the rolled tent until it formed a triangle over the island. The tent was then carefully unrolled down the guide wires until the island was covered (Figures 5-10).

Whereas wind had little effect upon manipulation of the tent in the scaffolding method, it was impossible to unfurl the tent from the tower in winds greater than 8 knots. Sandbags and stakes were used with both systems to help keep tent edges submerged.

Equipment used in the tower method was identical to that described on p.44 for the scaffolding method, and was similarly situated. The procedure was identical except that gas was administered from 1 lb. cans instead of 100 lb. cylinders and concentration and duration were increased to 28-33 oz./1000 cu. ft. for 2 1/2 hours on all islands but E1.

After fumigation the methyl bromide was released through tent seams as with scaffolding, but in the tower system tent removal was more difficult. At low wind speeds the tent could be laboriously refurled and gradually lowered to the boat. We fortuitously discovered that high winds, instead of causing extensive damage as we expected, could actually aid tent removal. The windward side of the tent was lifted by poles to about 8 ft. above water, whereupon sufficient wind entered the tent to lift it up over the tree and to

Figure 5: Tower over Island E2

Figure 6: Tent being lifted onto tower by block and tackle





Figure 7: Tent in furled position over Island E2

Figure 8: Tent opened over guide wires





Figure 9: Island E2 partially covered

Figure 10: Island E9 covered by tower method





drop it, partly extended, into the water on the leeward side of the island. Air trapped beneath the tent was sufficient to float it. It was then tied to a boat and pulled offshore, where it was manually lifted from the water.

El was fumigated in the daytime. For all remaining islands the tent was unrolled no earlier than 60 minutes before sundown, the fumigation was conducted between 8:00-12:00 P.M., the gas was removed by 1:00 A.M., and the tent was either off the island or refurled within 90 minutes of dawn. Effects on the mangrove trees of the fumigated islands are noted in Table 3.

The total destruction of the mangrove on E8 was probably due to two factors. First, since E8 is located on a wide, shallow mud bank the boat was anchored 110 yds. from the island. The meter pump drew the gas this distance to the meter (on the boat). It seems likely in retrospect that the pump had insufficient power and that consequently our readings (of 28-33 oz./1000 cu. ft.) represented only part of the actual concentration within the tent. Secondly, because of difficult working conditions (darkness, soft mud, and the frequent appearance of sharks) the gas could not be released until 3 hours at readings of 28-33 oz. had passed, instead of the planned 2 1/2 hrs. The use of E8 as an experimental island was discontinued.

All islands were examined immediately after tent removal

TABLE 3. Extent of damage to foliage and subsequent recovery on experimental islands

Island	Fumigation Date	Time	Extent of Damage (Burnt Leaves)	Damage Location	Recovery of Foliage
E1	3/13/67	day	50%	general	complete in 2 months, except for extreme upper canopy
E2	3/7/67	night	10%	upper canopy	complete in 2 months
E3	3/17/67	night	5%	upper canopy	complete in 2 months
E7	10/10/66	day	85%	all except one section	none
E8	4/17/67	night	100%	complete	none
E9	4/7/67	night	20%	upper canopy and one other section	little in upper canopy complete elsewhere in 2 months
ST2	4/20/67	night	5%	scattered	complete in 2 months

to ensure that the fumigation had been effective. No living animals were found on E1, E2, E8, and E9. The results from E7 have already been described. A single live curculionid larva was recorded on E3. On ST2 one living and at least 100 dead polyxenid millipedes (Lophoproctinus ?bartschi) were observed. Although we have no further direct evidence and know of no work on methyl bromide fumigation of millipedes, we suspect that all millipedes not destroyed immediately were killed by the delayed effect of methyl bromide discussed earlier. At no time in the later colonization of ST2 (or any other defaunated island, for that matter, and Lophoproctinus was found originally on E1, E2, E3, and ST2) was Lophoproctinus present, and an especial attempt at the first monitoring of ST2 to find polyxenids yielded only dead ones.

In sum, we feel that this fumigation technique kills all mangrove arthropods with the single possible exception of deep-boring beetle larvae.

MONITORING TECHNIQUE

Precautions were taken at all monitorings to prevent contamination of the experimental islands. At all islands except E2 (where this procedure was impractical because of the depth and nature of the bottom and unusually high

frequency of sharks) boats were never brought in contact with or tied to the islands but rather were anchored at least 40 ft. offshore. Before wading to an island experimenters examined clothing, equipment, and persons for animals, which were destroyed. To lessen the chance of phoresy investigators simply immersed themselves briefly early in the experiment but later substituted thorough spraying with "Off" insect repellent (N,N-diethyl-meta-toluamide). All equipment used on the island was sprayed weekly with a short-lived insecticide.

Absence of supratidal land simplifies the environment of the typical small mangrove island greatly. The following microhabitats dominate an island:

hollow twigs	leaves and flowers
living branches and twigs	green shoots
dead bark and tree holes	fruits

Because of the extremely small size of the experimental islands it was possible to study most microhabitats exhaustively for the predefaunation censuses. For example, on E3 we broke and examined 3500 of an estimated 5000 small hollow twigs, collected 90% of the fruits, and looked under at least 80% of the dead bark. Rhizophora has numerous limbs and our islands were relatively low, so that the greatest part and frequently all of the upper canopy was safely accessible if one climbed judiciously.

Our continued work in mangrove, after our surveys of E1, E2, E3, E6, and E7, but before the surveys of ST2, E8, E9, and E10 and before any defaunations, led us to believe that our study of the leaf and shoot fauna had been deficient. From that time greater emphasis was placed on these microhabitats. During fumigation we had serendipitous evidence for the completeness of our original surveys (with the exception just noted). The fumigant included 2% chloropicrin, which drives out even deep-boring and hollow twig-dwelling arthropods (cf. Lauck, 1965). In our experiment the animals either fell into the water or remained hanging from branches by spines or silk, tenuously and conspicuously. Those which fell generally remained afloat and, when a tent seam was opened after fumigation, flowed out in a stream where they could be seen easily with a flashlight and collected on a screen.

This technique was especially effective on E8, E9, and ST2 and indicated greater densities of both insects and spiders than we had suspected. Only on E8, however, were animals found that had not been noted in the original surveys. These consisted of four beetles:

Staphylinidae: gen. sp.

Carabidae: Bembidion sp. nr. contractum

Carabidae: Tachys occulator

Oedemeridae: Oxacis sp.

Of these the first three were apparently living in a patch of temporarily supratidal mud, which was submerged again two weeks later during a strong wind. Oxacis sp. is believed to have been a transient.

Defaunated islands were monitored every 18 days (approximately) for a 2 day period. The original census method was used with less breakage of twigs and peeling of dead bark. At each monitoring period approximately 10% of all hollow twigs were broken, and with this treatment the number of hollow twigs seemed to remain constant throughout the experiment. Only when gentle lifting failed to allow vision was dead bark removed and then only a part was peeled off. Small amounts of carbon tetrachloride and ammonia and tapping with a steel probe were used effectively to drive animals out from underneath bark and inside hollow twigs without damage to tree or colonist. Great care was taken to prevent the monitoring from being destructive and from altering the proportions of the respective microhabitats on an island.

Most colonists could be identified in the field because of the small subset of the Keys fauna which invades small mangrove islands and the completeness of our reference collection. Those which could not be recognized with certainty were treated in one of two ways. If the animal in question was obviously part of a sizable population, as with

many psocids and thrips, a small collection was made, one that did not exceed 2% of the estimated minimum size of the population. When an unknown colonist was not part of a large population we photographed it with a Medical-Nikkor lens on a Nikormat FS camera.

It was quickly discovered that the rate of finding colonizing species, at first very high, declined approximately linearly to near 0 at about 14 man-hours of searching:

$$\frac{d^2S}{dt^2} \cong C < 0,\ t \leq 14;\ \frac{dS}{dt} \cong 0,\ t > 14$$

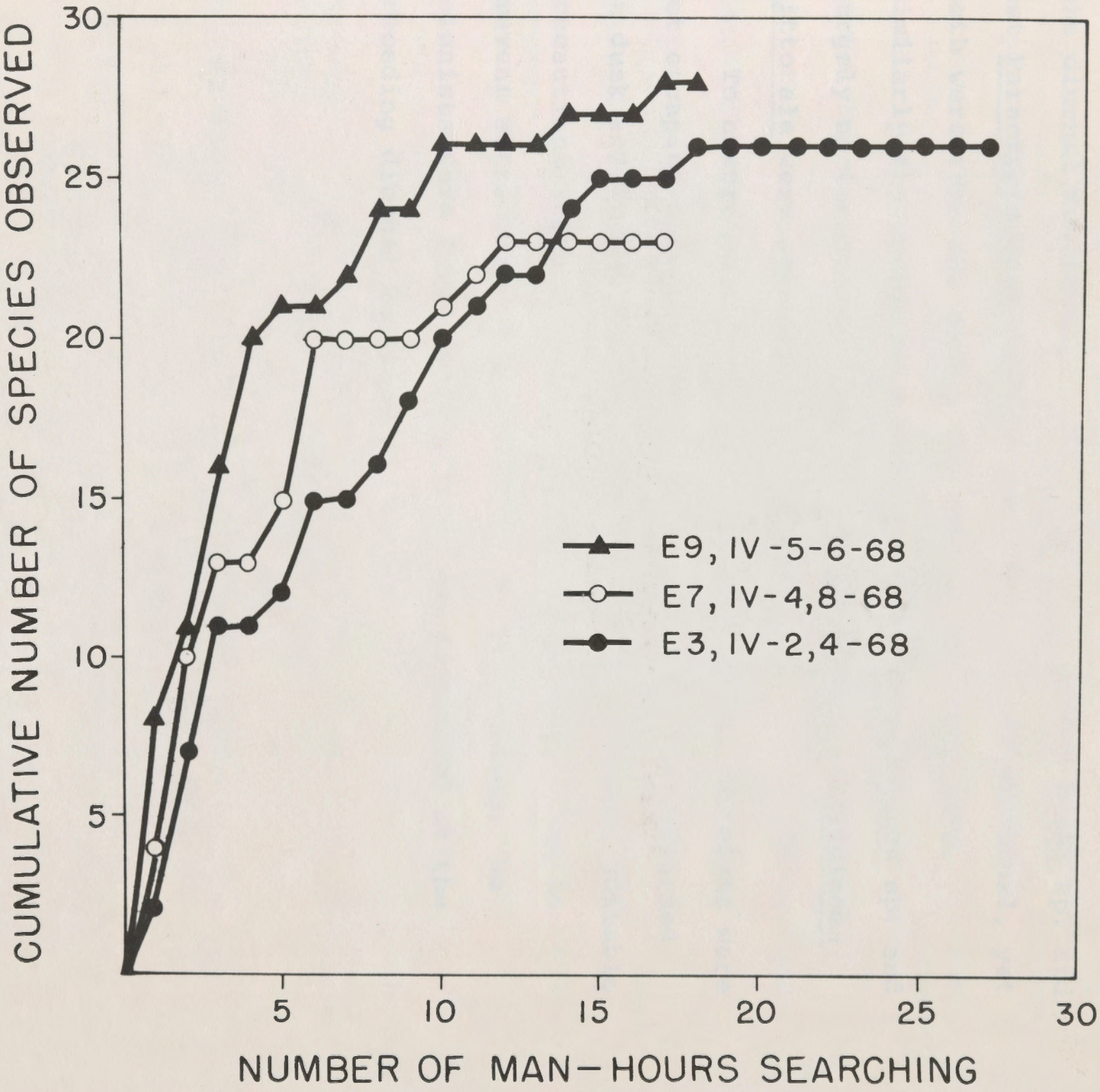
S = total # spp. seen during monitoring

t = time searching, in man-hours

C = constant

Beyond 14 man-hours previously unrecorded colonists were rarely found - a very few would be expected from immigration within the monitoring period. Graph 1 depicts the cumulative number of species observed vs. time for three representative monitorings. Different sizes of islands, weather conditions, and especially varying population sizes caused minor differences in the curves, but despite great change in species density throughout the experiment the curves remained remarkably similar; the above approximate equations continued to hold. A 2 day monitoring period (17-20 man-hours) was therefore chosen.

Graph 1: Cumulative species counts for three monitorings


CUMULATIVE NUMBER OF SPECIES OBSERVED
30
25
20
15
10
5
5
10
15
20
25
30
NUMBER OF MAN-HOURS SEARCHING
E9, IV-5-6-68
E7, IV-4,8-68
E3, IV-2,4-68

Because of the simplicity and very small size of the experimental islands we felt that all colonists having crepuscular or nocturnal activity were being recorded during the diurnal monitoring. The anyphaenid spider Aysha sp. and ant Paracryptocerus varians are both strictly nocturnal, yet both were recorded during the day in their retreats. Similarly the crepuscular braconid wasp Macrocentrus sp. and largely nocturnal ants Camponotus floridanus and Tapinoma littorale were repeatedly observed.

To ensure that nocturnal and crepuscular colonists were not escaping detection several monitorings were performed at dusk and during the first few hours of darkness, suitable precautions (such as narrow beam lights) being taken to prevent attraction of night fliers to the islands. No colonists were found which had not been recorded at the preceding diurnal monitoring.

ACKNOWLEDGMENTS

We thank the United States Department of the Interior for permission to fumigate the islands of this experiment. In particular, Mr. Jack Watson of the Great White Heron National Wildlife Refuge, Mr. Roger W. Allin and Dr. William B. Robertson of the Everglades National Park, and Dr. Robert M. Linn of the National Park Service encouraged this work. Mr. Steve Tendrich, Vice-President of National Exterminators, Inc. (Miami) coped imaginatively and effectively with the unique problems presented by this experiment. Dr. W. H. Bossert and Dr. P. B. Kannowski assisted in the original censuses. Maps and tables for all parts of this series were done by Mrs. Helen Lyman. The work was supported by NSF grant GB-5867.

REFERENCES

Alfken, J. D. 1924. Die Insekten des Memmert. Zum Problem der Besiedelung einer neuentstehenden Insel. Abh. Naturw. Ver. Bremen 25: 358.

Bowman, H. H. M. 1918. Botanical ecology of the Dry Tortugas. Carnegie Inst. Wash. Papers Dept. Marine Biol. 12: 111-138.

Chisholm, R. D. 1952. Nature and uses of fumigants. Insects-The Yearbook of Agriculture 1952: 331-339.

Dammerman, K. W. 1948. The fauna of Krakatau 1883-1933. Verhandel. Koninkl. Ned. Akad. Wetenschap. Afdel. Natuurk., (2) 44: 1-594.

Darlington, P. J. 1957. Zoogeography: the geographical distribution of animals. Wiley, New York. 675 pp.

Davis, J. H. 1940. The ecology and geologic role of mangroves in Florida. Papers from Tortugas Lab., Carnegie Inst. Wash. 32: 307-412.

Docters van Leeuwen, W. M. 1936. Krakatau, 1883 to 1933. Ann. Jard. Botan. Buitenzorg 56-57: 1-506.

Einarsson, E. 1967. Comparative ecology of colonizing species of vascular plants. Surtsey Research Progress Report III: 13-16.

Feekes, W. 1936. De ontwikkeling van de natuurlijke vegetatie in die Wieringermeer-Polder. Ned. Kruidk. Archief 46: 1.

French, R. A. 1964 (1965). Long range dispersal of insects in relation to synoptic meteorology. Proc. Interm. Congr. Entomol. 12th (London). 6: 418-419.

Fridriksson, S. 1967. Life and its development on the volcanic island, Surtsey. Proc. Surtsey Research Conf., 1967: 7-19.

Hermannsson, S. 1967. Introduction. Surtsey Research Progress Report, III:1.

Jacobson, E. R. 1909. De nieuwe fauna van Krakatau. Jarv. Top. Dienst Ned. Ind. 1908: 142.

LaRue, D. C. and T. T. Muzik 1954. Growth, regeneration and precocious rooting in Rhizophora mangle. Pap. Mich. Acad. Sci. Arts & Lett., I 39: 9-29.

Lauck, D. R. 1965. Chloropicrin for fast action with a Berlese funnel. Turtox News 43: 115.

Leege, O. 1938. Das staatliche Naturschutzgebiet Insel Memmert. Deutsche Vogelwelt 63: 101.

Lindroth, C. H., H. Andersen, H. Bodvarsson and S. H. Richter. 1967. Report on the Surtsey investigation in 1966. Terrestrial invertebrates. Surtsey Research Progress Report, III: 59-67.

MacArthur, R. H. and E. O. Wilson. 1963. An equilibrium theory of insular zoogeography. Evolution 17: 373-387.

MacArthur, R. H. and E. O. Wilson. 1967. The theory of island biogeography. Princeton University Press, Princeton. 203 pp.

Maguire, B. 1963. The passive dispersal of small aquatic organisms and their colonization of isolated bodies of water. Ecol. Mono. 33: 161-185.

Mainwaring, A. P. 1961. Some effects of methyl bromide on aphids and whitefly and their host plants. Doctoral thesis, London Univ., London, Engl.

Martens, E. von. 1867. Die landschnecken. Preuss. Exp. Ost-Asien, Zool. II: 447 pp.

Millspaugh, C. F. 1907. Flora of the Sand Keys of Florida. Field Columbian Museum Chicago Publ., Bot. Ser. 2: 191-192.

Monro, H. A. U. and R. Delisle. 1943. Further applications of methyl bromide as a fumigant. Sci. Agr. 23: 546-556.

Page, A. B. P. and O. F. Lubatti. 1963. Fumigation of insects. Ann. Rev. Entomol. 8: 239-264.

Patrick, R. 1967. The effect of invasion rate, species pool, and size of area on the structure of the diatom community. Proc. Nat. Acad. Sci. 58: 1335-1342.

Schaank, J. R. H. 1935-38. De broedvogels van den Wieringermeerpolder in 1935; idem 1936; idem 1937. Org. Club. Ned. Vogelk. 8: 43; Limosa 10:22; 11:7.

Wolfenbarger, D. O. 1946. Dispersion of small organisms. Am. Midland Naturalist 35: 1-152.

II. The Colonization of Empty Islands

ABSTRACT

The colonization of six small mangrove islands in Florida Bay by terrestrial arthropods was monitored continually for one year after defaunation.

Both the observed data and climatic considerations imply that seasonality had little effect upon the colonization curves of species present vs. time. By 250 days after defaunation the faunas of all but the most distant island had returned to a state not unlike that on untreated islands in species number and composition, although population densities were still abnormally low. Early colonists included both weak and strong fliers, but the former, particularly psocopterans, were usually the first to produce large populations. Among these same early invaders were the taxa displaying the highest extinction rates and also the greatest variability in species composition on the different islands. Ants, the ecological dominants of mangrove islands, were among the latest to colonize, but did so with the highest degree of predictability.

The colonization curves plus static observations on untreated islands imply strongly that a dynamic equilibrium number of species exists for any island. The colonization curves are believed best explained as the product first of colonization involving little if any interaction and then

a gradual decline as interaction becomes important, terminating in a lasting dynamic equilibrium. Equations are given for the early immigration, extinction, and colonization curves.

Dispersal to these islands is predominantly through aerial transport, both active and passive. Extinction of early colonists is probably rarely related to biotic interaction but rather to such physical factors as drowning or lack of suitable breeding site. As population sizes increase it is expected that competition and predation will become more important. Observed turnover rates showed wide variance, with most values between .05 and .50 spp./day. True turnover rates are probably much higher, with .67 spp./day the extreme lower limit on any island.

SPECIES COUNTS

For the species counts and discussion which follow these definitions will be used:

Colonization: the existence of at least one propagule of a species on an island

Extinction: the disappearance of a species from an island

Invasion: the arrival of one or more propagules on an island

Immigration: the arrival of a propagule on an island unoccupied by the species

Propagule: the minimum number of individuals of a species capable of breeding and population increase under ideal conditions for that species (unlimited food supply and proper habitat, no predators, etc.)

The distinction between invasion and immigration should be noted. It is incorrect to speak of an immigration rate for one species, since an immigration rate for an island is in units of spp./time. A species can have an invasion rate on a given island, however - this is simply the number of propagules of that species landing per unit time.

In analyzing species counts made at discrete intervals, as in our monitorings, every species for which at least one propagule exists is designated a colonist. It is also

designated an immigrant if it was not a colonist at the preceding count; every immigrant is also, by definition, a colonist. This definition says nothing about whether food and a breeding site exist; a species whose propagule lands on one of our islands is a colonist even if it is doomed to quick extinction for purely physical reasons, for example the absence of a suitable nest site for a given species of ant in the Rhizophora.

Because of the relative nearness of our experimental islands to source areas and, to a lesser extent, their small size and ecological simplicity, ambiguities concerning the state of colonization sometimes exist which would not arise if we were dealing with such truly distant and larger islands as Tristan da Cunha or Easter Island. Even in these places a very few birds might be seen rather frequently which are transients and do not breed on the islands, but in general any animal for which a propagule would be recorded on the island would "know" it was on an island. The island is not simply an extension in some sense of the mainland.

In our experiment a small percentage of the animal species, less than 10% of all species sighted, behave as though the distances to the experimental islands are not qualitatively different from the same distance overland. We wish to discount these species in our calculations, unless insularity becomes important in a specific instance.

Two classes of species can be recognized in this connection. Several species of insects (cicadas, odonates, hunting bees and wasps) treat small mangrove islands as part of a fine-grained foraging area, travelling readily and frequently among several islands and adjacent shore regions. A species of the wasp genus Polistes forages regularly over small mangrove islands but rarely nests there. When nesting does occur the wasps apparently restrict their foraging largely to the nesting island. Only an extant nest qualifies the Polistes as a colonist. In similar cases actual breeding, rather than just the presence of sufficient animals to breed under the most favorable conditions, was employed as the criterion for colonization. Transient adult butterflies, particularly Ascia monuste and Phoebis agarithe (Pieridae), in the course of active migration over and beyond the experimental islands occasionally skim briefly through an island proper but do not stop to breed there. These will not be considered colonists for reasons similar to those used to discount fine-grained foragers.

A second difficulty associated with the nearness of our islands concerns intermittent breeding by strong-flying insects combined with continuous foraging by adults. The moth Automeris io (Saturniidae) forages frequently on small mangrove islands and occasionally deposits eggs. The life cycle from egg to adult of Automeris on Rhizophora is about

2 1/2 months, and if (as may have happened on E3) adults breed on an island at intervals greater than that extinction rates would appear to be high. For after a brood matures, the survivors generally all disperse from the island and no new adults may breed there for a period. This is obviously not extinction in its classical sense--it is not caused by competition for food or space, predation, climatic catastrophe, etc.--but it does accord with our strict definition given above. This situation was fortunately rare, almost entirely restricted to a few Lepidoptera; species of this type will be considered colonists, with one immigration only and no extinction, until a definitive and extended absence is recorded. The behavior of the very few nesting birds listed earlier would place them in this category but they were nevertheless discounted in our analysis.

A few arthropods live in and among Rhizophora roots at or below the water level, some foraging on mud at low tide. These include the isopod Ligia exotica, an unidentified amphipod, and three insects: Trochopus plumbeus (Hemiptera: Veliidae), Axelsonia littoralis (Collembola: Isotomidae), and Anurida Maritima (Collembola: Poduridae). These will be excluded from the species counts because they are essentially part of a surface marine community and apparently do not interact significantly with the arboreal mangrove fauna. All are ubiquitous around small mangrove islands and

cannot be eradicated with certainty.

The impermanent mudbanks on E8 and E9 that remain wet but above water for several weeks in calm weather harbor a peculiar marine arthropod community, listed in Table 1. Most of the species are concentrated in washed up and wet debris and algae. That all but the earwig Labidura riparia are virtually marine and do not breed on the islands is indicated first by their never having been collected on Rhizophora (even when the mud is submerged and debris washed away by wind-driven high tide), second by most species having been observed swimming from one patch of mud or debris to another, and finally by the swift recolonization by large populations of most species observed after extinction caused by extended flooding. L. riparia is the only species found on the islands proper, and it is probably the only one whose energetic interaction with the mangrove and its arboreal fauna is significant. All the others apparently feed on seaweed or washed-up detritus, or else prey upon those which do. Consequently L. riparia alone is considered a colonist.

The tree snail Littorina angulifera and tree crab Aratus pisonii inhabit all but the upper canopy of small mangrove islands but will not be counted for the following two reasons. Neither can be removed--Littorina is unaffected by 50 oz./1000 cu. ft. of methyl bromide for 3 hrs., and Aratus simply drops to the water and may swim under the tent--

TABLE 1. Arthropod community of intermittently submerged mudbanks on small mangrove islands

INSECTS		
Collembola		
	Poduridae:	gen. sp.
Dermaptera		
	Labiduridae:	*Labidura riparia*
Coleoptera		
	Carabidae:	*Bembidion* sp. nr. *contractum*
		Tachys occulator
	Corylophidae:	*Anisomeristes* sp.
	Ptiliidae:	*Actinopteryx fucicola*
	Staphylinidae:	gen. sp.
Hemiptera		
	Saldidae:	*Pentacora sphacelata*
OTHER		
Acarina		
	Veigaiaidae:	*Veigaia* sp.
Isopoda		
	Oniscoidea:	*Ligia exotica*

and both have planktonic larvae. Again, the interaction of these species with the remainder of the arboreal community appears superficially not to be significant.

Our definition of a propagule dictates that animals with zero reproductive value (e.g., a male ant landing on an island after a nuptial flight) not be considered colonists.

Although birds were not counted here, bird parasites which establish breeding populations on the islands rather than wholly on the birds were listed as colonists. Specifically, the hippoboscid flies Olfersia sordida and Lynchia albipennis (whose puparia are commonly found in tree crevices) and the tick Argas radiatus (all stages of which live under dead mangrove bark) were counted.

Finally, except for the rare larvae and pupae, all Diptera were excluded. Monitoring of flies proved too difficult to warrant faith in the accuracy of species counts, and the extreme scarcity of immature stages indicates that small mangrove islands rarely support breeding dipteran populations.

Deep boring beetles were deemed valid colonists in this series. The uncertainty of extinction discussed above notwithstanding, the data imply that the few initially surviving cerambycid larvae were destroyed by a delayed effect, and that the weevils may have succumbed in the same way. In any event there are but four species involved,

and rarely were more than two found on a single island.

Conservatism was employed in counting acceptable colonists. In all instances of uncertainty about the number of species of a given taxon present the minimum possible number is taken. For example, occasionally the records for one monitoring revealed two thrips, Neurothrips magnafemoralis and Liothrips sp. (both Tubulifera), as well as larval thrips identifiable only to the suborder Tubulifera. Since the larvae could conceivably be ascribed to one of the two species known present, only two species are recorded for this period. Similarly the observations on E1 (V-29-67) of a moth caterpillar Bema ?ydda (Phycitidae), and a small adult moth similar to Bema but seen too briefly to be so recorded with certainty yield a species count of one only, since both individuals could belong to one species.

The presence of an immature animal need not imply breeding on an island; spiderlings balloon more readily than adults, and any insect larva could be blown or rafted to an island, although for some, of course, the probability of this is quite low . Similarly, an adult female does not constitute a propagule or part of one if she has not been fertilized, is not of a parthenogenetic species, and no male is present. Nevertheless, we assume here that an adult female, an adult of indeterminate sex, and an immature animal each imply the presence of a propagule. Adult males are not so counted.

The accompanying tables (2-7) of colonists on E1, E2, E3, ST2, E7, and E9 show the complete course of colonization on the defaunated islands. They are based over 90% on direct observation. In certain instances (hatched bars on the tables) animals were assumed present through one or more monitoring cycles when not actually observed. To ensure consistency in such interpolations the rules given in Table 8 were followed.

SEASONALITY

We must first discuss whether any aspects of the colonization depicted in Tables 2-7 (and Graphs 1-3) are artifacts of the particular season at which defaunation was performed. That is, if all the islands were fumigated in September instead of March would the tables and derived curves be qualitatively different?

This would obviously be so in much of the United States, where dispersal stages of most insects and spiders occur at short, distinct periods (usually in the summer). The Florida Keys are subtropical, however, with the mean temperature of the coldest month (69.6° F.) only 14° F. lower than that of the warmest month. Frost has never been recorded. The mean humidity of the driest month is but 8% lower than that of the most humid. Rainfall is less homogeneous, September-October averaging about 6 inches and December-January only

Table 2: Colonists on Island El

INSECTS	THYSANURA	Lepismidae	Lepisma sp.
	ORTHOPTERA	Blattidae	Latiblattella n. sp.
		Gryllidae	Cycloptilum sp.
			Tafalisca lurida
	DERMAPTERA	Labiduridae	Labidura riparia
	COLEOPTERA	Anthicidae	Sapintus fulvipes
		Curculionidae	Cryptorhynchus minutissimus
			Pseudoacalles sp.
			Gen. sp.
	THYSANOPTERA	Phlaeothripidae	Neurothrips magnafemoraus
		Thripidae	Pseudothrips inequalis
	CORRODENTIA	Peripsocidae	Ectopsocus sp. bμ
			Peripsocus pauliani
			Peripsocus stagnivagus
			Peripsocus sp. c
		Psocidae	Psocidus texanus
	HEMIPTERA	Aleyrodidae	Tetraleurodes sp.
		Coccidae	Ceroplastes sp.
		Miridae	Psallus conspurcatus
	NEUROPTERA	Chrysopidae	Chrysopa collaris
			Chrysopa rufilabris
	LEPIDOPTERA	Eucleidae	Alarodia slossoniae
		Hesperiidae	Phocides batabano
		Lymantriidae	Orgygia detrita
		Olethreutidae	Ecdytolopha sp.
		Phycitidae	Bema ydda
		Ptineidae	Nemapogon sp.
		Pyralidae	Gen. sp.
		Saturniidae	Automeris io
	DIPTERA	Hippoboscidae	Lynchia albipennis
			Olfersia sordida
	HYMENOPTERA	Bethylidae	Scleroderma macrogaster
		Chalcidae	Brachymeria psyche
		Eumenidae	Pachodynerus nasidens
		Formicidae	Camponotus tortuganus
			Colobopsis sp.
			Crematogaster ashmeadi
			Pseudomyrmex elongatus
		Ichneumonidae	Calliephialtes ferrugineus
			Casinaria texana
	ORDER UNK.	Fam. Unk.	Gen. sp.
ARACHNIDS	ARANEAE	Araneidae	Eustala sp. 1
			Nephila clavipes
		Salticidae	Hentzia palmarum
		Fam. Unk.	Gen. sp.
	ACARINA	Argasidae	Argas radiatus
		Ascidae	Arctoseius sp.
		Dermanyssidae	Ornithonyssus bursa
			Pellonyssus sp.
		Galumnidae	Galumna sp.
		Oribatulidae	Scheloribates sp.
		Phytoseiidae	Amblyseius sp.
OTHER	ISOPODA		Rhyscotus sp.
	DIPLOPODA	Polyxenidae	Lophoproctinus bartschi

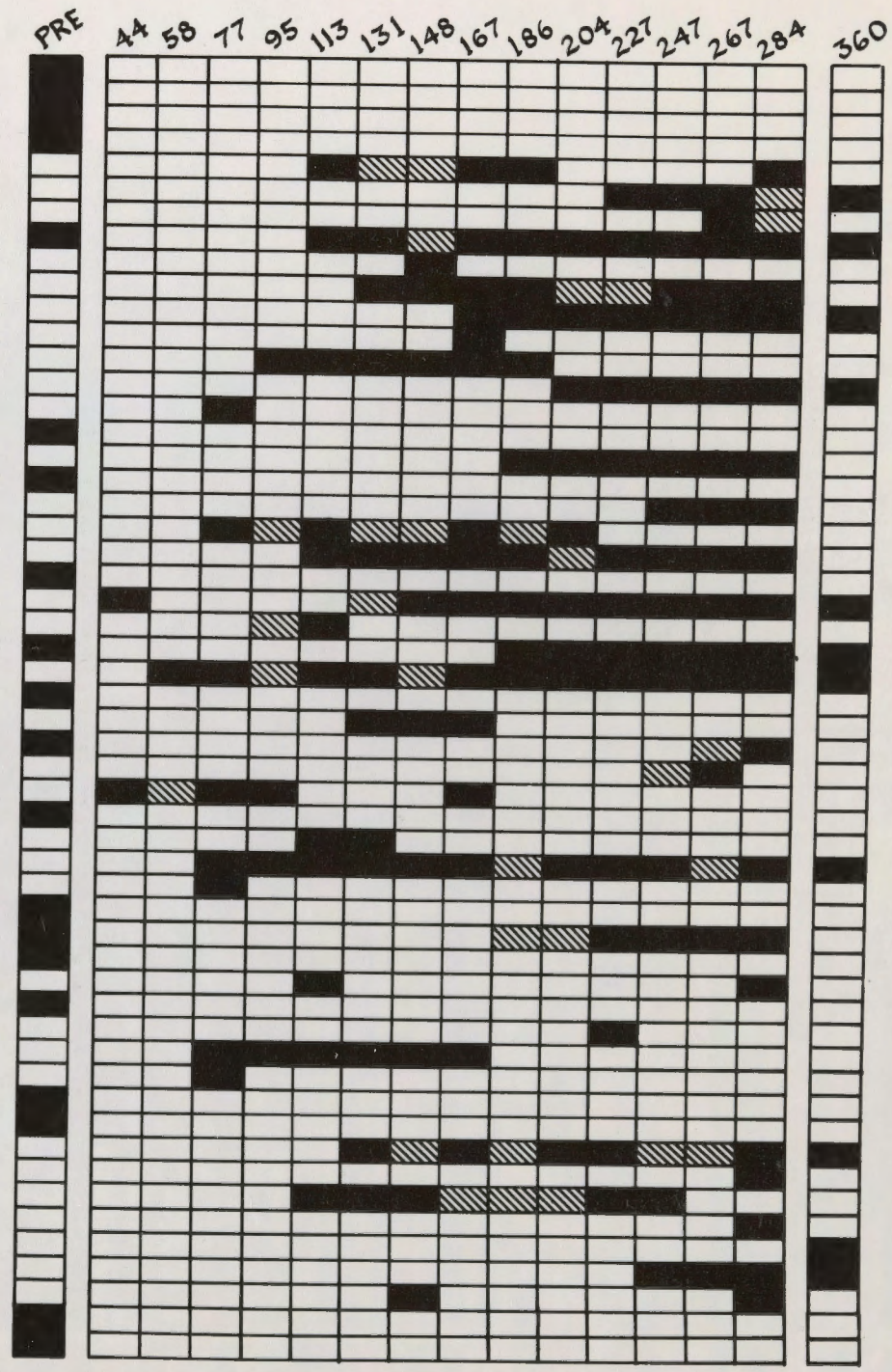


Table 3: Colonists on Island E2

INSECTS	EMBIOPTERA	Teratembiidae	Gen. sp.
	ORTHOPTERA	Blattidae	Aglaopteryx sp.
			Latiblattella n. sp.
			Latiblattella rehni
		Gryllidae	Cycloptilum sp.
			Cyrtoxipha sp.
			Orocharis gryllodes
			Tafalisca lurida
		Tettigoniidae	Turpilia rostrata
	ISOPTERA	Kalotermitidae	Kalotermes jouteli
			Neotermes castaneus
	COLEOPTERA	Anobiidae	Tricorynus sp.
		Anthicidae	Sapintus fulvipes
		Buprestidae	Actenodes aurovotata
			Chrysobothris sexfasciatus
			Chrysobothris tranquebarica
		Cerambycidae	Ataxia sp.
			Styloleptus biustus
		Chrysomelidae	Gen. sp.
		Cucujidae	Gen. sp.
		Curculionidae	Cryptorhynchus minutissimus
			Pseudoacalles sp.
		Lampyridae	Micronaspis floridana
		Oedemeridae	Copidita suturalis
			Oxacis sp.
			Oxycopis sp.
		Scolytidae	Poecilips rhizophorae
			Trischidias atoma
		Fam. Unk.	Gen. sp.
	THYSANOPTERA	Phlaeothripidae	Liothrips n. sp.
		Thripidae	Pseudothrips inequalis
		Fam. Unk.	Gen. sp.
	CORRODENTIA	Caeciliidae	Caecilius sp. n-b
		Lepidopsocidae	Echmepteryx hageni b
		Liposcelidae	Gen. sp.
		Peripsocidae	Peripsocus sp.
		Psocidae	Psocidus texanus
	HEMIPTERA	Acanaloniidae	Acanalonia latifrons
		Aleyrodidae	Aleurothrixus sp.
			Paraleyrodes sp. 1
			Paraleyrodes sp. 2
			Tetraleurodes sp.
		Cicadellidae	Scaphytopius sp.
		Cixiidae	Gen. sp.
		Flatidae	Flatoidinus punctatus
		Miridae	Psallus conspurcatus
		Pseudococcidae	Pseudococcus sp.
		Tropiduchidae	Neurotmeta brevieeps
		Fam. Unk.	Gen. sp.
	NEUROPTERA	Chrysopidae	Chrysopa collaris
			Chrysopa externa
			Chrysopa rufilabris
	LEPIDOPTERA	Geometridae	Oxydia sp.
		Hesperiidae	Phocides batabano
		Noctuidae	Melipotis sp.
		Olethreutidae	Eedytolopha sp.
		Phycitidae	Bema ydda
		Ptineidae	Nemapogon sp.
		Pyralidae	Gen. sp.
		Saturnidae	Automeris io
	DIPTERA	Cecidomyidae	Gen. sp.
		Culicidae	Aedes taeniorhynchus
		Syrphidae	Gen. sp.
		Fam. Unk.	Gen. sp.
	HYMENOPTERA	Bethylidae	Cephalonomia waterstoni
			Scleroderma macrogaster
		Braconidae	Apanteles hemileucae
			Callihormius bifasciatus
			Heterospilus sp.
			Iphiaulax epicus
		Chalcedectidae	Euchrysia sp.
		Chalcidae	Gen. sp.
		Encyrtidae	Ooencyrtus submetallicus
		Eumenidae	Pachodynerus nasidens
		Eupelmidae	Metapelma schwarzi
			Neanastatus sp.
			Gen. sp.
		Formicidae	Camponotus floridanus
			Camponotus tortuganus
			Crematogaster ashmeadi
			Monomorium floricola
			Paracryptocerus varians
			Pseudomyrmex elongatus
			Pseudomyrmex "flavidula"
			Tapinoma littorale
			Xenomyrmex floridanus
		Ichneumonidae	Calliephialtes ferrugineus
			Casinaria texana
		Sphecidae	Trypoxylon collinum
ARACHNIDS	ARANEAE	Araneidae	Argiope argentata
			Eustala sp. 1
			Eustala sp. 2
			Gasteracantha ellipsoides
			Gen. sp.
			Nephilia clavipes
		Clubionidae	Anyphaena sp.
			Aysha sp.
			Gen. sp. 1
		Gnaphosidae	Gnaphosa sp.
		Linyphiidae	Meioneta sp.
		Salticidae	Ballus sp.
			Hentzia palmarum
			Metacyrba undata
			Gen. sp. 11
		Segestriidae	Ariadna arthuri
		Tetragnathidae	Leucauge venusta
			Tetragnatha sp.
		Theridiidae	Gen. sp.
	ACARINA	Acaridae	Rhizoglyphus callae
		Bdellidae	Gen. sp.
		Cheyletidae	Cheyletia wellsi
		Dermanyssidae	Gen. sp.
		Entonyssidae	Entonyssus sp.
		Galumnidae	Galumna sp.
		Oribatulidae	Scheloribates sp.
		Phytoseiidae	Amblyseius sp.
		Tetranychidae	Tetranychus sp.
OTHER	ISOPODA		Rhyscotus sp.
	DIPLOPODA	Polyxenidae	Lophoproctinus bartschi

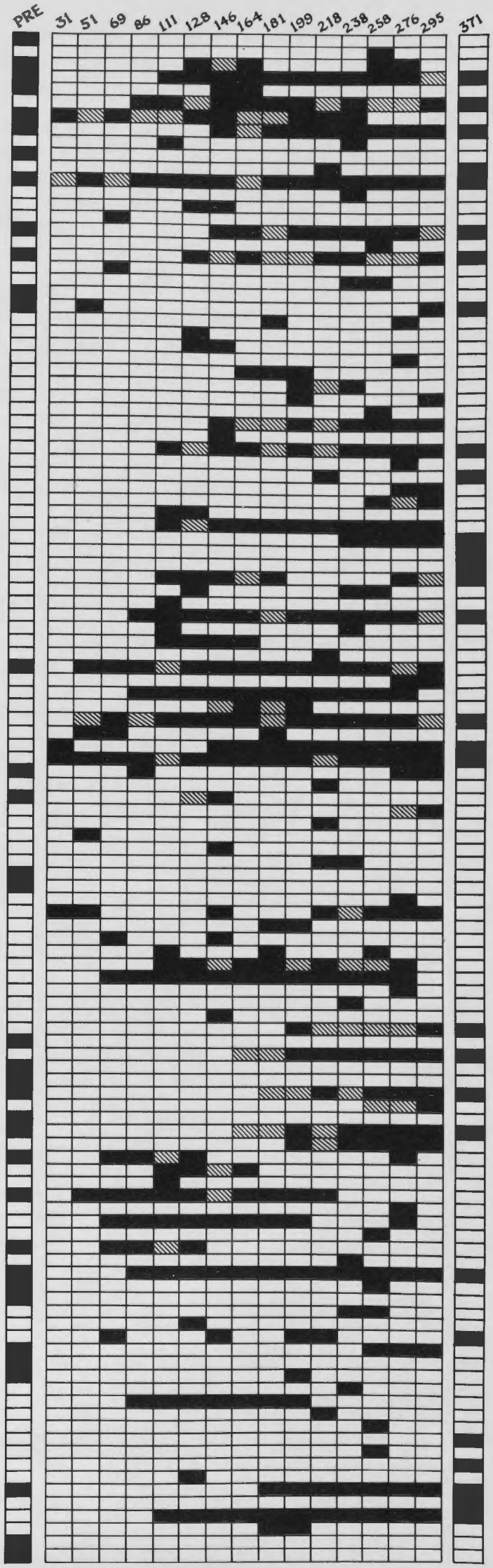
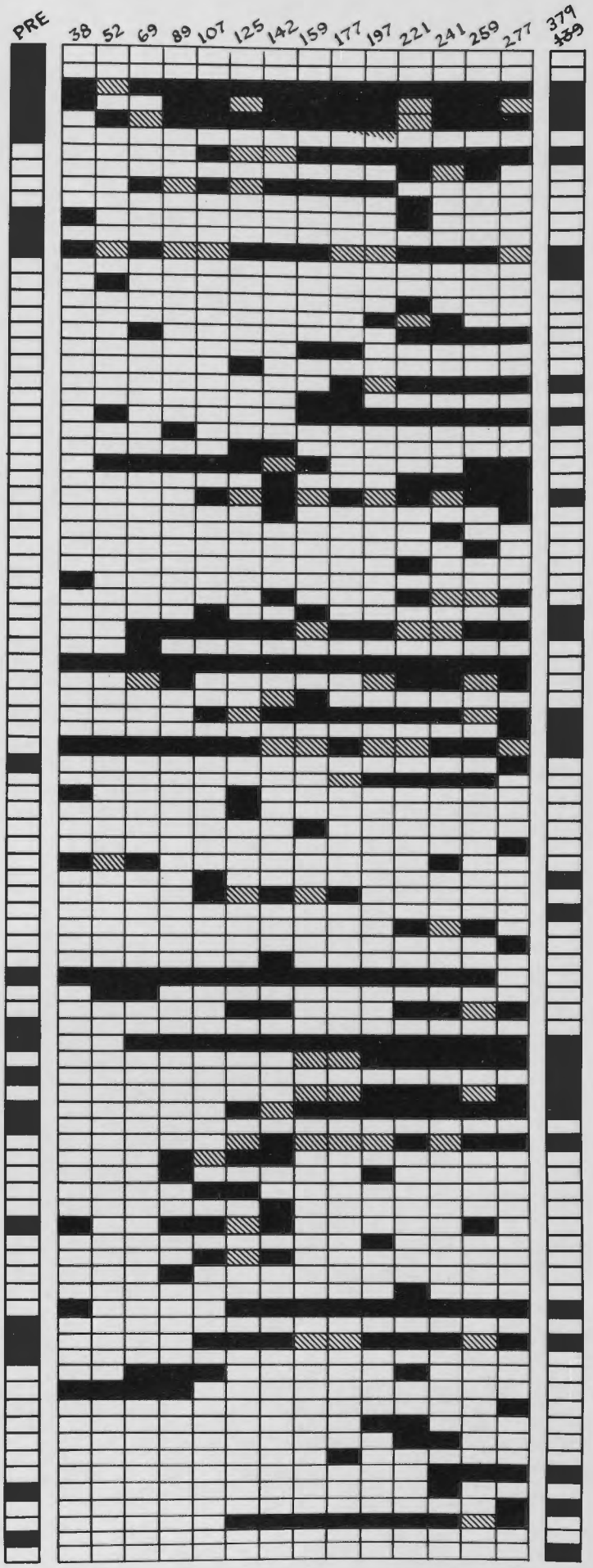


Table 4: Colonists on Island E3



INSECTS	COLLEMBOLA	Poduridae	Gen. sp.
	EMBIOPTERA	Teratembiidae	Diradius caribbeana
	ORTHOPTERA	Blattidae	Latiblattella n. sp.
		Gryllidae	Cycloptilum spectabile
			Tafalisca lurida
	ISOPTERA	Kalotermitidae	Kalotermes jouteli
	COLEOPTERA	Anobiidae	Tricorynus sp.
		Anthicidae	Sapintus fulvipes
		Buprestidae	Actenodes auroniata
			Chrysobothris tranquebarica
		Cerambycidae	Styloleptus biustus
		Curculionidae	Cryptorhynchus minutissimus
			Pseudoacalles sp.
		Lathridiidae	Melanophthalma floridana
		Oedemeridae	Oxacis sp.
			Oxycopis sp.
		Scolytidae	Trischidias atoma
	THYSANOPTERA	Phlaeothripidae	Haplothrips flavipes
			Liothrips n. sp.
			Neurothrips magnafemoralis
		Thripidae	Pseudothrips inequalis
		Fam. Unk.	Gen. sp.
	CORRODENTIA	Liposcelidae	Liposcelis bostrychophilus
		Peripsocidae	Ectopsocopsis cryptomeriae
			Ectopsocus sp. c
			Peripsocus pauliani
		Psocidae	Psocidus texanus
	HEMIPTERA	Aleyrodidae	Tetraleurodes sp.
		Anthocoridae	Dufouriellus afer
			Orius sp.
		Cicadellidae	Scaphytopius sp.
		Lygaeidae	Gen. sp. 2
		Membracidae	Gen. sp.
		Miridae	Psallus conspurcatus
		Nabidae	Carthasis decoratus
	NEUROPTERA	Chrysopidae	Chrysopa collaris
			Chrysopa externa
			Chrysopa rufilabris
	LEPIDOPTERA	Eucleidae	Alarodia slossoniae
		Geometridae	Oxydia sp.
		Hesperiidae	Phocides batabano
		Oiethreutidae	Ecdytolopha sp.
		Phycitidae	Bema ydda
		Ptineidae	Nemapogon sp.
		Saturniidae	Automeris io
	HYMENOPTERA	Bethylidae	Nesepyris floridanus
			Scleroderma macrogaster
			Gen. sp.
		Braconidae	Heterospilus sp.
			Iphiaulax epicus
			Macrocentrus sp.
		Chalcidae	Brachymeria psyche
			Gen. sp.
		Encyrtidae	Gen. sp.
		Eulophidae	Entedontini sp.
			Melittobia chalybii
		Eumenidae	Pachodynerus nasidens
		Eupelmidae	Gen. sp. 1
			Gen. sp. 2
		Formicidae	Colobopsis sp.
			Crematogaster ashmeadi
			Monomorium floricola
			Paracryptocerus varians
			Paratrechina bourbonica
			Pseudomyrmex elongatus
			Tapinoma littorale
			Xenomyrmex floridanus
		Ichneumonidae	Calliephialtes ferrugineus
			Casinaria texana
		Scelionidae	Probaryconus sp.
			Telonemus sp.
		Sphecidae	Trypoxylon collinum
		Vespidae	Gen. sp.
ARACHNIDS	ARANEAE	Araneidae	Eustala sp. 1
			Gasteracantha ellipsoides
		Clubionidae	Anyphaena sp.
			Aysha sp.
		Gnaphosidae	Sergiolus sp.
		Salticidae	Hentzia palmarum
		Segestriidae	Ariadna arthuri
		Tetragnatnidae	Leucauge venusta
			Tetragnatha antillana
		Theridiidae	Gen. sp.
	ACARINA	Acaridae	Tyrophagus putrescentiae
		Ascidae	Asca sp.
		Dermanyssidae	Gen. sp.
		Eupodidae	Eupodes sp. nr. fusifer
		Galumnidae	Galumna sp.
		Oribatulidae	Scheloribates sp.
		Phytoseiidae	Amblyseius sp.
OTHER	DIPLOPODA	Polyxenidae	Lophoproctinus bartschi
	ISOPODA		Rhyscotus sp.

Table 5: Colonists on Island ST2

INSECTS	EMBIOPTERA	Teratembiidae	Diradius caribbeana
	ORTHOPTERA	Blattidae	Latiblattella n. sp.
		Gryllidae	Cycloptilum sp.
			Cyrtoxipha sp.
			Tafalisca lurida
	ISOPTERA	Kalotermitidae	Kalotermes jouteli
	COLEOPTERA	Anobiidae	Tricorynus sp.
		Anthicidae	Gen. sp.
		Buprestidae	Gen. sp.
		Cerambycidae	Styloleptus biustus
		Curculionidae	Cryptorhynchus sp.
			Pseudocalles sp.
		Lathrididiidae	Melanophthalma floridana
		Oedemeridae	Oxycopis sp.
	THYSANOPTERA	Phlaeothripidae	Haplothrips flavipes
			Liothrips n. sp.
		Thripidae	Pseudothrips inequalis
	CORRODENTIA	Liposcelidae	Liposcelis bostrychophilus
		Peripsocidae	Ectopsocus sp.
			Peripsocus pauliani
			Peripsocus stagnivagus
		Psocidae	Psocidus texanus
	HEMIPTERA	Aleyrodidae	Tetraleurodes sp.
		Lygaeidae	Blissus insularis
			Gen. sp. 2
	NEUROPTERA	Chrysopidae	Chrysopa collaris
			Chrysopa externa
			Chrysopa rufilabris
	LEPIDOPTERA	Eucleidae	Alarodia slossoniae
		Geometridae	Gen. sp.
		Hesperiidae	Phocides batabano
		Lymantriidae	Orgygia detrita
		Olethreutidae	Ecdytolopha sp.
		Phycitidae	Bema ydda
		Ptineidae	Nemapogon sp.
		Pyraustidae	Gen. sp.
	DIPTERA	Fam. Unk. 1	Gen. sp.
		Fam. Unk. 2	Gen. sp.
	HYMENOPTERA	Bethylidae	Scleroderma macrogaster
		Braconidae	Iphiaulax epicus
			Macrocentrus sp.
			Gen. sp.
		Chalcidae	Brachymeria psyche
			Gen. sp.
		Eumenidae	Pachodynerus nasidens
		Eupelmidae	Gen. sp.
		Formicidae	Camponotus floridanus
			Colobopsis sp.
			Crematogaster ashmeadi
			Crematogaster atkinsoni
			Paracryptocerus varians
			Pseudomyrmex elongatus
			Tapinoma littorale
			Xenomyrmex floridanus
		Ichneumonidae	Calliephialtes ferrugineus
			Casinaria texana
		Sphecidae	Trypoxylon collinum
		Apocrita	Gen. sp.
ARACHNIDS	ARANEAE	Araneidae	Eustala sp. 1
			Eustala sp. 2
			Gasteracantha ellipsoides
			Nephila clavipes
		Clubionidae	Anyphaena sp.
			Aysha velox
		Salticidae	Hentzia palmarum
		Segestriidae	Ariadna arthuri
		Tetragnathidae	Leucauge venusta
			Tetragnatha sp.
		Theridiidae	Theridion sp.
	ACARINA	Ascidae	Arctoseius sp.
			Asca sp.
		Bdellidae	Bdella sp.
		Eupodidae	Eupodes sp. nr. fusifer
		Oribatulidae	Scheloribates sp.
		Phytoseiidae	Amblyseius sp.
		Veigaiidae	Veigaia sp.
		Fam. Unk.	Gen. sp.
	CHELONETHIDA	Cheliferidae	Tyrannochelifer n. sp.
OTHER	PAUROPODA		Gen. sp.
	DIPLOPODA	Polyxenidae	Lophoproctinus bartschi

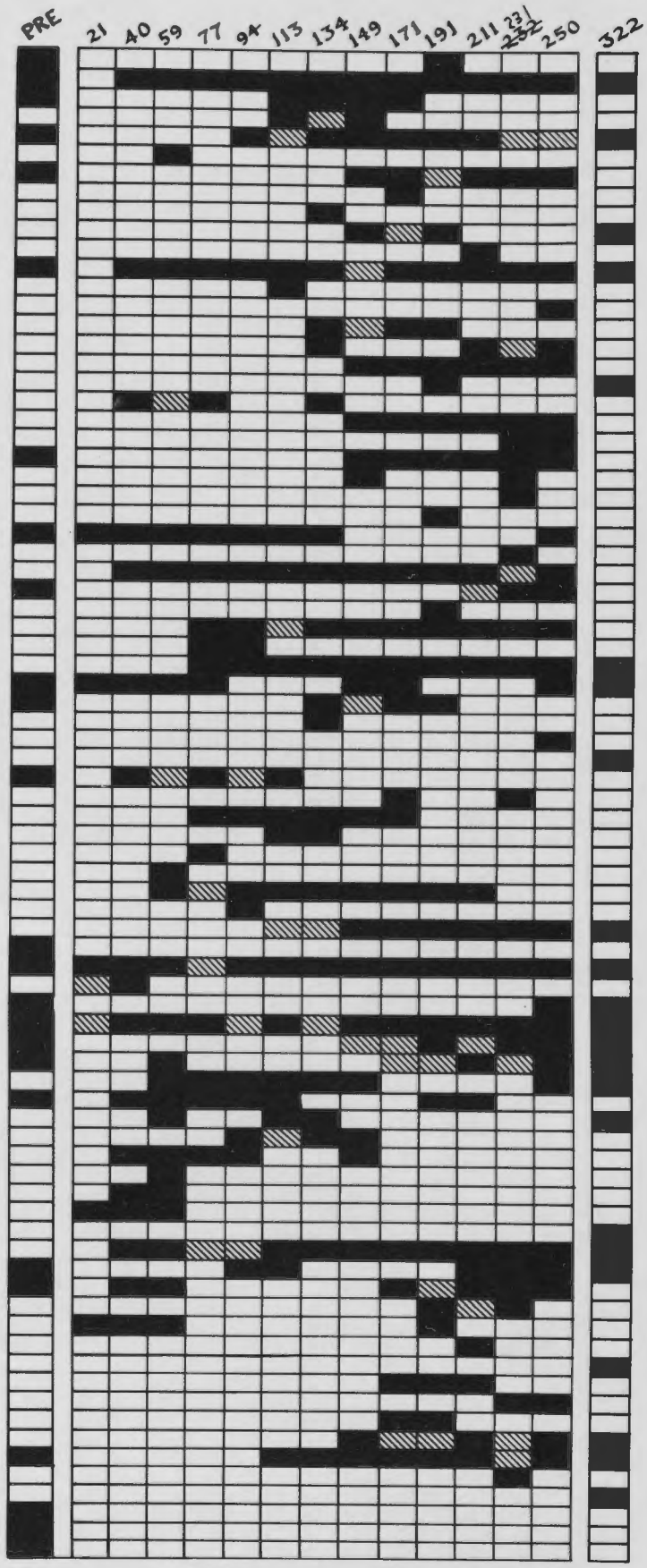


Table 6: Colonists on Island E7

INSECTS	EMBIOPTERA	Teratembiidae	Gen. sp.
	ORTHOPTERA	Blattidae	Latiblattella n. sp.
		Gryllidae	Cycloptilum sp.
			Tafalisca lurida
	DERMAPTERA	Labiduridae	Labidura riparia
	COLEOPTERA	Anobiidae	Tricorynus sp.
		Anthicidae	Gen. sp.
		Buprestidae	Actenodes auronotata
			Chrysobothris tranquebarica
			Gen. sp.
		Cerambycidae	Leptostylus sp.
			Styloleptus biustus
		Cucujidae	Gen. sp.
		Curculionidae	Pseudocalles sp.
		Oedemeridae	Gen. sp.
		Scydmaenidae	Gen. sp.
	THYSANOPTERA	Phlaeothripidae	Haplothrips flavipes
			Neurothrips magnafemoralis
		Thripidae	Pseudothrips inequalis
	CORRODENTIA	Archipsocidae	Archipsocus panama
		Liposcelidae	Embidopsocus laticeps
			Liposcelis bostrychophilus
		Myopsocidae	Lichenomima sp. b
			Gen. sp.
		Peripsocidae	Ectopsocopsis cryptomeriae
			Ectopsocus maindroni
			Peripsocus pauliani
			Peripsocus stagnivagus
			Peripsocus sp. b
			Peripsocus sp. c
		Psocidae	Psocidus texanus
			Psocidus sp. nr. bisignatus
			Psocidus sp. 1
			Psocidus sp. 2
	HEMIPTERA	Nabidae	Carthasis decoratus
			Metatropiphorus belfragei
		Pseudococcidae	Pseudococcus sp.
	NEUROPTERA	Chrysopidae	Chrysopa collaris
			Chrysopa rufilabris
	LEPIDOPTERA	Hesperiidae	Phocides batabano
		Lymantriidae	Orgygia detrita
		Olethreutidae	Ecdytolopha sp.
		Phycitidae	Bema ydda
		Pyralidae	Nemapogon sp.
	HYMENOPTERA	Bethylidae	Cephalonomia waterstoni
			Scleroderma macrogaster
		Braconidae	Aparteles hemileucae
			Iphiaulax epicus
		Chalcedectidae	Euchrysia sp.
		Chalcidae	Gen. sp.
		Eumenidae	Pachodynerus nasidens
		Formicidae	Camponotus floridanus
			Camponotus planatus
			Crematogaster ashmeadi
			Hypoponera opacior
			Paracryptocerus varians
			Paratrechina bourbonica
			Pseudomyrmex elongatus
			Pseudomyrmex "flavidula"
			Xenomyrmex floridanus
		Ichneumonidae	Calliephialtes ferrugineus
			Casinaria texana
		Scelionidae	Probaryconus sp.
		Sphecidae	Trypoxylon collinum
		Vespidae	Gen. sp.
ARACHNIDS	ARANEAE	Araneidae	Argiope argentata
			Eustala sp. 1
			Eustala sp. 2
			Gasteracantha ellipsoides
			Mangora sp.
			Nephila clavipes
		Clubionidae	Aysha sp.
		Dictynidae	Dictyna sp.
		Gnaphosidae	Sergiolus sp.
		Pisauridae	Dolomedes sp.
		Salticidae	Hentzia palmarum
			Maevia vittata
			Paraphidippus flavus
			Stoidis aurata
		Segestriidae	Ariadna arthuri
		Tetragnathidae	Leucauge venusta
			Tetragnatha antillana
		Theridiidae	Argyrodes nephilae
			Theridion adamsoni
			Theridion atropunctatum
		Thomisidae	Misumenops sp.
		Uloboridae	Uloborus sp.
		Fam. Unk.	Gen sp.
	ACARINA	Acaridae	Tyrophagus putrescentiae
		Ascidae	Proctolaelaps hypudaei
			Proctolaelaps pygmaeus
		Dermanyssidae	Ornithonyssus bursa
		Galumnidae	Galumna sp.
		Phytoseiidae	Amblyseius sp.
		Sarcoptidae	Gen. sp.
		Tydeidae	Triophtydeus sp.
	CHELONETHIDA	Cheliferidae	Tyrannochelifer sp.
OTHER	ISOPODA		Rhyscotus sp.
	CHILOPODA	Oryidae	Orphnaeus brasilianus

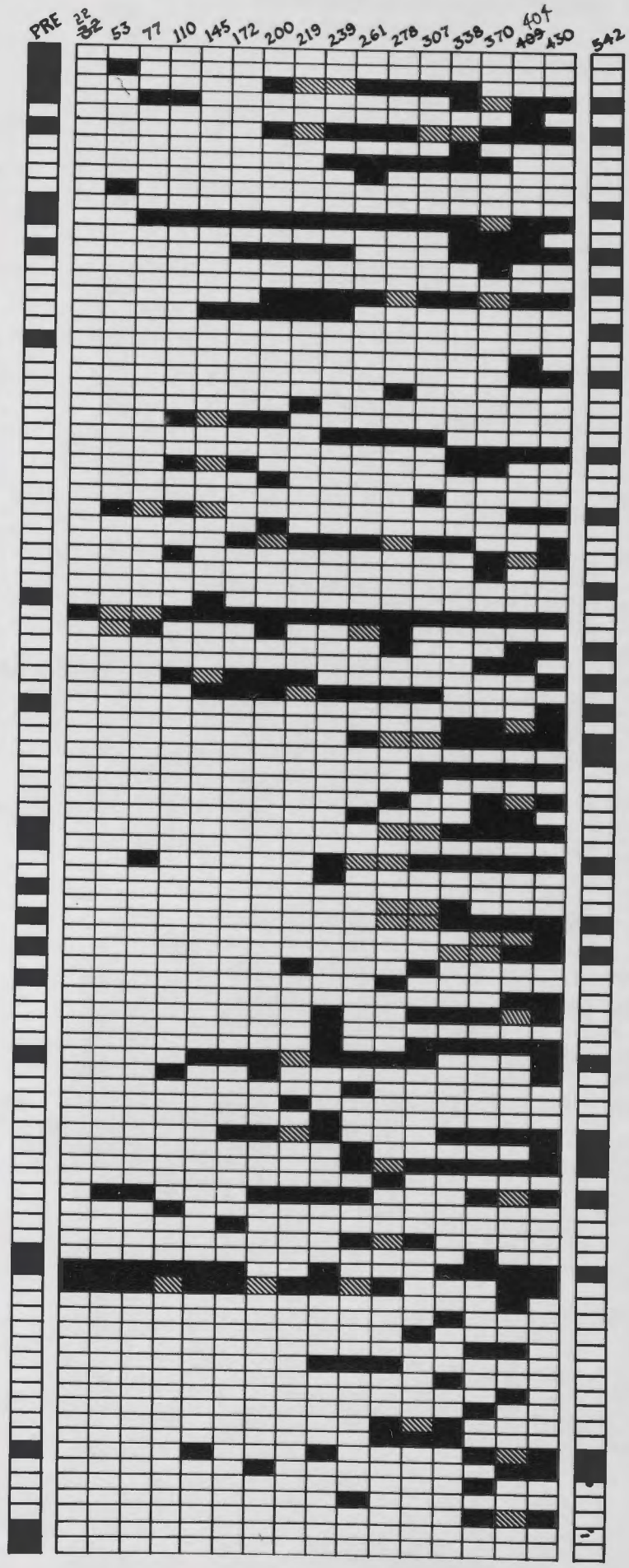


Table 7: Colonists on Island E9

INSECTS	ORTHOPTERA	Gryllidae	Cycloptilum sp.
			Cyrtoxipha confusa
			Orocharis sp.
	DERMAPTERA	Labiduridae	Labidura riparia
	COLEOPTERA	Anobiidae	Cryptorama minutum
			Tricorynus sp.
		Anthicidae	Sapintus fulvipes
			Vacusus vicinus
		Buprestidae	Actenodes auronotata
			Chrysobothris tranquebarica
		Cantharidae	Chauliognathus marginatus
		Cerambycidae	Styloleptus biustus
		Curculionidae	Cryptorhynchus minutissimus
			Pseudoacalles sp.
		Lathridiidae	Holoparamecus sp.
		Oedemeridae	Oxacis sp.
		Fam. Unk.	Gen. sp.
	THYSANOPTERA	Phlaeothripidae	Haplothrips flavipes
			Neurothrips magnafemoralis
		Thripidae	Pseudothrips inequalis
	CORRODENTIA	Caeciliidae	Caecilius sp. np.
		Lachesillidae	Lachesilla n. sp.
		Lepidopsocidae	Echmepteryx hageni b
		Liposcelidae	Belaphotroctes okalensis
			Embidopsocus laticeps
			Liposcelis sp. not bostrychophilus
		Peripsocidae	Ectopsocus sp. bμ
			Peripsocus stagnivagus
		Psocidae	Psocidus texanus
			Psocidus sp. 1
		Trogiomorpha	Gen. sp.
	HEMIPTERA	Anthocoridae	Dufouriellus afer
		Cixiidae	Oliarus sp.
		Miridae	Psallus conspurcatus
		Pentatomidae	Oebalus pugnax
		Fam. Unk.	Gen. sp.
	NEUROPTERA	Chrysopidae	Chrysopa collaris
			Chrysopa externa
			Chrysopa rufilabris
	LEPIDOPTERA	Eucleidae	Alarodia slossoniae
		Olethreutidae	Ecdytolopha sp.
		Phycitidae	Bema ydda
		Psychidae	Oiketicus abbottii
		Ptineidae	Nemapogon sp.
		Pyralidae	Tholeria reversalis
		Saturniidae	Automeris io
		Fam. Unk.	Gen. sp.
	DIPTERA	Hippoboscidae	Olfersia sordida
		Fam. Unk.	Gen. sp.
	HYMENOPTERA	Braconidae	Apanteles hemileucae
			Apanteles marginiventris
			Callihormius bifasciatus
			Ecphylus n. sp. nr. chramesi
			Iphiaulax epicus
		Chalcidae	Gen. sp. 1
			Gen. sp. 2
			Gen. sp. 3
			Gen. sp. 4
		Eulophidae	Euderus sp.
		Eumenidae	Pachodynerus nasidens
		Eupelmidae	Gen. sp.
		Formicidae	Brachymyrmex sp.
			Camponotus floridanus
			Camponotus sp.
			Crematogaster ashmeadi
			Monomorium floricola
			Paracryptocerus varians
			Pseudomyrmex elongatus
			Pseudomyrmex "flavidula"
			Tapinoma littorale
			Xenomyrmex floridanus
			Gen. sp.
		Ichneumonidae	Calliephialtes ferrugineus
			Casinaria texana
		Pteromalidae	Urolepis rufipes
		Sphecidae	Trypoxylon collinum
		Vespidae	Polistes sp.
ARACHNIDS	ARANEAE	Araneidae	Argiope argentata
			Eriophora sp.
			Eustala sp.
			Gasteracantha ellipsoides
			Metepeira labyrinthea
			Nephila clavipes
		Clubionidae	Aysha sp.
		Dictynidae	Dictyna sp.
		Gnaphosidae	Sergiolus sp.
		Linyphiidae	Meioncta sp.
		Lycosidae	Pirata sp.
		Salticidae	Hentzia palmarum
		Scytodidae	Scytodes sp.
		Tetragnathidae	Leucauge venusta
			Tetragnatha antillana
			Tetragnatha sp. 2
		Theridiidae	Gen. sp.
		Uloboridae	Uloborus sp.
	ACARINA	Argasidae	Argas radiatus
		Ascidae	Lasioseius sp.
			Melichares sp.
		Bdellidae	Bdella sp.
		Carpoglyphidae	Carpoglyphus lactis
		Erythraeidae	Sphaerolophus sp.
		Galumnidae	Galumna sp.
		Phytoseiidae	Amblyseius sp.
OTHER	ISOPODA		Rhyscotus sp.
	CHILOPODA	Oryidae	Orphnaeus brasilianus

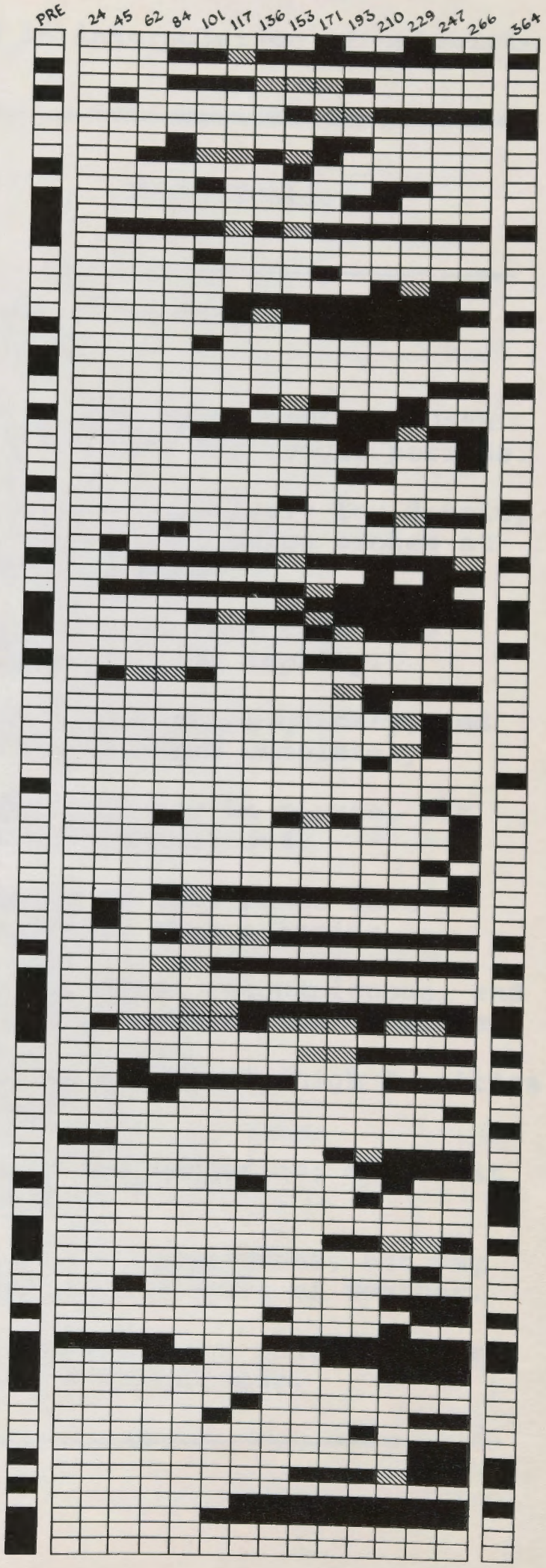


TABLE 8. General rules applied in interpolation of colonists

Animal	# cycles Interpolated	Justification
Ants. Workers seen first	2 (previous)	Conservative on physiological grounds
Ants. Queen seen first	indefinite	Obvious for short periods. Data of E9 support for longer periods.
Deep-boring beetles	2+	Present in relatively low density and only 10% of twigs broken at each monitoring.
Small leaf dwellers	1-2	Inconspicuous, but densities usually increase rapidly.
Bark-dwellers	1	Often become dense quickly, and habitat examined completely.
Araneids	1	Spiderlings may be minute, but webs are conspicuous.
Tetragnatha	2	Position of webs makes less conspicuous than araneids.
Salticids	2-3	Furtive, often inconspicuous, and usually present in low densities.
Anyphaenids	1	Build up relatively high densities quickly.
Small crawlers	2	Usually low densities; difficult to record.
Fliers	2	Frequently conspicuous, but may be inactive because of weather.
Caterpillars	1 (usually)	No generalization possible; large ones are conspicuous.

1.5 inches. The precise amount for all months is quite variable, however, and there are obviously no extreme dry or wet seasons. Wind is also relatively constant over the year in both speed and direction: it averages about 11 mph from the eastern quadrant.

In those species whose dispersal period is not governed by an endogenous annual cycle (probably the majority of the Keys pool), the relative climatic uniformity should dictate continued year-long dispersal. Another consideration is that about half the species of the Florida Keys terrestrial arthropods are of antillean rather than nearctic origin, and their tropical character would tend to produce dispersal throughout the year.

These theoretical arguments are buttressed by several experimental observations. First was the presence of all life stages, including dispersal forms, of many species of insects and spiders throughout the year. We can make no quantitative assertions, but it was observed that there were no striking seasonal decreases among the common mangrove inhabitants in either number or activity (including flight) except for mosquitoes, which were much more numerous in the summer.

We had the good fortune to be present February 26, 1967, when the temperature at Key West fell briefly to 49° F., the lowest reading in several years. Our surveys during that

cold spell revealed no apparent mortality or even great lessening of activity of mangrove inhabitants other than a decrease in flight activity quite normal for the prevailing wind speed.

Finally, that propagules were constantly hitting our islands is incontrovertible from the data summarized in Tables 2-7. Moreover, these data provide no clear indication of seasonality in the dispersal of any taxon. The colonization of E7, defaunated approximately half a year before the other islands, should certainly have manifested any strong seasonal component. Yet in both form and specifics (Table 6 and Graph 2) it is consistent with the colonization of the other islands.

PATTERNS OF COLONIZATION

As would be expected in a system involving but one plant, succession in its usual sense, a progression of discrete and relatively stable communities, did not occur. This does not imply a lack of order in the time course of colonization; indeed, the invasion of species was remarkably regular. But it was not accompanied by wholesale extinction of distinct animal associations.

Several broad patterns are nevertheless evident. First, the earliest immigrants on all islands included both strong

fliers (especially moths and wasps) and weak or non-fliers (particularly psocopterans, chrysopids, and spiders), but the latter built up large populations more rapidly and became numerically dominant. That wind should transport many of the early invaders is not surprising. The first animal recorded on Krakatau after its eruption was a spiderling (Cotteau, 1885), while psocopterans (including wingless nymphs) and spiders are prominent in aerial plankton samples (Glick, 1939). But their success in colonization deserves further comment. The food supply for psocopterans, algal and lichen growth on the mangrove itself, is evidently sufficient to allow much larger populations than one normally finds on undisturbed Rhizophora islands. This implies that on untreated islands there may be predation by animals not present on recently defaunated islands. In fact, we have observed the ants Pseudomyrmex elongatus and Pseudomyrmex "flavidula" (both of which colonized later) carrying apparently freshly killed psocopterans to their nests. Running and jumping spiders can, of course, eat the psocopterans. Maevia vittata (Salticidae) was seen catching a Psocidus texanus adult on E7, while the webs of even small araneid spiderlings commonly trapped transient flies, especially tipulids and ceratopogonids.

Although it still involves only a relatively small subset of the entire Florida Keys fauna, colonization by these

early weak fliers was more variable than in other classes of arthropods, both in time on individual islands and at any given time among islands. The psocopterans were particularly opportunistic; from the second month after defaunation there were usually 1-4 species on each island at any monitoring period, but over the course of the experiment a total of 24 species were involved. Although certain psocopterans, especially species of Psocidus and Peripsocus, were generally more prominent than others there was little correlation among the sets of psocopterans found on different islands. Furthermore, as can be seen on the Corrodentia sections of Tables 2-7, many psocopterans persisted for less than a month. As a group they invaded and multiplied readily, and went extinct almost as readily. On E7 (Table 6) only five species of the 15 colonists remained as long as two months.

Spiders as a group were less opportunistic than psocopterans but their colonization was much more variable than that of most later colonists. Although the majority of the 36 spider species which colonized the islands followed the pattern just described for the psocopterans - that is, they immigrated readily and were extinguished quickly, and occurred on but one or two islands - a few species behaved quite differently. Eustala sp., Tetragnatha sp., Leucauge venusta, Hentzia palmarum, and Aysha velox in particular colonized most of the islands and usually persisted for at least several months.

These include most of the spiders found on the islands before defaunation.

Wasps present a similarly heterogeneous picture of colonization, many species appearing on one or two islands and vanishing rapidly while a few, notably Pachodynerus nasidens, Scleroderma macrogaster, and Calliephialtes ferrugineus, colonized many islands and were not swiftly extinguished. Mites did not invade as early as did wasps and spiders but displayed the same pattern of many transients occurring with a few persistent and recurring colonists. Most of the 20-odd species of Acarina were recorded from one or two islands only and disappeared within a month, while Amblyseius sp. and Galumna sp. were omnipresent and their populations long-lived.

In view of evidence that the majority of the arthropod species are obligate transients on these tiny islands, destined for extinction within a few days, and that many colonizations (perhaps 2/3) are not recorded (Simberloff, 1968), it seems probable that the apparent correlation in the spiders, mites, and wasps between mean length of persistence and number of islands colonized is artifactual. For if a species with a very high initial probability of extinction and another with a very low initial probability of extinction (long expected persistence time) each invaded equally frequently all six islands, we would expect to see the former on one or two islands only and the latter on most or all of them.

In sharp contradistinction to the relatively unordered patterns of colonization previously described is the regularity of colonization by thrips, lepidopterans, orthopterans, and ants. The last three groups, particularly the ants, are ecological dominants of an undisturbed mangrove animal community.

Only five species of thrips colonized the islands, of which four were widespread among the islands, and almost all invasions occurred 4-5 months after defaunation. Most thysanopteran colonizations endured for at least three months; large populations were occasionally produced but rarely persisted - the late colonizing ants may have attacked thrips. All species commonly immigrated about the same time; in other words, there was no consistent order of colonization.

Of about 30 lepidopteran species known from mangrove and a few hundred from the general Keys fauna, only eight commonly colonized the experimental islands, if we do not count the two or three fine-grained foragers discussed earlier. All eight were recorded more than once, and six were widespread. Most colonizations were sustained and many involved sizable populations. There was a somewhat predictable order of invasion, with Phocides batabano, Bema ?ydda, and Ecdytolopha sp. the normal first arrivals, Nemapogon sp. somewhat later, and Alarodia slossoniae and Automeris io usually not seen until about 200 days.

The orthopteroids colonized still more predictably. Of perhaps 25 species that occur in mangrove and 60 or more that occur in the Keys as a whole, only nine invaded the experimental islands. If the two very near islands (E2 and E7) are discounted, only four species were involved and all have multiple records. These four were rarely extinguished and two, the green tree cricket Cyrtoxipha confusa and roach Latiblattella n. sp. produced large populations. The small number of species precludes a statistically sound statement on order of colonization, but it seemed subjectively that all were capable of early invasion.

The ants displayed the most orderly pattern of colonization. These insects are also numerically and probably energetically the dominant animal on all small mangrove islands. Of the more than 50 species found in the Keys, 20 species inhabit Keys red mangrove and about 12 of these normally occur on small islands. The pre-defaunation surveys revealed a highly ordered fall-off of ant species in two directions. First, on islands of equal size but varying distance from source area the most distant islands contain Crematogaster ashmeadi, those somewhat nearer both the Crematogaster and Pseudomyrmex elongatus, those nearer still these two species plus Paracryptocerus varians, Tapinoma littorale, and Camponotus (Colobopsis) sp., and islands near shore most or all of the above species plus one or more

species of Camponotus, Pseudomyrmex "flavidula", Monomorium floricola, and Xenomyrmex floridanus.

If instead one fixes a distance (usually small) from the source area and examines islands of increasing size, he generally finds on the smallest bush (ca. 2 ft. high) Crematogaster ashmeadi; on slightly larger bushes C. ashmeadi and/or Pseudomyrmex elongatus; on small trees these two with perhaps two species drawn from among Paracryptocerus, Tapinoma, Colobopsis, Xenomyrmex, and Monomorium; and on islands the size of our experimental ones the full complement expected on an island of the appropriate distance from source. In short, the ability to colonize increasingly smaller islands parallels closely the ability to colonize increasingly distant ones.

The order of colonization by ants of the experimental islands (Table 9) indicates a curious zoogeographic analog of Haeckel's biogenetic law. In almost every instance Crematogaster ashmeadi was the first colonist, even on the two near islands (E2 and E7) where it was not present before defaunation. On all but the most distant island (E1) Pseudomyrmex elongatus was an early and prominent colonist. Moreover, the small subset of the mangrove ants which comprised the remainder of the colonists was almost identical to that found on small islands as one moves nearer to the source areas. Only three extinctions were observed, and two

TABLE 9. Colonization of experimental islands by ants

Island	E1	E2	E3	E7	E9	ST2
Ants before defaunation	5 6 11	3 8 9 11 13 14	5 6 9 11 13	1 2 9 11 14	4 8 9 11 12 13	5 6 9 11 13 14
Ant colonists in order of colonization	6	6 14 11 1	6 11 14 8 10 9	6 16* 1 10 11 14 12	12 15* 1 6 11 14 9	6 7* 11 14 1 13 9

* = extinction

1 - Camponotus floridanus
2 - Camponotus planatus
3 - Camponotus tortuganus
4 - Camponotus sp.
5 - Camponotus (Colobopsis) sp.
6 - Crematogaster ashmeadi
7 - Crematogaster atkinsoni
8 - Monomorium floricola
9 - Paracryptocerus varians
10 - Paratrechina bourbonica
11 - Pseudomyrmex elongatus
12 - Pseudomyrmex "flavidula"
13 - Tapinoma littorale
14 - Xenomyrmex floridanus
15 - Brachymyrmex sp.
16 - Hypoponera opacior

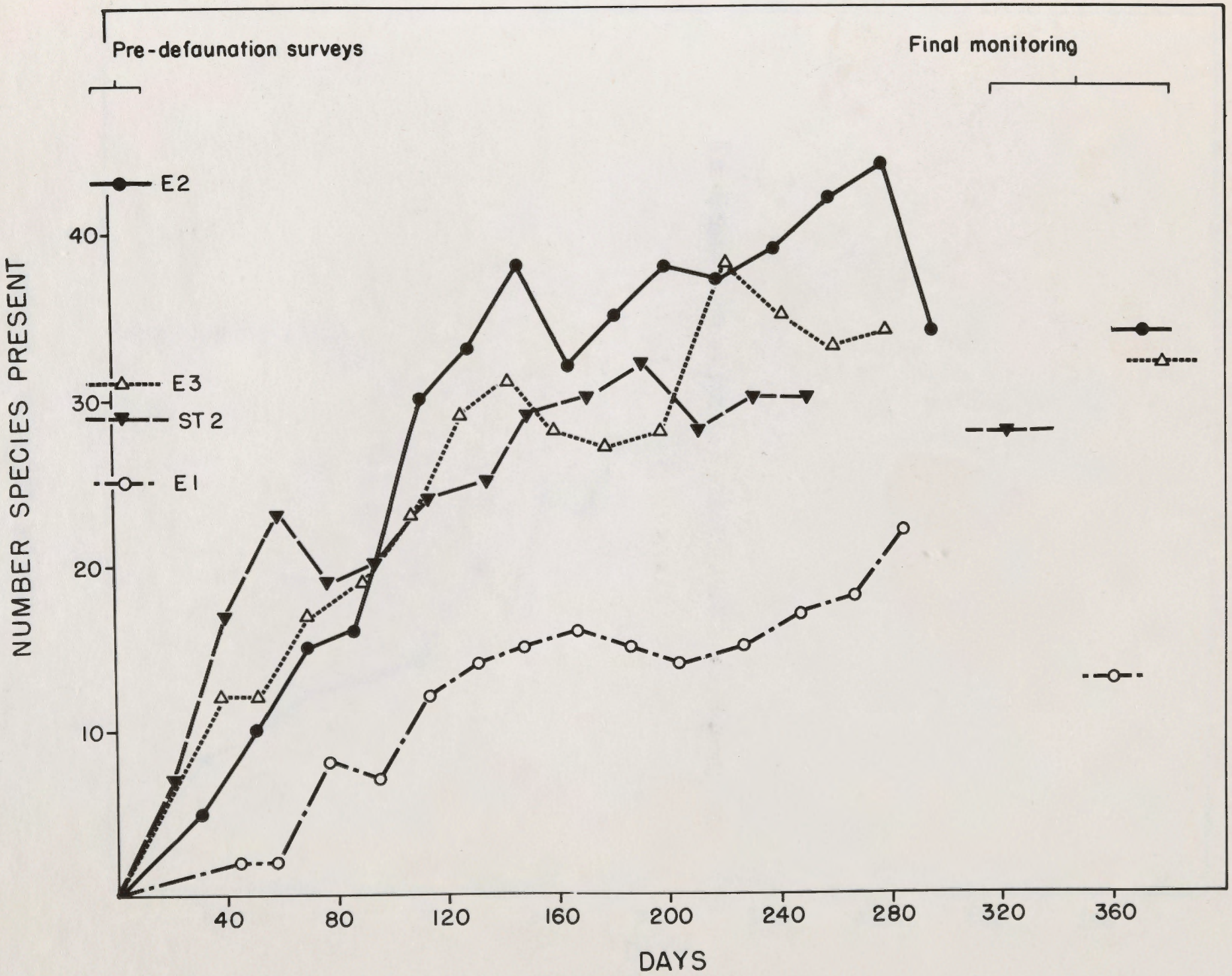
were of species believed unable to nest in mangrove. As a group the ants colonized later than most other taxa and at the close of the first phase of our study (April 1968) few species had built up populations numerically similar to those on untreated islands.

COLONIZATION CURVES

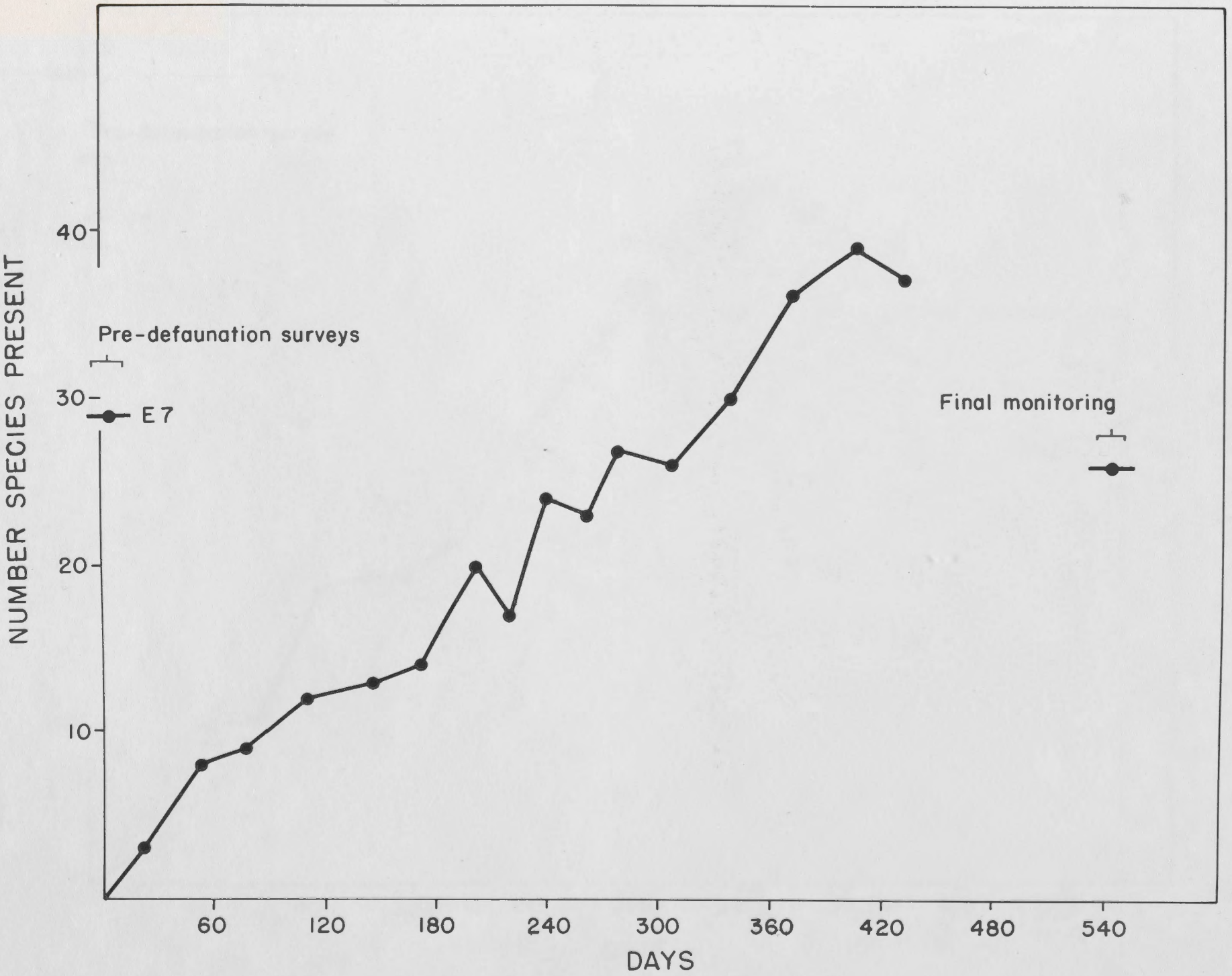
Graphs 1-3 show the original numbers of species present and the colonization curves (#spp. present vs. time) for the experimental islands.

Estimation of the number of species present before defaunation and after regular monitoring had ended is complicated by two factors. First, as can be seen from Tables 2-7, a few colonists are inferred present at each regular post-defaunation monitoring period without actually having been observed because they were recorded at both preceding and subsequent periods. Since there was but one pre-defaunation survey, its total species number must be increased by the mean number of species inferred present without having been observed for all regular post-defaunation monitorings after an approximate equilibrium $\hat{S}$ had been reached. The last four regular monitorings were used for this purpose, since the population structure then was probably closest to that before defaunation. A similar correction

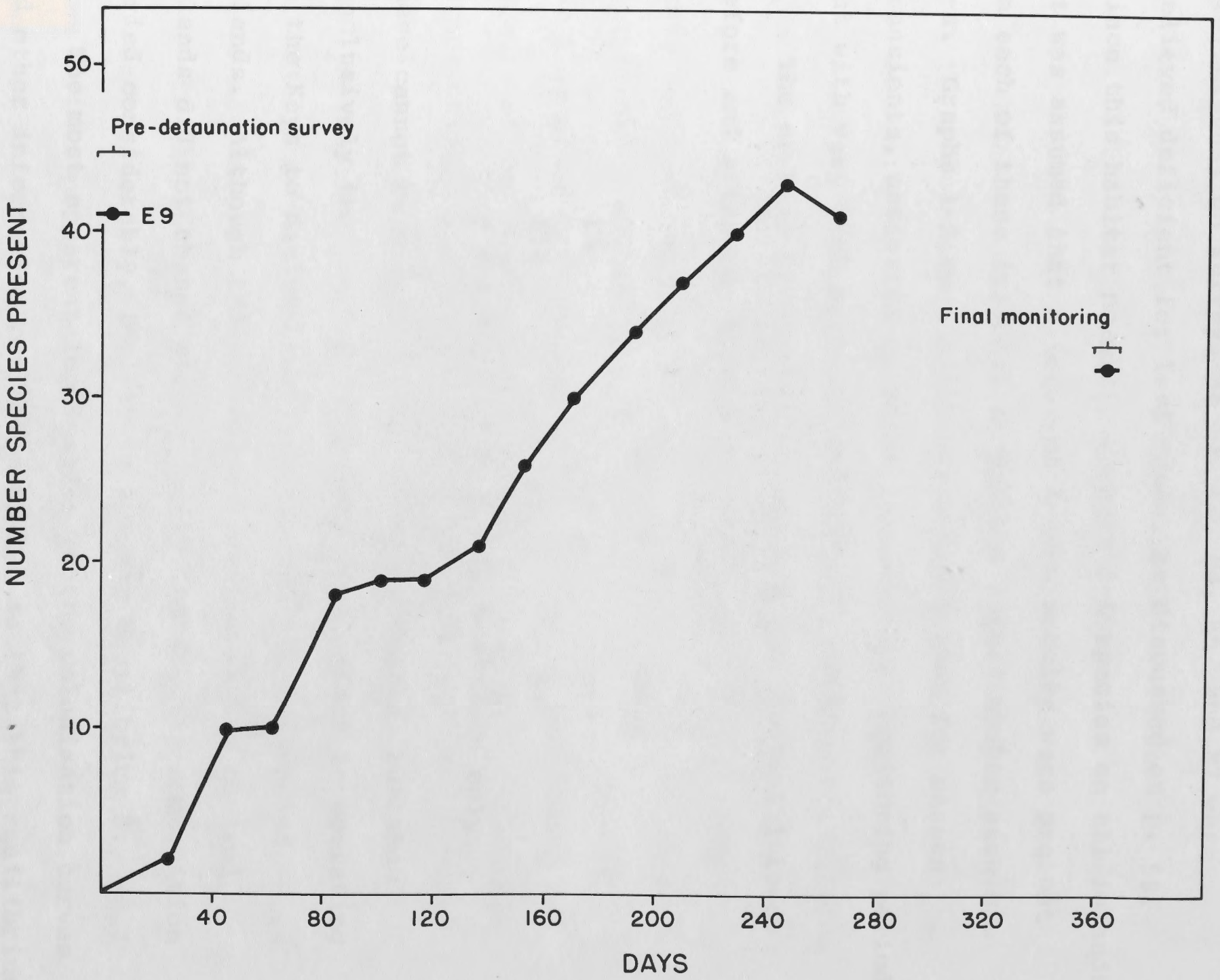
Graph 1: Colonization curves of series 1 islands


Pre-defaunation surveys
Final monitoring
E2
E3
ST 2
E1
NUMBER SPECIES PRESENT
40
30
20
10
40
80
120
160
200
240
280
320
360
DAYS

Graph 2: Colonization curve of Island E7


NUMBER SPECIES PRESENT
40
30
20
10
Pre-defaunation surveys
E7
Final monitoring
60
120
180
240
300
360
420
480
540
DAYS

Graph 3: Colonization curve of Island E9


50
40
30
20
10
NUMBER SPECIES PRESENT
Pre-defaunation survey
E9
Final monitoring
40
80
120
160
200
240
280
320
360
DAYS

must of course be made for the final census, after regular monitorings had ended. In addition to this correction, the pre-defaunation surveys of E1, E2, E3, E6, and E7 were believed deficient for leaf fauna, as discussed on p. 58. Since this habitat normally harbors 3-5 species on all islands, it was assumed that a total of 4 such species were present on each of these islands, though the actual number seen was 1-4. Graphs 1-3 do not include a correction for unseen transients, estimated at about 2 species per monitoring period but with very high variance (Simberloff, 1968).

The numbers of species recorded on the control islands before and after the experiment were:

	before	after
E6	30	28*
E10	20	23

* + 9 spp. in bird nest berlesate only

These cannot be corrected for unseen colonists, but show conclusively that no important long term effect is operating in the Keys to distort the results from the defaunated islands. Although the numbers of species on the control islands did not change significantly the species composition varied considerably, implying a dynamic equilibrium $\hat{S}$.

The most apparent implication of the colonization curves and other information presented so far is that this equilibrium

$\hat{S}$ does exist. Three lines of evidence are relevant. First is the fact, just mentioned, that S on the control islands did not change greatly during the year-long period in which the nearby experimental islands were being colonized. Second is the static observation that untreated islands with similar area and distance from source have similar $\hat{S}$ (note E3 and ST2 before defaunation); that $\hat{S}$ varies consistently with those parameters allows other inferences which will be touched upon in a later article (Simberloff, 1968).

Perhaps the most convincing argument for an equilibrium $\hat{S}$, however, is the increase of species present on all our islands to approximately the same number as before defaunation, and then rough oscillation about this number. This $\hat{S}$ may be only a pseudo-equilibrium - that is, the curve of S vs. time after $\hat{S}$ is reached may not be truly stationary - because of two long-term processes. The first is that when an approximate $\hat{S}$ is first reached the population structure of the particular set of species on the island is still changing rapidly; some species are represented by few individuals and may have large r (intrinsic rate of increase). Others may have abnormally large populations. Population sizes are generally fluctuating much more rapidly than on untreated islands. We have already indicated one manifestation of this process in our experiment: psocopterans colonized early and built up immense populations before

presumed ant predators appeared in number. The effect of this extreme population fluctuation on the colonization curve is that species may be eliminated and added at a rate systematically different from that on an untreated island. The concept of a dual dynamic equilibrium - of species number and population structure - will be discussed briefly in this paper and is treated in more detail by Simberloff (1968).

The joint evolution of the particular constellation of species on an island ought logically to raise $\hat{S}$ systematically (Wilson and Taylor, 1967), but we will neglect this effect because the time course of such a change is obviously beyond that of this experiment. Also, the invasion rates for most species on our islands are probably too high to allow significant genetic alteration to occur in populations on individual islands; in other words, they are not isolated in an evolutionary sense.

The curves of Graphs 1-3, except for that of E1, are believed best explained by the equation:

$$E(S(t)) = \sum_{\alpha=1}^{P} \frac{i_\alpha}{i_\alpha + e_\alpha} \left(1-e^{-(i_\alpha + e_\alpha)t}\right)$$

where $E(S(t))$ = the expected number of colonists present at time t

P = number of species in the pool

i_α = invasion rate of species α

e_α = intrinsic probability of extinction for species α

The derivation of this equation and a discussion of the concepts involved are found elsewhere (Simberloff, 1968). The important aspects of this theory are as follows:

The variance of S(t) is high:

$$\text{var } S(t) = \sum_{\alpha=1}^{P} E(S_\alpha(t))\,(1-E(S_\alpha(t))$$

S_α is a species indicator variable, which equals 1 when species α is present and 0 when species α is absent. Simberloff (1968) shows that

$$E(S_\alpha(t)) = \frac{i_\alpha}{i_\alpha + e_\alpha}\left(1-e^{-(i_\alpha + e_\alpha)t}\right)$$

Once the number of species on these particular islands is between ca. 75% and 90% of the equilibrium value of $E(S(t)) \left(=\sum_{\alpha=1}^{P} \frac{i_\alpha}{i_\alpha + e_\alpha}\right)$ the major premise of the theory, namely non-interaction of species, is invalidated. From this point onward S(t) declines slightly, at a slow rate which cannot yet be predicted well stochastically. It equilibrates ultimately at an enduring $\hat{S}$ partly determined by interaction and close to the number that existed before

defaunation. The decrease on all islands in number of species present for the final census (after regular monitoring had ended) is believed to be a manifestation of this decline.

El was so distant from its presumed source area that a few early invaders were able to build up large populations before their probable competitors arrived. Interactions thus became important before even a small fraction of the non-interaction $\hat{S}$ was achieved, and on El the colonization curve will probably ascend slowly and irregularly to an equilibrium near the pre-defaunation $\hat{S}$. This enduring equilibrium will be the same one to which the colonization curve of El would ultimately have descended had interactions not become important until a large fraction of $\hat{S} = \sum_{\alpha=1}^{P} \frac{i_\alpha}{i_\alpha + e_\alpha}$ had been achieved, as on the nearer islands.

As island distance from source increases the non-interaction $\hat{S}$ $(= \sum_{\alpha=1}^{P} \frac{i_\alpha}{i_\alpha + e_\alpha})$ decreases because of decreases in the i_α. Furthermore, the time necessary to reach any given percentage of the non-interaction $\hat{S}$, though not readily expressed mathematically, can be shown to increase with increasing distance from source. If this increase in time is sufficiently large the few early colonists are able to produce large enough populations to interact significantly with later immigrants. This in fact is what happened on El.

The colonization curve of E7 (graph 2) must be considered in light of the fact that 85% of the tree was killed by the fumigation (Wilson and Simberloff, 1968). The dead portion did not disappear, but rather deteriorated until by the end of one year the wood was brown and dry and much of the bark was peeling. Thus the island was not a constant factor, and the relative proportions of the various microhabitats changed drastically until ultimately there was far more dead wood and bark and far less leafy canopy than on an untreated island. If a consistent measure of area existed for these islands it would probably have remained unchanged on E7, but the expected number of species would not because the different microhabitats normally support different numbers of species. In particular dead bark shelters numerous species while mangrove leaves rarely support more than four species on a single island. Before its gradual decline, the colonization curve of E7 rose to a far higher percentage of the original $\hat{S}$ (135%) than did that of any other island. In addition, it was still rising quite monotonically a year after defaunation, when those of all other islands but E1 had levelled off. Arachnids (excluding orb-weavers) and psocopterans were the animals largely responsible for the higher S near the end of the experiment. Both groups are primarily bark dwellers.

All the above considerations imply that one of the determinants of the shape of the colonization curve on this

island alone was variation of the island itself, and that the enduring $\hat{S}$ which will ultimately be achieved on E7 may be higher than the pre-defaunation figure.

DISPERSAL

The agents of dispersal for few specific immigrations can be given with assurance, but the evidence implies that aerial transport, passive and active, is the major mode of invasion.

For the several parasites of vertebrates which breed on the islands proper zoochorous transport is certain. These include the hippoboscid flies Olfersia sordida and Lynchia albipennis and tick Argas radiatus on E1 and E9. All three species parasitize the cormorants and pelicans which roost on these islands. A number of mite colonists could also have arrived on transient higher animals. This appears to be so for Entonyssus sp. on E2; it is an obligate parasite in snake lungs, and a Natrix was recorded sloughing on E2. The invasions of E1, E3, and E7 by the mite Ornithonyssus bursa, an avian parasite, were probably ornithocorous.

A more interesting possibility involves phoresy on birds, particularly by some of the psocopterans prominent among early immigrants. Mockford (1967) has hypothesized that phoresy may be a more efficient means of insular invasion than wind

transport, especially for smaller species. Among four species found on Asian birds he lists Ectopsocopsis cryptomeriae, which has also colonized E3 and E7. Whether phoresy is a significant phenomenon in the Keys remains to be determined.

Other arthropods that may utilize phoresy are the pseudoscorpion Tyrannochelifer sp. found on E7, and free-living mites on all islands. These could have been transported by larger insects as well as by birds.

A related transport mechanism utilizes nesting material carried by birds. We suspect without proof that several mites in our experiment arrived in this fashion. Two beetle larvae were found in deep excavations in green heron nest twigs soon after the nests were built: Chrysobothris tranquebarica on E3 and ?Sapintus fulvipes on ST2 (the latter in a twig not of Rhizophora). It seems certain that both were in the twigs when the birds constructed their nests. Meyerriecks (1960) has observed green herons using twigs from other trees and from the nest tree itself. It is our impression that most nesting material that goes into new nests on small mangrove islands is brought from elsewhere. This was assuredly so for the non-mangrove twig on ST2.

Hydrochorous transport, either free or on rafts, was not as important as aerial transport in the invasion of our islands. Many mangrove colonists remain afloat almost

indefinitely in salt water, but only the orthopteroids seem able to achieve significant independent oriented motion. Furthermore, most floating insects and spiders of all sizes are rapidly devoured by fingerlings which are immensely numerous about all mangrove islands; even actively swimming crickets and earwigs frequently meet this fate, attracting more attackers by the very vigor of their efforts.

Nevertheless, at least one invasion (though not immigration, as the species was already present) occurred this way and there are other pertinent observations. An adult female Cyrtoxipha cricket was seen floating from Upper Snipe Key to E2, a distance of perhaps 6 ft. She successfully climbed a root and disappeared into the lower canopy. That a winged individual fully capable of oriented flight should actively choose to disperse by water is dubious, but at least over this short a distance the method is feasible in case the animal accidentally lands in the water.

Four Automeris io caterpillars were seen to float from one end of E9 to the other, a distance of about 50 ft. Three of them lodged on roots and eventually climbed up out of the water. The weakening of leaves attacked simultaneously by several large Automeris caterpillars (a common occurrence) might cause them to fall into water occasionally. Also, the caterpillars release their hold readily when the branch is shaken, apparently a defensive maneuver. It seems doubtful,

however, that a high proportion of those that land in the water could successfully travel between islands. Aside from fish attack, they would be plagued by their inability to direct their motion and to climb readily from the water.

Occasionally earwigs (Labidura riparia) were seen swimming from one root to another within an island. We do not know how well this species flies, but its swimming ability seems adequate for aquatic travel of considerable distance and it readily climbs out of the water. Fish would still be a hazard, however.

Our experiments resulted in no unequivocal invasions by rafting. In fact, several considerations imply that rafting must play a minor role in mangrove colonization. There is rarely land on which rafts can lodge, since Rhizophora islands generally have no supratidal ground. Drifting wood usually hits an island, gets trapped temporarily among roots, and eventually floats away. Even more importantly, green Rhizophora wood sinks immediately and many dead twigs also fail to float, thus precluding rafting by much of the wood-boring fraction of the fauna. Finally, except during hurricanes there is very little floating debris in Florida Bay - far less than the amount found at river mouths.

The preceding considerations lead, by elimination, to the inference that aerial transport must be an important means of dispersal to our islands. Several observations of

actively flying propagules support this hypothesis. Buprestid and cerambycid beetles, lepidopterans, wasps, and a lacewing have all been seen to land on the islands after flight from an outside source. Many other mangrove colonists are evidently carried passively by wind, especially psocopterans, thrips, neuropterans, and most spiders. Many of these more or less passively dispersed organisms are minute and direct evidence on their invasion method is therefore scarce. Occasionally spiderlings and psocopterans were found in the air around our islands. In general, they are usually important components of aerial plankton (Glick, 1939), and it is known from numerous anecdotal records (e.g., Bristowe, 1958) that ballooning for the distances involved in our experiment is regularly achieved by some spiders. So far, the small sizes of most of these animals has made it impossible to follow a flight visually from source to island. One suggestive record, however, is that of spider dragline stretching the six feet between Upper Snipe Key and E2.

An attempt to correlate Graphs 1-3 with hourly wind data of the U. S. Weather Bureau station at Key West was inconclusive, but this piece of negative evidence is hardly damaging to the thesis of dominance of aerial transport. For such data gives only timed readings at one nearby point, while dispersal depends largely on specific gusts at odd times in highly circumscribed areas about the islands.

Furthermore the published wind data are from a single fixed anemometer while the entire wind profile would be necessary to describe dispersal.

IMMIGRATION AND EXTINCTION RATES

Simberloff (1968) demonstrates that many immigrations and extinctions (perhaps 2/3) are not observed, the species involved being obligate or near-obligate transients which immigrate and are extinguished all within one interval between two monitoring periods. For this reason immigration and extinction curves cannot be derived from the observational data.

The observed immigration and extinction curves for all islands were highly variable, with no apparent pattern except for generally higher immigration rates on nearer islands during the first 150 days. Rates were usually between .05 and .50 spp./day. Simberloff (1968) shows that the very least the expected error in immigration and extinction rates could be is .67 spp./day, and furthermore that the variance about the "expected" immigration and extinction curves is very high. The observed curves are consequently of limited interest, as they yield only an extreme lower limit for turnover rates and cannot be used to intuit shapes of the "expected" curves.

The presumed agents of observed immigrations have just been discussed; there is no reason to suppose that those invasions not observed occurred largely by different means.

than those which were recorded. The assumption that most propagules arrive by air is therefore probably valid. The evidence against a seasonal component of dispersal, including the fact that wind direction and velocity are approximately constant throughout the year in the Keys, is given on p.78. In sum, we have a large body of information which implies that i_α (invasion rate of species α) is constant through time for all α. What we lack at present is quantitative information on the sizes and distribution of the i_α.

Simberloff (1968) has deduced that extinction rates, at least during most of the rise of the colonization curve from 0 to a large fraction of $\hat{S} = \sum_{\alpha=1}^{P} \frac{i_\alpha}{i_\alpha + e_\alpha}$, are adequately represented by the unchanging, species-characteristic e_α, without an additional S-dependent or density dependent factor included. The main arguments behind this assertion are:

i) Most of the species in the Florida Keys pool are obligate transients on these small mangrove islands. For a variety of reasons not directly related to their own densities or to other species they are doomed to swift extinction.

ii) Population sizes during most of the rise of S from 0 to near $\hat{S} = \sum_{\alpha=1}^{P} \frac{i_\alpha}{i_\alpha + e_\alpha}$ are uniformly low.

The observed data from this experiment provide rough quantitative information on both the distribution and sizes of the e_α, unlike with the i_α. This information has been incorporated into a simulation developed by Simberloff (1968).

Whatever the i_α and e_α the expected curve of immigration rate vs. time is represented during the rise of S from 0 to a large fraction of the non-interaction $\hat{S}$ by:

$$E(I(t)) = \sum_{\alpha=1}^{P} i_\alpha - \frac{i_\alpha^2}{i_\alpha + e_\alpha}\left(1 - e^{-(i_\alpha+e_\alpha)t}\right) = \sum_{\alpha=1}^{P} i_\alpha - i_\alpha E(S_\alpha(t))$$

while the expected curve of extinction rate vs. time during the same period is:

$$E(Ex(t)) = \sum_{\alpha=1}^{P} \frac{i_\alpha\, e_\alpha}{i_\alpha + e_\alpha}\left(1 - e^{-(i_\alpha+e_\alpha)t}\right) = \sum_{\alpha=1}^{P} e_\alpha E\left(S_\alpha(t)\right)$$

Beyond this point accurately predicted curves are impossible, but during the slight decline of S to an endurig $\hat{S}$ ex(t) must be, on the average, slightly greater than I(t), while after the equilibrium is reached the two must remain approximately equal. On any real island, of course, the two curves would cross and recross indefinitely. It also seems reasonable that after interactions become important, the Ex(t) and I(t) curves still do not change much,

since the contribution from their common major component, the transients, does not change with time.

The explicit derivation of the Ex and I curves is given by Simberloff (1968).

Whereas evidence on the specific agents of dispersal, and hence on immigration, has been plentiful during this study, observation on the causes of extinction was meager. Obviously the probability of witnessing the death or disappearance of the last member of a population is exceedingly low. Some inferences can be drawn from observed means of population decrease.

Population decline should be most apparent when associated with interaction, especially predation, yet the small sizes of most populations during our experiment reduced interactions enormously. A few cases of predation have already been mentioned (p. 88). Insectivorous birds, particularly warblers and red-winged blackbirds, were frequently observed eating numerous insects of many species. Wasps, both parasitic and non-parasitic, were seen to destroy several insects and spiders. Some of these attacks may have led directly to extinction, when the prey populations were small. Examples include the parasitism on Automeris io caterpillars by Apanteles hemileucae (Braconidae) and the destruction of the salticids Hentzia palmarum and Stoidis aurata by Trypoxylon collinum (Sphecidae).

Exclusion can also provide indirect evidence of extinction through interaction. A possible instance is the apparent predation of crickets on E9 by a large population of the centipede Orphnaeus brasilianus. E8, with no centipedes, had immense populations of four cricket species. After defaunation of E9 removed Orphnaeus, a large population of the cricket Cyrtoxipha confusa was rapidly established.

From observation of the pre-defaunation distribution of ant species numbers and population sizes on the various islands it seems probable that when one ant species is able to build up large populations before other species invade, it can exclude one or more other species. However, direct evidence of aggressive behavior among the mangrove ants is lacking; the observed exclusion may have been the result of nest site pre-emption.

Most extinctions were probably not the result of interactions, at least during the initial rise of the colonization curves, but rather resulted from the inability of most species in the Florida Keys pool to colonize these tiny mangrove islands under any conditions (Simberloff, 1968). Lack of proper food or nest site and hostile physical conditions are probably common causes. An example was the observation of a dealate queen of Brachymyrmex sp. on E9. Since this species nests in soil, which is lacking on the experimental islands, it is not surprising that no workers

were subsequently observed, despite the fact that the queen landed in a totally ant-free environment.

Even species which can survive on small mangrove islands have high probabilities of extinction not related to interaction. A number of animals have been found drowned during this experiment, including entire small ant colonies, numerous lepidopterous larvae, beetles, and psocopterans. It seems probable that during the hurricanes which periodically buffet these islands such deaths would be commonplace.

Similarly, numerous mangrove colonists inhabit hollow twigs and even under normal conditions many of these fall into the water. Certainly such events are multiplied during storms. The ant Camponotus floridanus and oedemerid beetle Oxycopis sp. seem particularly vulnerable in this respect - they typically inhabit largely low, weakly anchored, hollow roots.

ACKNOWLEDGMENTS

We wish to thank Dr. Joseph A. Beatty and Dr. Edward L. Mockford for identification of specimens and advice on experimental technique. Mr. Robert E. Silberglied performed the survey of Keys arthropods and aided in monitoring. S. Peck, H. Nelson, and R. B. Root participated in island censuses. Mr. John Ogden cultured many arthropod colonists. The following specialists gave generously of their time to identify animals encountered during the experiment: D. M. Anderson, E. W. Baker, J. R. Barron, J. C. Bequaert, L. Berner, B. D. Burks, J. A. Chemsak, K. A. Christiansen, W. J. Clench, C. M. Clifford, B. Conde, R. E. Crabill, P. J. Darlington, G. W. Dekle, H. Dybas, H. E. Evans, J. G. Franclemont, R. C. Froeschner, A. B. Gurney, J. L. Herring, W. Herrnkind, R. W. Hodges, R. L. Hoffman, D. G. Kissinger, J. P. Kramer, J. F. Lawrence, H. W. Levi, J. E. Lloyd, E. G. MacLeod, P. M. Marsh, R. Matthews, W. B. Muchmore, S. B. Mulaik, L. Pinter, C. C. Porter, E. S. Ross, L. M. Roth, L. M. Russell, R. L. Smiley, T. J. Spilman, L. J. Stannard, R. L. Usinger, B. D. Valentine, G. B. Vogt, T. J. Walker, L. M. Walkley, R. E. Warner, D. M. Weisman, F. G. Werner, R. E. White, S. L. Wood, R. E. Woodruff, P. W. Wygodzinsky. The work was supported by NSF grant GB-5867.

REFERENCES

Bristowe, W. S. 1958. The World of Spiders. Collins, London. 308 pp.

Cotteau, E. 1885. A week at Krakatau. Proc. Geogr. Soc. of Australia, N. S. W. and Victorian branches, II.

Glick, P. A. 1939. The distribution of insects, spiders, and mites in the air. U. S. D. A. Techn. Bull. 673. 151 pp.

Meyerriecks, A. J. 1960. Comparative breeding behavior of four species of North American herons. Publ. Nuttall Ornithological Club, No. 2. 158 pp.

Mockford, E. L. 1967. Some Psocoptera from plumage of birds. Proc. Ent. Soc. Wash. 69: 307-309.

Simberloff, D. 1968. Experimental zoogeography of islands. III. A theory of insular colonization. Doctoral thesis, Harvard Univ., Cambridge, Mass.

Wilson, E. O. and D. Simberloff. 1968. Experimental zoogeography of islands. I. Defaunation and monitoring techniques. In press.

Wilson, E. O. and R. W. Taylor. 1967. An estimate of the potential evolutionary increase in species density in the Polynesian ant fauna. Evolution 21: 1-10.

III. A Model for Insular Colonization

Abstract

A distinction is made between immigration rate (in spp./time) for an island and invasion rate (in propagules/time) for a species and an island. An analogous distinction is drawn between an island extinction rate and a species extinction rate (or intrinsic probability of extinction in a given time interval). It is claimed that the most objective definition for "propagule" is any animal or group capable of population increase under any conceivable circumstances. Immigration and island extinction curves are unique only if plotted against time, not against number of species.

Most members of the Florida Keys species pool are obligate transients on small mangrove islands (often because of inadequate food or microhabitat) and those which can survive were present on the defaunated islands in such low densities that extinction was probably initially rarely due to interaction. Drowning of entire small populations probably occurred frequently.

A model for non-interactive colonization is discussed, and its equilibrium $\hat{S}$ derived. It is shown that data from the defaunated Florida Keys can be interpreted as arising from non-interactive colonization to an S near the non-interactive $\hat{S}$ (and to a point above a more enduring interactive $\hat{S}$), followed by a slow decline in S (as population

sizes and interaction increase) to an enduring $\hat{S}$ near that obtaining before defaunation.

The effect on this scheme of increasing distance from source area is shown, and a simulation of the non-interactive part of the scheme was performed which corroborates that part of the model.

Explicit equations for the "expected" colonization, immigration, and island extinction curves are given for non-interactive colonization, and predictions are given about the general changes on these curves as interaction becomes significant.

SYMBOLS USED IN TEXT

$C(t)$ colonization rate, in species/time, at time t

$e_{t_0}(\alpha)$ probability that species α, if present, is extinguished in time period of length t_0

e_α species extinction rate of species α, defined analogously to i_α (q.v.); $\lim_{t_0 \to 0} \frac{e_{t_0}(\alpha)}{t_0}$; if species α were replaced immediately upon extinction, e_α would be the frequency of extinctions/time

$Ex(t)$ island extinction rate, in species/time, at time t

$Ex_\alpha(t)$ contribution to island extinction rate of species α; defined in text

$i_{t_0}(\alpha)$ probability that species α invades in time period of length t_0

i_α invasion rate of species α, in propagules/time

$I(t)$ immigration rate, in species/time, at time t

$I_\alpha(t)$ contribution to immigration rate of species α; defined in text

P number of species in species pool

$S(t)$ number of species on island at time t

$\hat{S}$ equilibrium number of species for island

$S_\alpha(n)$ species indicator variable for species α

= 1 if species α present on island during time period n

= 0 otherwise

A discussion of theoretical zoogeography must be based on clear definitions of the following often ambiguous terms:

Colonization: the existence on an island of at least one propagule of a species.

Extinction: the disappearance of a species from an island.

Immigration: the arrival of a propagule on an island unoccupied by that species.

Invasion: the arrival of one or more propagules on an island, whether or not the island is occupied by that species.

Propagule: the minimum number of individuals of a species capable of breeding and population increase under ideal conditions for that species (unlimited food supply, proper habitat, no predators, etc.).

Probably the most frequently confused of these concepts are "invasion" and immigration". I wish to distinguish between two rates: the rate (in species/time) of new species arriving on an island and the rate (in propagules/time) of propagules of a given species landing on an island, whether or not that species is present on the island already. The former could be called "island immigration rate" since it refers to a given island, and the latter "species immigration

rate" since it is a species characteristic, but to avoid ambiguity I follow the convention of MacArthur and Wilson (1963) and reserve "immigration" for the rate of new species arriving on an island. For the rate of arrival of propagules of a given species on a given island I propose the term "invasion", heretofore used less precisely.

To recapitulate, an immigration rate (in species/time) involves a given island, while an invasion rate (in propagules/time) involves a given island and a given species. The total rate of arrival of propagules on an island regardless of species can be called "total invasion rate".

An analogous situation holds logically for extinction rate, but here there has been little confusion since all previous zoogeographic references to extinction rate have been to extinction of species on an island, in species/time. This is a direct result of the tacit assumption that a species alone on an island has a very low intrinsic rate of extinction, and that its extinction or persistence is almost completely interdependent with those of other species on the island - in short, that extinction is determined almost entirely by competition, or at least by interaction. In this paper I will give evidence for the existence of an intrinsic probability of extinction for a given species on a given island which exists even in the absence of interaction and which is not directly related to density of the species, and

will use this concept in proposing a tentative general theory of insular colonization. Since no prior term for extinction analogous to "invasion" exists, I will hence-forth refer to an "island extinction rate" Ex (or simply "extinction rate") and a "species extinction rate" e_α.

The concept of colonization has been represented more or less interchangeably by two distinct curves, both denoted "colonization curve" (e.g. - MacArthur and Wilson, 1967). The first, which I term the "colonization rate curve", plots the change in the number of species present per time vs. time - i.e.: $\Delta S/\Delta t$ vs. t ($\Delta S/\Delta t$ has also been plotted vs. S; this is treated on p.126). For continuous immigration and extinction rate curves, C(t) = I(t)-E(t). With discrete time intervals of length t_0, for a given interval i, C_i = (# immigrants - # spp. extinguished)/t_0.

The other curve, which I will call the "colonization curve", simply plots the number of species present on an island vs. time - S vs. t. Clearly, for continuous data $S(t) = \int_0^t (I(t)-E(t))dt = \int_0^t C(t)dt$, while for discrete data with time intervals i = 1,2,...., all of length t_0, $S(t_n) = \sum_{i=1}^{n}$ (# immigrants in interval i - # spp. extinquished in interval i) = $t_0 \sum_{i=1}^{n} C_i$.

The least precise of the above definitions is that of "propagule". In order for meaningful comparisons of immigration, extinction, and invasion rates to be possible, what constitutes a propagule must be made independent of the physical and biological properties of the island upon which it lands. Were this not so, the size of a propagule of one species would vary on a single island (depending partly on how many and which species were already present) and among different islands (depending on whether suitable microhabitat, food, etc., were present and in what amounts).

A probabilistic definition (e.g. - MacArthur and Wilson, 1963) similarly leads to a variable propagule size. If we say arbitrarily that a propagule is the minimum combination of individuals with probability x of initial increase to a specified (large) population size, then we must also specify precisely all relevant ecological conditions. Aside from the difficulty even in defining these conditions for certain species, such a procedure renders comparisons among species suspect. For any given species every set of conditions would be associated with a distinct propagule size, yet to define a standard set of hypothetical conditions and thence to derive the propagule sizes of all species from this set would certainly yield unrealistically large, and perhaps not even meaningful, propagule sizes for species whose normal niche characteristics vary widely from the standard set.

A more objective criterion, adopted herein, denotes as a propagule a combination of individuals capable under any imaginable circumstances of initial population increase. That is, no standard set of conditions is invoked, but rather for any species the most favorable circumstances are assumed for that species. This leads for most species to a definition of a propagule as a single pair of opposite sexed individuals or one fertilized female.

THE INDEPENDENT VARIABLE IN RATE CURVES

Immigration and extinction rates have been plotted against both the number of species present on an island (S) and time (t) (MacArthur and Wilson, 1963, 1967). For the colonization of a given island from zero species to a dynamic equilibrium this is not inconsistent so long as the colonization curve increases monotonically, but once S is fluctuating about $\hat{S}$ (that is, once monotonicity ceases) the reality of the plots of I and Ex vs. S must be questioned. Similarly, hypothetical curves of I and Ex vs. S for a series of similar islands at a single point in time are suspect.

Consider first the curve of Ex vs. S. Its validity rests on the association with every S of a unique Ex, but it is difficult to make this association from two viewpoints.

Questions of population size aside, there is no reason to expect that every constellation of n species on a given island should produce the same extinction rate. Whatever interactions are occurring among a particular n species it is unlikely that their extinguishing effect should equal that of a different set of n species. And the species extinction rates defined earlier are certainly not equal for all species and hence as a sum would not contribute equally to an island extinction rate for all sets of n species.

And, still neglecting population sizes, even if an extinction rate could be associated with each of the $\binom{P}{n}$ sets of n species in a species pool of size P, it is not possible directly to average them and thus perhaps to claim that some sort of an average Ex(n) is less than an average Ex(n + 1). For each of the $\binom{P}{n}$ sets cannot be weighted equally - surely some are in reality highly improbable. To find a relative probability for all sets is not yet possible; it requires in particular a more complete knowledge of static distributions of colonists on several series of islands.

Yet the most important defect of the Ex vs. S curve is that it fails to take account of population structure. A given set of n species will have associated with it numerous extinction rates, as many as there are conceivable combinations of sizes of the n populations, and to measure their relative probabilities seems a hopelessly complicated task. A

stochastic model can be conceived which can yield the relative probabilities of each possible combination of population sizes, but the biological knowledge necessary to make it predictive will be lacking for the foreseeable future, if not forever.

An immigration rate vs. S is not subject to this last consideration since invasion rates, and consequently immigration rates, are unaffected by the sizes of the populations already on the island in question. But it still suffers from its failure to account for different sets of n species present on the island, and hence different sets of (P-n) species of potential immigrants. Again, if the relative probability of each of the $\binom{P}{n}$ sets of n species were known a meaningful average I(n) could be calculated in theory, but it would require that the invasion rates of all P species in the pool be known for the given island. Although such information does not seem altogether out of reach it is certainly unavailable now. For the present I as a function of S has limited utility.

The concept of intersecting plots of I and Ex vs. S, the former monotonically decreasing and the latter monotonically increasing, may still be didactically useful in two distinct situations. If one monitored two times, separated by a fairly long interval, each of a series of islands that were large enough to avoid small numbers problems and distant enough from a source area (for reasons given below), his

data would consist of one value of S (that of the first monitoring), one value of Ex, and one value of I for every island. I and Ex could then be plotted against S and would probably display the expected monotonicities.

Similarly, if one observed a single such island at long intervals from a defaunate condition through $\hat{S}$ he would get for each monitoring period i an S_i, I_i, and Ex_i. If the I_i and Ex_i were then plotted against the S_i we would probably again have a monotonically increasing Ex curve and monotonically cally decreasing I curve. These curves would not be the same as those discussed in the preceding paragraph, however, because of obvious radical differences in population structure. And the nearer the islands were to their source area the more different the two sets would become because of drastic changes in the latter (single island) set, in a manner to be explained later. Furthermore, in neither instance is it possible to predict from first principles the shape of the Ex curve. Though one might logically deduce characteristics of the I curves this will not be feasible practically until much more is known about both species dispersal characteristics, and therefore invasion rates, and static distributions of species, in order to estimate relative probabilities of distinct sets of species.

Curves of I and Ex vs. time, by contrast, are unambiguous for a given island monitored at discrete points in time,

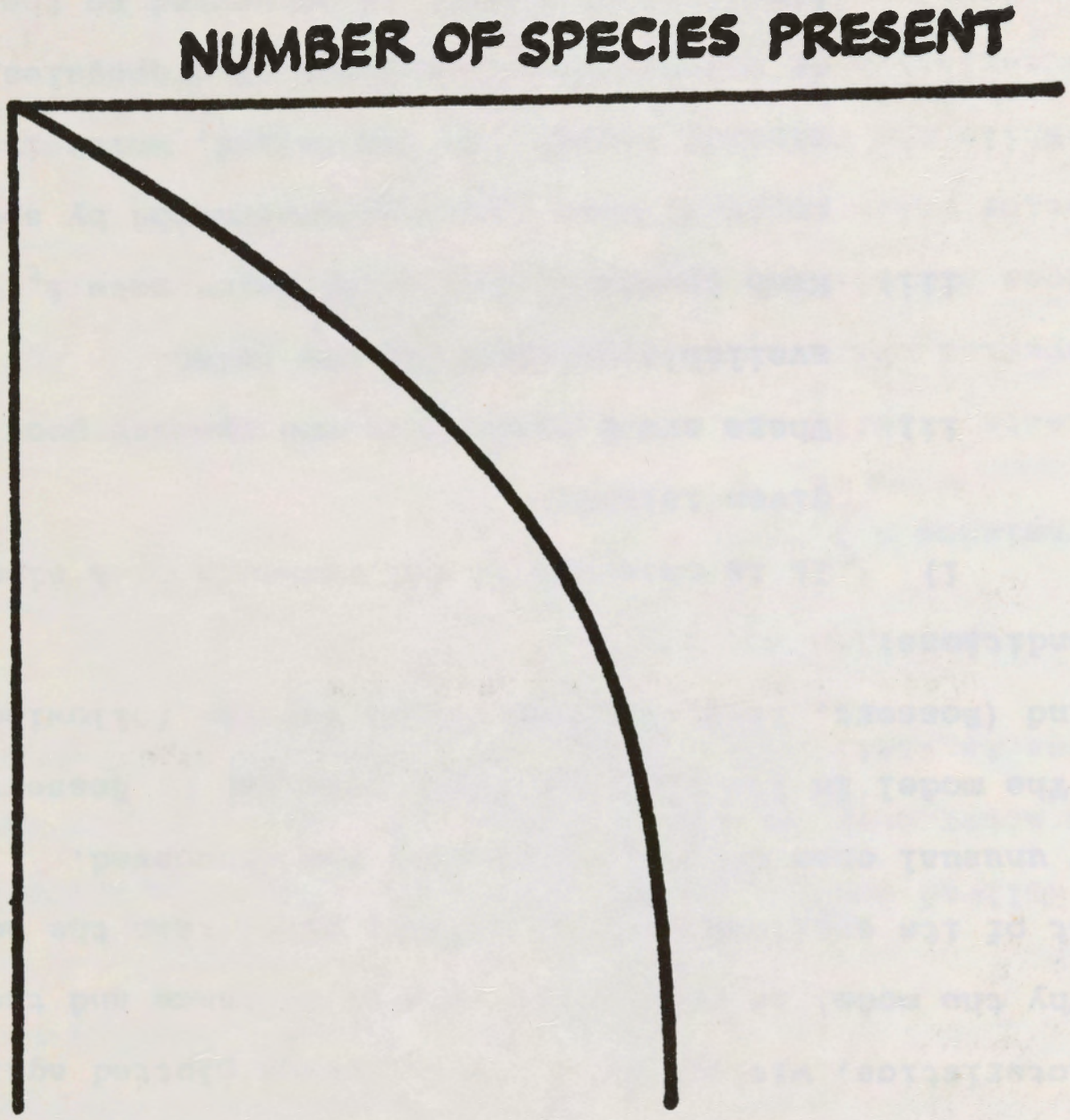
instead of discrete numbers of species S. They simply plot the average rates (I_i and Ex_i) for a series of time periods i vs. the position of those periods in the time continuum. The only arbitrary decision is what length to make the time periods. In an experiment such as that described herein, this is determined by the interval chosen between monitorings. The longer the interval the less accurate the observed I and Ex rates because of species immigrating and going extinct all within one interval; a discussion of the inaccuracy thus introduced is found on p. 151.

Given the reality of the curves of I, Ex, and S vs. t, one would wish to predict their interdependent shapes in advance. A previous attempt by MacArthur and Wilson (1963, 1967) yielded for the latter curve $S = \hat{S}(1-e^{-Gt})$ with G a constant, whose general form is given in Graph 1. They found that the ratio of $\frac{\text{variance}}{\text{mean}}$, if this colonization curve were found experimentally on a series of identical islands, would fall from 1 near time 0 to about 1/2 as the islands approached their equilibrium $\hat{S}$.

Both the shape of their curve and the constant G are derived from characteristics of the I and Ex vs. S curves, the limitations of which have just been discussed. In particular they utilize the doubtful analogy between an untreated island with S_1 species and a defaunated island of similar size (and presumably shorter distance to source

Graph 1: $S = \hat{S}(1-e^{-Gt})$

from MacArthur and Wilson (1967)



131

area) whose colonization curve rises to S_1 species en route to a higher $\hat{S}$.

A MODEL FOR COLONIZATION OF THE SMALL ISLANDS IN THE KEYS

A model will be discussed here which predicts a major part of these experimental curves directly from species characteristics, without recourse to curves plotted against S. Why the model is predictive in this instance and the extent of its applicability to islands other than the admittedly unusual ones of this experiment are discussed.

The model in its simplest form, proposed by Bossert and Holland (Bossert, 1968; Holland, 1968) has the following preconditions:

i) It is relevant to colonization of a single given island.

ii) There are P species in the species pool available to colonize the island

iii) Each species α has an invasion rate $i_{t_0}(\alpha)$ constant over time and unaffected by species already present on the island, which instead of being defined in terms of propagules/time (as on p.102) is converted to the probability that one or more propagules land on the island in one interval. This, of course,

is dependent upon the length of the time interval which is used in the experiment; once this t_0 is chosen the $i_{t_0}(\alpha)$ are uniquely determined by the i_α.

iv) Every species α has a species extinction rate $e_{t_0}(\alpha)$, constant over time and unaffected by species already present, similarly defined as the probability that this species will go extinct in one interval.

Holland deals largely with the shape of the colonization curve after many intervals have elapsed (i.e. - once the process is stationary), in particular finding that there is a non-interactive equilibrium $S = \sum_{\alpha=1}^{P} \frac{i_{t_0}(\alpha)}{i_{t_0}(\alpha) + e_{t_0}(\alpha)}$ and variance $= \sum_{\alpha=1}^{P} \frac{i_{t_0}(\alpha) e_{t_0}(\alpha)}{(i_{t_0}(\alpha) + e_{t_0}(\alpha))^2}$

He treats briefly the effects on the colonization curve as the species characteristics $i_{t_0}(\alpha)$ and $e_{t_0}(\alpha)$ are modified and does not discuss the problem of varying island characteristics while keeping the species pool constant.

While the model is manifestly derived from the species characteristics i_α and e_α, any simulation utilizing it automatically provides the information necessary to compute the island characteristics I and Ex, and the model has been programmed to provide this data; that is, to yield for a

given input set of $e_{t_0}(\alpha)$ and $i_{t_0}(\alpha)$ not only a curve of S vs. t, but also of I and Ex vs t. Also, although Holland does not treat the effects of varying island parameters (especially island area and distance from source) while maintaining one species pool, this can be done readily by modifying the species characteristics systematically (for instance, lowering the $i_{t_0}(\alpha)$ as distance of the island from source increases).

Each of the preconditions will now be considered in turn, and its applicability to general situations and the Florida Keys defaunation experiment in particular discussed.

Condition (i) is simply a convention of the model, that only one island will be considered at a time. As mentioned above, the colonization of different islands can be compared by varying the species characteristics; this is discussed on p.

Condition (ii) is similarly a mere convention.

Condition (iii) seems incontrovertible unless seasonality or some other factor introduces a periodicity into the dispersal characteristics of a major proportion of the species in the pool. It defines a unique, real measure of the probability that at least one propagule of a given species will land on a given island in a given amount of time. There is no reason to believe that those animals already present on an island would in any way modify the rate of arrival of animals from

elsewhere. Both prior consideration of Keys climatic information and the colonization data from the defaunated islands in the Keys indicate strongly that dispersal of the majority of potential colonists is relatively uniform over time (Simberloff and Wilson, 1968), so in this respect the model seems applicable. For islands where fluctuation in the i_{t_0} (α) is expected there is no reason why the model could not be programmed to simulate this, provided the fluctuation characteristics were known.

More doubtful is condition (iv). Probably no one would question that every species on an island has a finite probability of extinction from causes not related to food-limitation or competition - one could imagine every member of a population drowned during a torrential downpour, say, or buried under lava from a volcanic eruption. What may be doubted is that such events, in the aggregate, contribute significantly to species extinction rates and hence to an island extinction rate. That such extinction probabilities are so important that food limitation and competition can be neglected entirely and a useful model still result may seem preposterous. Yet the model says exactly this, for it provides for extinction only through the comparison of uniform random numbers with the e_{t_0} (α). The failure to allow either for change through time of the e_{t_0} (α) (by making them intrinsic species characteristics) or for the inclusion of a separate time- or

S-dependent term in calculating extinction probabilities is tantamount to discounting all inter- and intraspecific interactions.

As regards the experiment in the Florida Keys, however, two considerations seem strongly to imply that the model accurately depicts extinction at least during a major part of the rise of the colonization curve from 0 to the non-interactive $\hat{S}$, and hence to a point above a more permanent $\hat{S}$ to be derived later. Eventually (certainly by the time the colonization curve becomes truly stationary) its validity is dubious; this will be discussed.

The first factor is that many colonizations (and hence immigrations and extinctions) throughout the experiment were by transients. Most animals in the source fauna cannot successfully colonize small red mangrove islands for a variety of reasons - lack of adequate nest site, absence of proper plant food, insufficient prey, hostile physical conditions, etc. They invade but quickly go extinct; in short, their $e_{t_0}(\alpha)$ are very high. Of an estimated 600-700 species in the pool, 236 were observed to have colonized the islands after defaunation (not counting the final monitoring period); 110 of the 236 were extinguished within a single monitoring period (18 days), and 134 within two. Many of these immigrated and went extinct more than once. The fraction of the total colonizations comprised of these transients did not change

systematically throughout the experiment.

The error incurred in estimating total immigration and extinction rates from observed colonizations is discussed later, but it can be briefly noted here that one must assume that a sizable fraction of the total extinction (and immigration) rate, perhaps as large as two thirds, is not seen in observational data because it consists of propagules landing and going extinct all within one time interval, between two monitoring periods. Most of this fraction is due to the same class of transients just described, and this will obviously strengthen the assertion that most colonizations are by transients.

A further consideration, which leads to the same conclusion, is that all the species eliminated from consideration as colonists by Simberloff and Wilson (1968) because they were judged to be treating the defaunated islands as part of a fine-grained foraging system, would if included in the species counts appear as transients - that is, all would become extinct within one monitoring period, and many would reinvade and be extinguished repeatedly.

It seems probable from the above arguments that the majority of colonizations, perhaps about 75%, were by obligate transients. The species in this class all have high e_{t_0} (α). But the remaining 102 of the 236 observed species, those not extinguished within two monitoring periods, were not a uni-

form lot; many of these accomplished sustained colonization on one or two occasions only, their invasions otherwise resulting in swift extinction. Of a total of 391 distinct colonizations by these species, 158 lasted only one or two intervals. If the experimental time course is divided in half there is apparently some change in extinction rates caused by interactions, for 30% of these colonizations initiated in the first half were transient while 51% of those in the last half were transient. Even this difference may be artifactual during the major part of the initial climb of S for two reasons. First, there are a few species in the pool (perhaps 10-15) which have very low e_{t_0} (α) - once they colonize they are rarely extinguished. Most of these immigrated in the first half of the experiment, tending to lower the percentage of short-lived colonizations in the first half and, by their unavailability for new colonizations, to raise this percentage in the second half. Secondly, the second half includes for every island except El a portion of differing length during which S had already begun to fluctuate and perhaps gradually to decline, and it was during these portions that some population sizes may have been large enough for interactions to occur. This is discussed below.

In sum, the first consideration which implies that precondition (iv) of the model may have biological validity for the Keys experiment is the majority of obligate transients

in the species pool, and that all but a few of the remaining species, even though capable of sustained existence, apparently persist in at best half their colonizations. Even many of these disappear within two months. And at least during most of the rise of S these characteristics do not change significantly in time (or therefore with S).

The second consideration supporting precondition (iv) may explain the apparent lack of inter- and intraspecific interactions during this period (i.e. - that the unchanging $e_{t_0}(\alpha)$ adequately represent the total extinction probability for most species). This is that, except for colonists on E1 (discussed later), population sizes during the entire monotonic rise of the colonization curves toward an equilibrium $\hat{S}$, and in varying degree through the first few fluctuations, were uniformly very low - strikingly so compared to those on most untreated islands.

Accurate quantitative estimates are unavailable for this experiment - indeed, they may not yet be possible for these mangrove islands - but it was readily apparent that densities on the defaunated islands were extraordinarily low. Whereas on normal red mangrove islands one sees without manipulation numerous small arthropods constantly and almost instantly, for at least four months after defaunation he would see at most one or two animals per hour without active searching. Even active manipulation only accentuated the

animal paucity. Small mangrove twigs, both living and dead, normally harbor a plethora of both wood-borers and species which inhabit the hollow twigs which the borers produce; breakage of such twigs on defaunated islands for at least several months yielded almost no animals at all. Before defaunation approximately 20 twigs/100 yielded colonists (mean over all islands), while in the five months immediately after defaunation a maximum of 2 twigs/100 (and usually less) contained animals. Similarly, dead bark ordinarily houses large populations of several species on any single island; for months after defaunation this microhabitat was essentially empty. Although the low densities were most striking in these two microhabitats (since they normally contain more animals than the others) all microhabitats showed the same trend.

All colonists were present in low densities during this period (with occasional exceptions, such as ephemeral population explosions of some psocopterans and thrips), but the most dramatic scarcity was of ants, the undisputed ecological dominants of untreated mangrove islands. The ants as a group not only immigrated late (Simberloff and Wilson, 1968) but were very slow in building up populations (in both colony numbers and colony sizes) to anything approaching the great size often achieved on these islands. At the last monitoring of all islands, about one year after defaunation, ant populations

were still abnormally low - certain expected colonists were rarely present (Paracryptocerus varians, Tapinoma littorale) and only Crematogaster ashmeadi and more rarely Pseudomyrmex elongatus had sufficient workers (and these only on some of the islands) to appear common. On no island were ant populations nearly so dense as those before defaunation.

And it is precisely the ants that one would expect to be involved most frequently in competition, predation, and interactions in general. Except for a very few observations of spiders (particularly salticids) eating psocopterans and roaches, and of several wasp species preying on various lepidopterous larvae and araneids, all direct observations of interaction in this experiment have involved ants (and almost all these have been near the end of the experiment as densities were rising noticeably). All interactions, of course, were more common during the later monitorings, and as population sizes continue to rise I expect that interactions will play an increasingly greater role.

To reiterate the second consideration, then, the overwhelming weight of observational evidence in the Keys experiment implies that population sizes were almost all low during the rise of the colonization curve from 0 to a large fraction of the non-interactive equilibrium. Interactions were correspondingly greatly reduced from those on an untreated island.

The generality of this condition is doubtful. The relatively short distances from source area to the experimental Keys (2 yards to ca. 1 mile) are directly responsible for its applicability in this instance, for they allow extremely high total invasion rates (and therefore high immigration rates) which in turn means that many species can be present before any can build up large populations. Undoubtedly if one defaunated more distant islands (say, 30 or more miles from source) this situation would not pertain and to simulate colonization of such islands an additional extinction factor, dependent on which species are present and in what densities (and including information on food availability), would have to be incorporated. Of course such experiments have not been performed - the results from one such event, the eruption of Krakatau, are inconclusive (Wilson and Simberloff, 1968).

It should also be noted that on islands larger than the tiny ones in the Keys the invasion rates would be much higher than for a tiny island equidistant from the same source. Just what the relative weights of island distance and island area are in determining invasion rates and how much one factor can compensate for the other must be determined by further experimentation. In particular more must be known about gross dispersal characteristics such as the normal and exponential dispersal patterns of MacArthur and Wilson (1967) and about behavioral components of insular invasion, including

the ability of potential invaders to orient themselves toward an island and to discriminate from a distance among different types of islands.

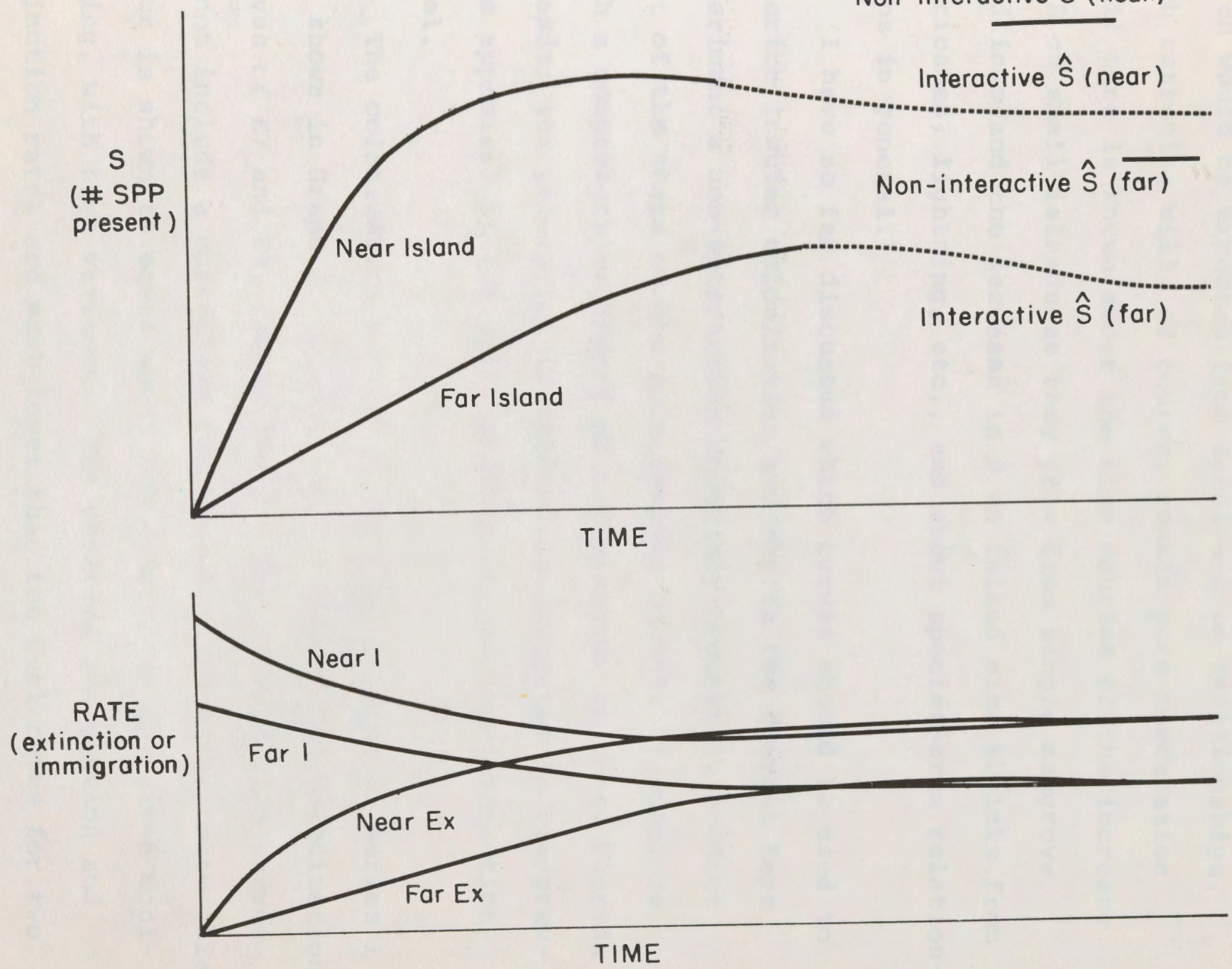
In the Keys experiment a possible exception to the rule that a large fraction of the non-interactive equilibrium $\hat{S}$ is achieved before population sizes are large enough to allow significant interactions may be the island E1 in series 1. This is by far the most distant island in the series, and its present small size is apparently but a fraction of that only a century ago (Wilson and Simberloff, 1968). The equilibrium theory to be presented here predicts that, as the farthest island, E1 would be expected to have the lowest non-interactive $\hat{S}$, and further that it might be expected to take longest to reach any set fraction of that $\hat{S}$. The interesting possibility is that E1 may be so far from its presumed source areas that when it finally does equilibrate, it may be around an $\hat{S}$ lower than that before defaunation. Although the colonization curves of the other three islands in series 1 (E2, E3, and ST2) have apparently risen to near their respective non-interactive $\hat{S}$'s and started oscillating or even declining slightly (see below), that of E1 was still erratically rising a year after defaunation. Since in general on all other islands in this experiment population sizes seemed to be approaching those on undisturbed islands by one year, it may be that what few potential long-term

colonists have succeeded in reaching E1 will be able to produce abnormally large populations before their presumed competitors invade. This in turn could render these late invaders, which might otherwise be persistent colonists, transients doomed to swift extinction. That is, though their intrinsic e_{t_0} (α) may still be relatively low, interactions may cause their total probability of extinction to be high.

That the resulting equilibrium $\hat{S}$ on E1 should be lower than that before defaunation is a consequence of the general colonization curve derived later and pictured in Graph 2. It is sufficient for now to note that after an initial approach to near the non-interactive $\hat{S}$, there is a gradual decline to a slightly lower, more enduring $\hat{S}$ determined partly by interaction. Since E1 appears to be leveling off much lower than the pre-defaunation $\hat{S}$, one might expect a quasi-equilibrium $\hat{S}$ (Wilson and Taylor, 1967) which will rise slowly and in an as yet unpredictable fashion to the same enduring $\hat{S}$ to which it would have descended from near the non-interactive equilibrium. That is, the E1 colonization curve will first equilibrate at a level lower than the pre-defaunation $\hat{S}$ and then very gradually and possibly not monotonically climb to this long-term equilibrium level.

It is even possible that the enduring equilibrium to which it ascends will be somewhat lower than the pre-defaunation

Graph 2: Generalized colonization curve, and effect of varying distance from source area

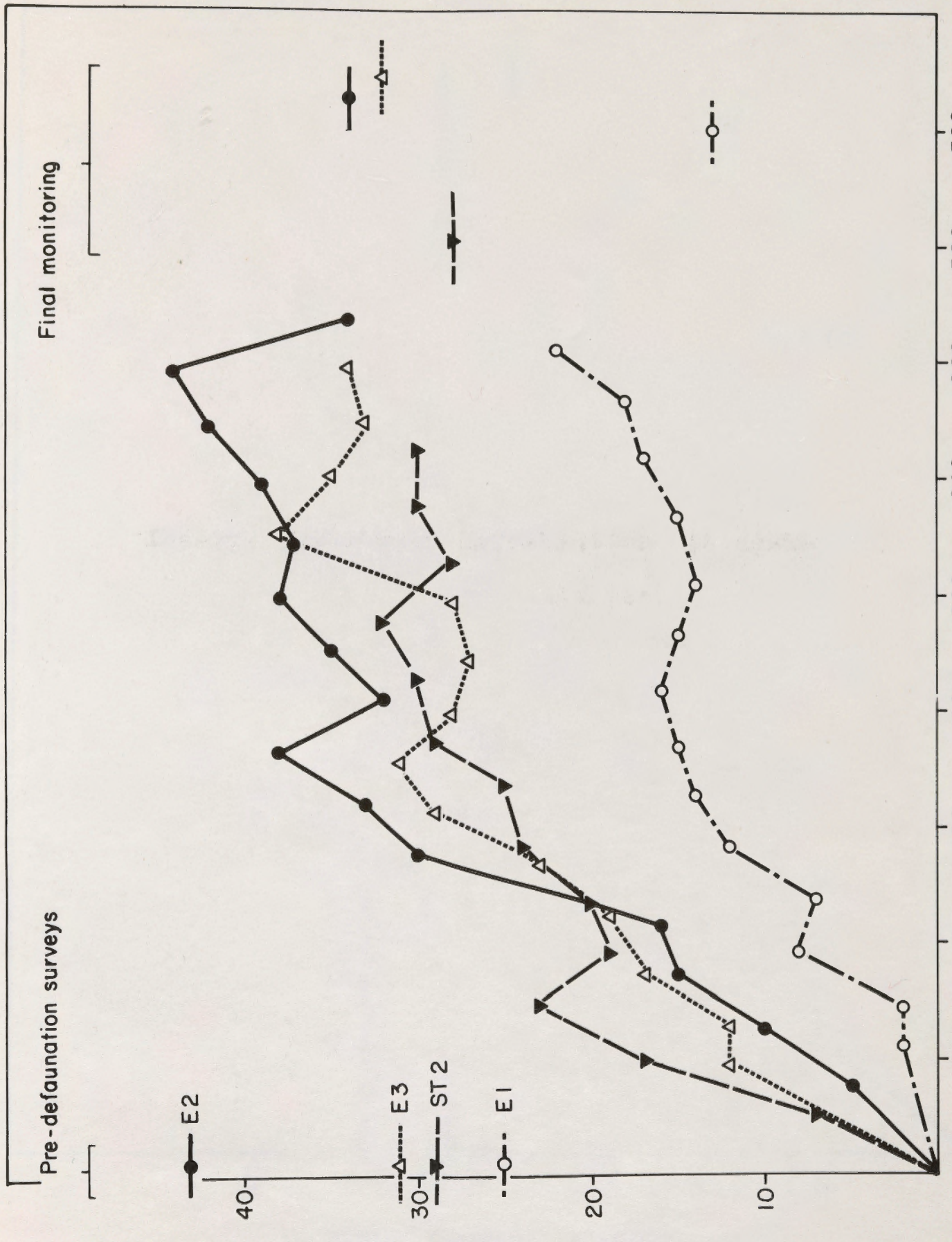

Non-interactive Ŝ (near)
Interactive Ŝ (near)
Non-interactive Ŝ (far)
Interactive Ŝ (far)
S
(# SPP
present)
Near Island
Far Island
TIME
RATE
(extinction or
immigration)
Near I
Far I
Near Ex
Far Ex
TIME

$\hat{S}$. This rests on the tenuous but not unreasonable assumption that as the size of El shrank during the past 100 years there was a considerable lag in the decrease of $\hat{S}$ to that which would be expected from species-area relationships. Such reasoning will, of course, remain pure speculation until more is known about the time courses of the increase in $\hat{S}$ on small islands as they grow from single mangrove seedlings and the decrease in $\hat{S}$ as island size shrinks from hurricanes, lightning, etc., and about species-area relationships in general.

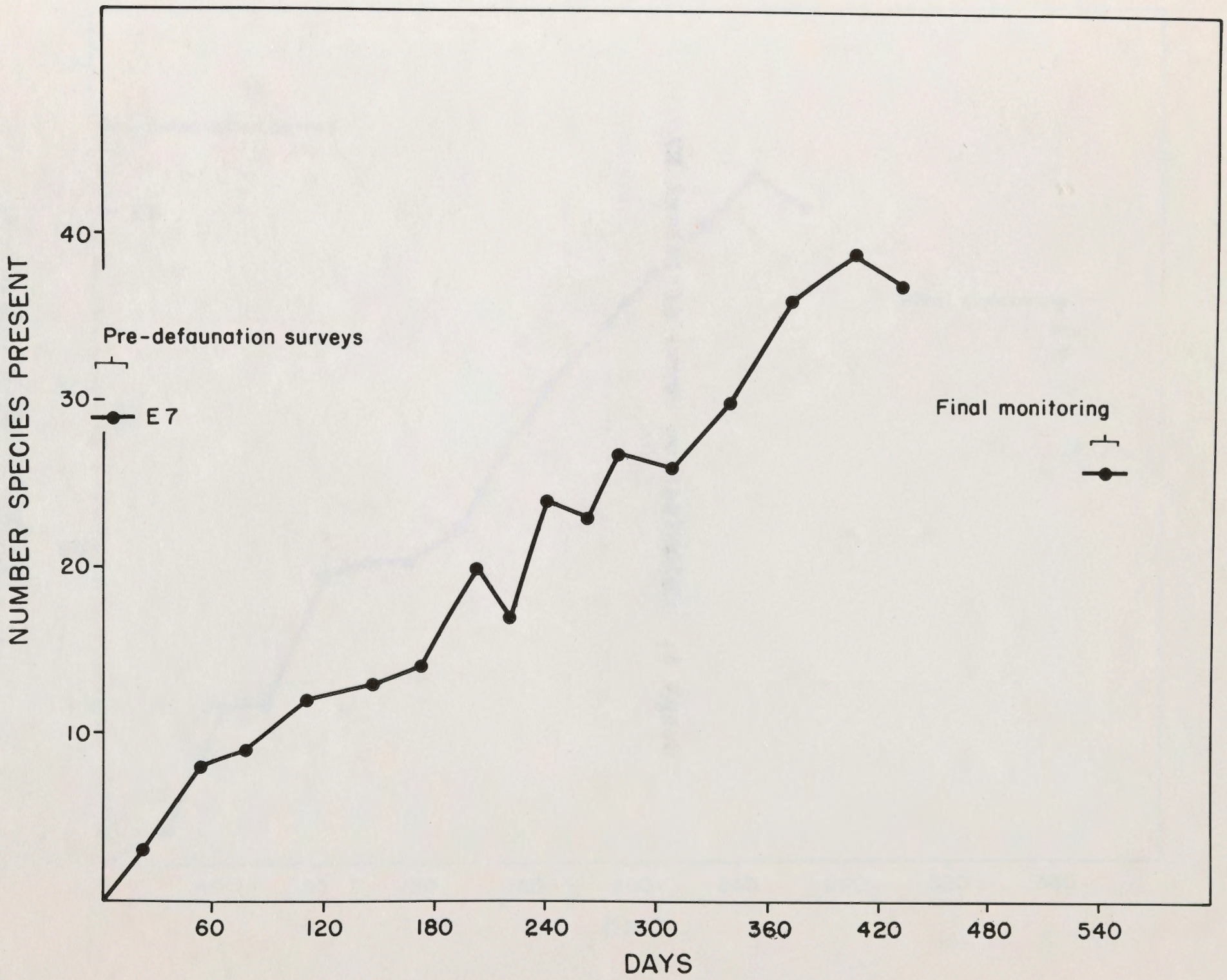
I have so far discussed which curves should be used to describe insular colonization and why in the Florida Keys experiment a non-interaction model may accurately predict part of the shape of the colonization curves. I conclude with a comprehensive theory of colonization of these Florida islands; its generality is limited as indicated in the previous appraisal of the applicability of the non-interaction model.

The colonization curves of the four islands in series 1 are shown in Graph 3. Graphs 4 and 5 depict the colonization curves of E7 and E9, respectively. The colonization curves do not include a correction for unseen transients; below this error is shown to equal about two species at any given monitoring, with high variance. The observed immigration and extinction rates are much lower than the real rates for two

Graph 3: Colonization curves of series 1 islands

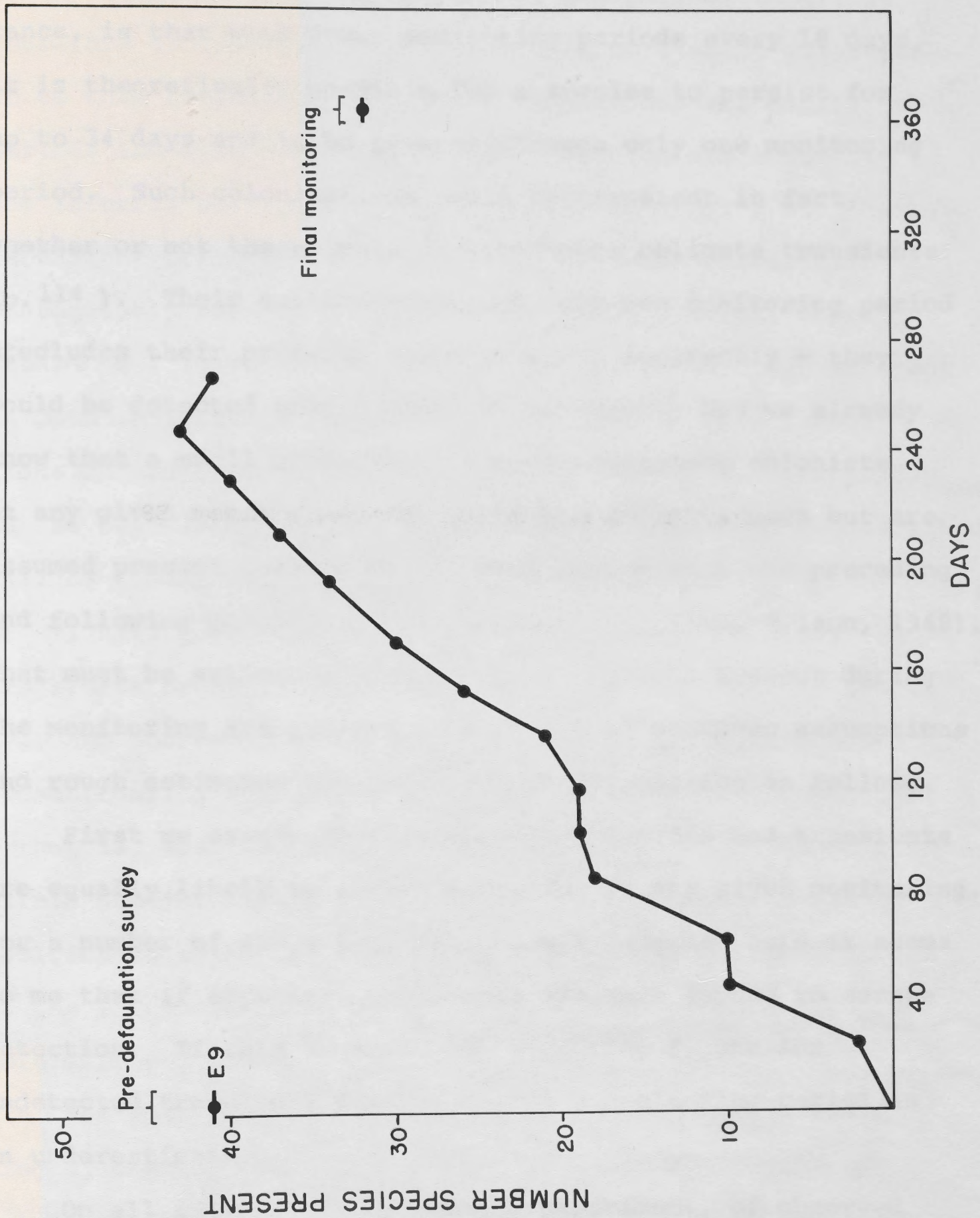

Final monitoring
Pre-defaunation surveys
E2
E3
ST 2
E1
NUMBER SPECIES PRESENT
40
30
20
10
40
80
120
160
200
240
280
320
360
DAYS

Graph 4: Colonization curve of Island E7


NUMBER SPECIES PRESENT
40
30
20
10
Pre-defaunation surveys
E7
Final monitoring
60
120
180
240
300
360
420
480
540
DAYS

1483

Graph 5: Colonization curve of Island E9


NUMBER SPECIES PRESENT
10
20
30
40
50
40
80
120
160
200
240
280
320
360
DAYS
E 9
Pre-defaunation survey
Final monitoring

reasons, and consequently are not shown.

First, and probably of little relative numerical importance, is that with 2-day monitoring periods every 18 days, it is theoretically possible for a species to persist for up to 34 days and to be present through only one monitoring period. Such colonizations would be transient in fact, whether or not the animals involved were obligate transients (p.114). Their existence through only one monitoring period precludes their presence being inferred indirectly - they could be detected only through observation. Now we already know that a small proportion of more persistent colonists at any given monitoring period are not actually seen but are assumed present because of observations at both the preceding and following monitoring periods (Simberloff and Wilson, 1968). What must be estimated is how many transients present during the monitoring are not seen. A series of unproven assumptions and rough estimates can provide a crude solution as follows.

First we assume that persistent colonists and transients are equally likely to escape detection at any given monitoring. For a number of subjective reasons not defended here it seems to me that if anything, transients are more likely to escape detection. If this is true, the resulting figure for undetected transients present during a monitoring period is an underestimate.

On all islands throughout the experiment, of <u>observed</u>

colonists at any given monitoring period at least one third were transients (present for one or two periods only) and therefore at most two thirds were more persistent colonists. If we then estimate that for all islands and all monitoring periods the mean number of species observed was about 24 and inferred was about 4, then for the 16 (=2/3 x 24) observed persistent colonists there were 4 unobserved colonists. Consequently for the 8 observed transient species, there should be 2 (=4/16 x 8) unobserved transients. The increment in both immigration and extinction rate from this source alone should therefore average 2 spp./18 days = .11 spp./day, but an estimate from this source and a second one now described will be calculated which is much greater.

I have just dealt with the error incurred through transients present during a monitoring period but not seen. A second source of error is introudced by transients not present during any period (and hence, of course, never seen) - that is, species which immigrate and are extinguished all within one interval between two monitoring periods. In addition to being far more important numerically than errors of the first class, this second sort of error is considerably more difficult to estimate. Two methods have been used.

The first is purely probabilistic and necessitates a single, crucial measure - the distribution of lengths of colonizations lasting from 1 through 34 days. In the absence

of evidence on this distribution the calculation was done on the assumption that it is uniform - i.e.: that colonizations lasting for 1,2,....., 34 days are equiprobable. There are again rather subjective reasons which will not be defended here for believing that this is not so, but that instead colonizations lasting 1 or 2 days are far more frequent than those lasting 34 days. The extent of monotonicity of the curve cannot yet be quessed, however, so the uniform distribution was used for simplicity of calculation. Again a deviation from uniformity in the direction indicated would tend to raise greatly the number of immigrations and extinctions not observed and so the estimate of inaccuracy introduced through this source is also a lower limit, probably a gross underestimate.

Granted the uniform distribution, it is a routine matter to calculate for a given species present for x days ($1 \leq x \leq 34$) the relative probabilities that it will be present during 0,1, or 2 2-day monitoring periods, respectively, and thence to calculate how many transients were present during no monitoring period given a certain number present at one monitoring period (this last figure, of course, must be estimated from the number observed plus the correction indicated on p. 78). The net result of this procedure is that for every colonist known present through one monitoring period only, there were 0.42 colonists which were present during no

monitoring period. And whereas that one colonist known present had an expected persistence time of 17.1 days, the estimated 0.42 colonists not present during any monitoring period had an expected persistence time of 6.0 days. In sum, whereas we had estimated 1 transient with mean time to extinction of 17.1 days, we now estimate a lower limit of 1.42 transients with mean time to extinction of 13.8 days.

Again looking at a typical island during one monitoring period with 24 observed species present, we earlier estimated that if 8 of those were transients there were also 2 unobserved transients, or a total of 10 transients. We must now estimate a total of at least 14 (=1.42 x 10) transients, and the 4 species added have an even greater extinction rate than the original 10 transients. In addition, this probably greatly underestimates the number of transients (as explained above) and a more realistic estimate would probably be at least 20 total transients during one interval for 8 transients observed during the monitoring period at the end of that interval. To guess at the total increment in immigration and extinction rates from this estimate is exceedingly difficult because, as has just been indicated, not all transients have the same extinction rate and the unobserved ones tend to have higher rates. But the very least the increment could be from this line of reasoning is (20 spp. - 8 spp.)/18 days = .67 spp./day.

The second estimate of the error introduced into extinction

rate measurements through transients not being present during any 2-day monitoring period when monitoring is performed every 18 days (though not of the lesser error introduced through observational failure) is provided by the colonization simulation described below. This estimate was derived by generating data on immigration and extinction every two days for 190 days, and then looking first at the total number of simulated immigrations and extinctions during an 18 day interval (an average daily extinction rate for an interval = total extinctions for all 18 days/18 days) and then at the number of immigrations and extinctions recorded if only the data from a single 2-day monitoring period every 18 days are available (average daily extinction rate for an interval = (total spp. present at any time during the first 2-day period but never during the second 2-day period)/18 days). That is, the same random events were used - in the first instance all these events were observed, while in the second only a subset were observed.

It should be noted that, whereas the previous method extimated the minimum possible error in observed I and Ex rates, the simulation yields a maximum since it assumes that the presence of a species through n consecutive periods does not increase the probability of its persistence through n+1 consecutive periods, surely a pessimistic outlook. That is, this method overestimates the ratio of the observed 2-day

rates to the observed 18-day rates.

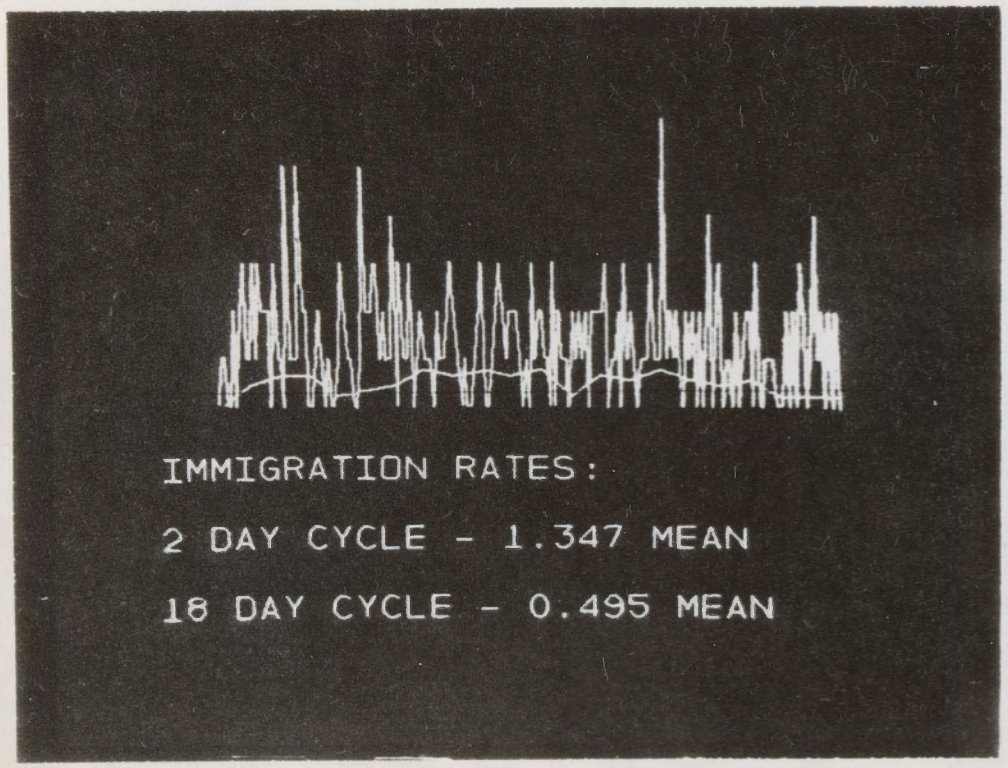
The invasion and species extinction rates used in this simulation, given in Table 2, were chosen as described in a later section to accord with the observed crude distribution of persistence times and immigration rates for the Keys defaunation experiment and the approximate non-interactive equilibrium indicated for island E2. As will be discussed, storage considerations necessitated a simulation of only half the Keys species pool, but the approximate distribution of the $e_{t_0}(\alpha)$ and $i_{t_0}(\alpha)$ were unchanged.

Results of the simulation are pictured in Figures 1 and 2 and summarized in Table 3. In the figures, the jagged line represents the average I and Ex rates when 2-day monitoring periods are continuous, while the lower (usually), smoother line represents the average rates when monitoring consists of a single 2-day monitoring period every 18 days.

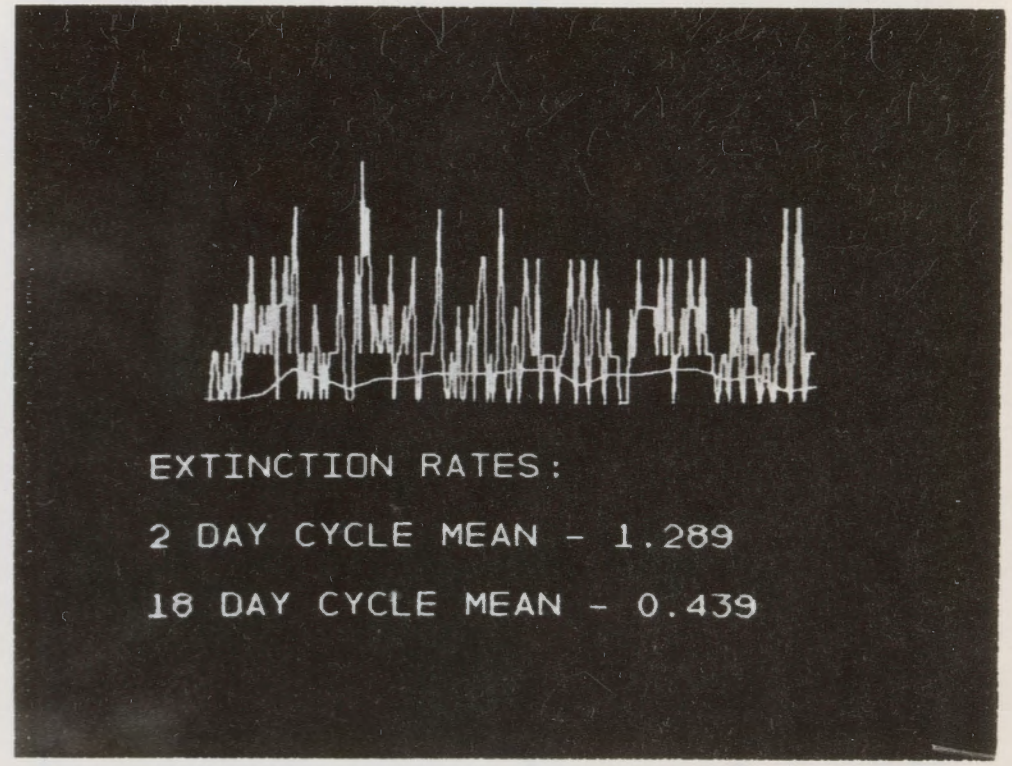
The important numbers in Table 3 are not the rates themselves, which are certainly lower by a factor of 2 (since the species pool was halved) and furthermore are distorted by the inaccuracies of the assumed distributions of the $i_{2\text{-day}}(\alpha)$ and $e_{2\text{-day}}(\alpha)$. The significant column rather is the last, since the ratios of observed rates are unaffected by the halving of the species pool and are much less sensitive than the rates themselves to the exact values of the invasion and species extinction rates. It can be seen that

Figure 1: Immigration rates observed from intermittent and continual monitoring

Figure 2: Extinction rates observed from intermittent and continual monitoring


IMMIGRATION RATES:
2 DAY CYCLE - 1.347 MEAN
18 DAY CYCLE - 0.495 MEAN

1


EXTINCTION RATES:
2 DAY CYCLE MEAN - 1.289
18 DAY CYCLE MEAN - 0.439

2

156

TABLE 2. Invasion and species extinction rates used in simulation to determine errors in observed I and Ex rates.

# of α	$e_{2\ day}(\alpha)$	$i_{2\ day}(\alpha)$
6	5.724×10^{-4}	
16	8.800×10^{-3}	
63	4.968×10^{-2}	
215	5.309×10^{-1}	
300		5.000×10^{-3}

TABLE 3. Differences in observed immigration and extinction rates over 190 days between 2-day monitoring cycle and 18-day monitoring cycle (2-day monitoring period in all instances)

	2-day cycle	18-day cycle	ratio (2-day/18 day)
I max	6.000	0.778	7.712
I mean	1.347	0.495	2.721
Ex max	5.000	0.667	7.496
Ex mean	1.289	0.439	2.936

All rates in spp./day.

the upper limits for the true mean I and Ex rates on the defaunated Keys over long periods of time (at least several months) are the observed rates gotten by monitoring every 18 days multiplied by 2.5-3.0.

It is apparent from either estimate, then, that the error in the observed immigration and extinction rates is so large as to render them almost useless as a measure of true immigration and extinction rates, except possibly for order of magnitude; the error is at least 0.67 spp./day - equal to or larger than the observed rates themselves. Mean turnover rates at equilibrium are probably between 1.5 and 3.0 x the observed rates. The only remaining worth of the observed rates will be to compare them in general size and shape (fluctuations, etc.) to the appropriately derived curves in the simulation; if the agreement is good it will serve as supporting evidence that the rules used in the simulation correspond closely to those in nature.

The observed immigration and extinction curves for all experimental islands were highly variable, with no apparent pattern except for generally higher immigration rates on nearer islands during the first 150 days. Rates were usually between 0.05 and 0.50 spp./day, which is less than the minimum expected error just derived. It will be shown later that the variance about the "expected" immigration and extinction rates is high. If we take 0.35 spp./day as an

approximate mean observed extinction rate near equilibrium, the estimates derived above indicate that true turnover rates at equilibrium for these islands are probably:

$$0.52 \text{ spp./day} = 0.35 \text{ spp./day} \times 1.5 \leq \text{true turnover rate} \leq 0.35 \text{ spp./day} \times 3.0 = 1.05 \text{ spp./day}$$

We must therefore concentrate on the observed colonization curves - since they depict S at a series of discrete points (namely, the monitoring periods) there is no error introduced through species immigrating and going extinct all between two monitoring periods. The monitoring procedure and the evidence for its completeness are discussed in detail elsewhere (Simberloff and Wilson, 1968). The major source of error is undetected transients, which we have just seen probably averages only about 2 species per monitoring period. That the distribution of the number of transients present, though having high variance, changes relatively little through time is a feature of the theory now to be described.

I feel that these observed curves are best explained as the product of colonization first according to the tenets of the non-interaction model, to a level near the equilibrium $\hat{S}$ predicted by that model (and above that determined partly be interaction); thence a slow, irregular decline to a more enduring equilibrium, determined in part by interactions and similar to that obtaining before defaunation. That El may not fit this pattern has already been discussed.

E7 may also deviate somewhat from this scheme. Change in the island itself probably acted to raise both the non-interactive $\hat{S}$ and the interaction-determined $\hat{S}$, and also to prolong the entire colonization process (Simberloff and Wilson, 1968).

The part of the curve determined by the non-interaction model can be predicted in great detail, but once population sizes are sufficiently large for interactions to become significant (which occurs on these experimental islands after a very few oscillations of the colonization curve in its approach to the non-interactive $\hat{S}$) this model breaks down, and data on interaction in general seems insufficient to allow a predictive stochastic model for later colonization even with so simple an island ecosystem as that of the tiny Florida mangrove keys.

It must be reiterated that the non-interaction model produces an equilibrium number of species determined entirely by the $i_{t_0}(\alpha)$ and $e_{t_0}(\alpha)$ in the total absence of interaction. To predict this equilibrium $\hat{S}$ and the expected value of the colonization curve at any point for a given island requires that the $i_{t_0}(\alpha)$ and $e_{t_0}(\alpha)$ for all species in the pool be known. Although this requirement cannot be satisfied directly for any of the experimental islands, it is nevertheless possible to make reasonable estimates of all necessary parameters, and thence to calculate

i) The curve of expected value of S vs. t

ii) The variance of the curve of S vs. t

iii) The equilibrium value of S

and to give the mathematical equation for this "expected" colonization curve. The experimental curve can then be compared to a confidence band about the "expected" colonization curve to see if the hypotheses behind this latter, theoretical curve could reasonably explain the experimental curve. In addition, stochastic simulations utilizing these hypotheses and the data used to calculate the "expected" colonization curve can be performed and the resulting colonization curves compared to the experimental curve.

First let us derive the "expected" colonization curve and its parameters, then discuss the estimates inserted into the resulting equations.

In addition to the measures described above, Bossert and Holland define for each species α a species indicator variable $S_\alpha(n)$ by

$S_\alpha(n) = 1$ if species α is on the island during period n

$S_\alpha(n) = 0$ otherwise

Then for every species α and time period t,

$$(1) \qquad E(S_\alpha(t)) = Pr(S_\alpha(t) = 1)$$

In any discrete simulation a decision must be made about

whether to apply first the $i_{t_0}(\alpha)$ or $e_{t_0}(\alpha)$: whether to invade first and then to extinguish at each discrete time period or vice versa. As the intervals approach 0 (i.e. - as the rates become instantaneous) this difficulty of course disappears; consequently the theoretical discussion to be presented later is unaffected by the convention chosen. For all simulations, however, extinction was performed first and then invasion for every simulated time interval - this was because, as has been shown, most members of the species pool are obligate transients (high $e_{t_0}(\alpha)$) and if extinction were performed after invasion these species would very rarely manifest themselves in the output.

Given this convention,

$$(2)\quad E(S_\alpha(t+1)) = E(S_\alpha(t))(1-e_{t_0}(\alpha)) + (1-E(S_\alpha(t)))i_{t_0}(\alpha) + E(S_\alpha(t))e_{t_0}(\alpha)i_{t_0}(\alpha)$$

$$= E(S_\alpha(t))(1-e_{t_0}(\alpha)-i_{t_0}(\alpha)+ e_{t_0}(\alpha)i_{t_0}(\alpha)) + i_{t_0}(\alpha)$$

Even with fairly large time intervals the products $e_{t_0}(\alpha)i_{t_0}(\alpha)$ are small enough to be omitted without loss of accuracy. This will be done here, though the calculations could as easily be performed with these terms included. In any event, when we pass to the limit below, these terms would be excluded.

We then have

$$(3)\quad E(S_\alpha(t+1)) = E(S_\alpha(t))(1-e_{t_0}(\alpha)-i_{t_0}(\alpha)) + i_{t_0}(\alpha)$$

An equilibrium is attained when

$$E(S_\alpha(t+1)) = E(S_\alpha(t)),$$

which by equation (3) implies that

$$(4)\quad \hat{S}_\alpha(t) = E(S_\alpha(t)) = \frac{i_{t_0}(\alpha)}{i_{t_0}(\alpha) + e_{t_0}(\alpha)}$$

But since we have postulated independence of the species, the expected value of the colonization curve at any given time t is simply

$$(5)\quad E(S(t)) = E\left(\sum_{\alpha=1}^{P} S_\alpha(t)\right) = \sum_{\alpha=1}^{P} E(S_\alpha(t))$$

which approaches as $t \longrightarrow \infty$ (from equation (4))

$$(6)\quad \hat{S}(t) = \sum_{\alpha=1}^{P} \frac{i_{t_0}(\alpha)}{e_{t_0}(\alpha) + i_{t_0}(\alpha)},$$

the result deduced by Bossert and Holland.

Since

$$S_\alpha(t) = (S_\alpha(t))^2,$$

$$E(S_\alpha(t)) = Pr(S_\alpha(t)=1) = Pr((S_\alpha(t))^2=1) = E((S_\alpha(t))^2)$$

Then

$$(7)\quad var(S_\alpha(t)) = E((S_\alpha(t))^2) - E^2(S_\alpha(t))$$

$$= E(S_\alpha(t)) - E^2(S_\alpha(t))$$

We can therefore calculate var $(S_\alpha(t))$ stochastically simultaneously with $E(S_\alpha(t))$. Var $(S_\alpha(t))$ also has an equilibrium, as $S_\alpha \longrightarrow \hat{S}_\alpha$ with increasing t. By substituting equation (4)

into equation (7) we see that

$$(8)\quad \text{var}\,(S_\alpha(t)) \xrightarrow[t\to\infty]{} \frac{i_{t_0}(\alpha)\,e_{t_0}(\alpha)}{(i_{t_0}(\alpha)+e_{t_0}(\alpha))^2}$$

Again, the independence of the species allows us simply to add the variances of the individual curves of $E(S_\alpha(t))$ vs. t to yield the variance of the curve S vs t:

$$(9)\quad \text{var}(S(t)) = \sum_{\alpha=1}^{P} E(S_\alpha(t)) - E^2(S_\alpha(t))$$

$$= \sum_{\alpha=1}^{P} E(S_\alpha(t))(1-E(S_\alpha(t)))$$

Although we now have sufficient information to perform a stochastic simulation for comparison with the experimental data, we first digress to find a general mathematical equation to fit the "expected" colonization curve.

Starting with equation (3):

$$(3)\quad E(S_\alpha(t+1)) = E(S_\alpha(t))(1-e_{t_0}(\alpha) - i_{t_0}(\alpha)) + i_{t_0}(\alpha)$$

$$(10)\quad E(S_\alpha(t+1)) - E(S_\alpha(t)) = -(e_{t_0}(\alpha)+ i_{t_0}(\alpha))E(S_\alpha(t)) + i_{t_0}(\alpha)$$

We may then divide both sides of the above equation by Δt, but before passing to the limit we must recall that the species invasion and extinction rates, i_{t_0} and e_{t_0}, decrease with decreasing time intervals t_0 (since they are defined as the probabilities that a species invades or goes extinct,

respectively, within one interval t_0). Earlier i_α and e_α were defined as the rates per time of invasion and extinction, respectively. Working only with invasion, from the Poisson distribution for random events it follows that:

$$i_{t_0}(\alpha) = \Pr(\text{species } \alpha \text{ invades in interval } t_0) =$$

$$1-\Pr(\text{species } \alpha \text{ does not invade in interval } t_0)$$

$$= 1 - \frac{(i_\alpha t_0)^0 e^{-i_\alpha t_0}}{0!} = 1 - e^{-i_\alpha t_0}$$

$$\text{Consequently } \lim_{t_0 \to 0} \frac{i_{t_0}(\alpha)}{t_0} = \lim_{t_0 \to 0} - \frac{e^{-i_\alpha t_0} - e^{-i_\alpha 0}}{t_0 - 0}$$

$$= - \left. \frac{de^{-i_\alpha t}}{dt} \right|_{t=0} = i_\alpha$$

An analogous treatment for extinction yields

$$\lim_{t_0 \to 0} \frac{e_{t_0}(\alpha)}{t_0} = e_\alpha$$

With this in mind, dividing equation (10) by Δt yields:

$$\frac{E(S_\alpha(t+1)) - E(S_\alpha(t))}{\Delta t} = \frac{-(e_{t_0}(\alpha)+i_{t_0}(\alpha))E(S_\alpha(t)) + i_{t_0}(\alpha)}{\Delta t}$$

which on passing to the limit ($\Delta t \longrightarrow 0$) gives

$$(11) \quad \frac{dE(S_\alpha(t))}{dt} = i_\alpha - (e_\alpha + i_\alpha)E(S_\alpha(t))$$

Rearrangement and integration yield:

$$\int_0^{S(t)} \frac{dE(S_\alpha(u))}{i_\alpha-(i_\alpha + e_\alpha)E(S_\alpha(u))} = \int_0^t du$$

And since $E(S_\alpha(0)) = 0$ for a defaunated island, we find:

$$(12) \quad E(S_\alpha(t)) = \frac{i_\alpha}{i_\alpha + e_\alpha} (1-e^{-(i_\alpha + e_\alpha)t})$$

which defines the curve approached by $E(S_\alpha(t))$ as the time intervals used approach 0.

Because of the independence of the species,

$$(13) \quad \lim_{t_0 \to 0} E(S(t)) = \sum_{\alpha=1}^{P} \frac{i_\alpha}{i_\alpha + e_\alpha}(1-e^{-(i_\alpha+e_\alpha)t}) \xrightarrow[t\to\infty]{} \sum_{\alpha=1}^{P} \frac{i_\alpha}{i_\alpha+e_\alpha}$$

Although only for carefully chosen sets of i_α and e_α can this curve be represented in the form derived by MacArthur and Wilson (1963, 1967):

$$(14) \quad E(S(t) = \hat{S}(1-e^{-Gt}) \quad (\text{where } G = \frac{dEx}{dS} - \frac{dI}{dS} \text{ at an } S$$

near $\hat{S}$, for curves of I and Ex vs. S, not t).

the curve determined by any set of i_α and e_α is very similar in shape to (some) curve fitting equation (14). That is, because of the monotonicity and shape of each term in the sum

$$\sum_{\forall i} C_{1i}(1-e^{-C_{2i}t})$$

the sum itself resembles a curve of the form $C_1(1-e^{-C_2t})$, where the C_{1i} and C_{2i} are all arbitrary constants and C_1 and C_2 are fitted constants.

The theoretical basis for the similarity of equations (13) and (14) is the assumption of MacArthur and Wilson in deriving equation (14) that for S near $\hat{S}$, the curves I(s) and Ex(S) are at least locally straight, which is exactly equivalent to saying that the species are independent and no interactions are occuring (the underlying assumption of equation (13)). Then dEx/dS is simply the (positive) increment in island extinction rate per species, and dI/dS the (negative) increment in immigration rate per species already on the island. This tacitly assumes that all species have the same (intrinsic) extinction and invasion rates. But if all the i_α were equal and all e_α were equal in equation (13), we would have

$$(15)\quad \lim_{t_0 \longrightarrow 0} E(S(t)) = \frac{Pi_\alpha}{i_\alpha + e_\alpha}(1-e^{-(i_\alpha + e_\alpha)t}),$$

and since MacArthur and Wilson (1968) find $\hat{S} = \frac{IP}{I+E}$ (I and E functions of S), which when inserted into equation (14) gives:

$$(16)\quad E(S(t)) = \frac{PI}{I+E}\left(1-e^{-\left(\frac{dEx}{dS}-\frac{dI}{dS}\right)t}\right),$$

the two equations (15 and 16) are equivalent, for I have just shown that under the hypothesis invoked by MacArthur and Wilson in their derivation:

$$\frac{dEx}{dS} = \text{average extinction rate/species} = e_\alpha,$$

(equal for all species)

and similarly for immigration rates.

Equation (13) is thus a more general equation for the colonization curve, reducing to equation (14) when all species have the same characteristics

By substituting equation (13) into equation (9) we derive for the variance of the colonization curve at any time t:

$$(17)\quad \text{var}\,(S(t)) = \sum_{\alpha=1}^{P}\left(\frac{i_\alpha}{i_\alpha+e_\alpha}\right)\left(1-e^{-(i_\alpha+e_\alpha)t}\right)\left(1-\left(\frac{i_\alpha}{i_\alpha+e_\alpha}\right)\left(1-e^{-(i_\alpha+e_\alpha)t}\right)\right)$$

If for all α , $i_\alpha = e_\alpha$, then the last factor in the sum goes from 1 at time 0 to 1/2 at time ∞ . Under these circumstances, then, the ratio variance/mean goes from 1 at time 0 to 1/2

at time ∞, as noted by MacArthur and Wilson (1967). More generally, if $i_\alpha = Ce_\alpha$ for all α, then the ratio variance/mean goes from 1 at time 0 to $\frac{1}{C+1}$ at time ∞; for any combination of e_α and i_α, the ratio falls from 1 at time 0 to

$$\sum_{\forall\alpha} \frac{i_\alpha}{i_\alpha + e_\alpha} \left(1 - \frac{i_\alpha}{i_\alpha + e_\alpha}\right) \Big/ \sum_{\forall\alpha} \frac{i_\alpha}{i_\alpha + e_\alpha}$$

at time ∞, and can be calculated explicitly for any t from equation (17).

We have thus far given the characteristics of the colonization curve for so long as inter- and intraspecific interactions are of minimal significance. As has already been discussed, for all islands but E1 populations apparently reached sufficient size for this condition to break down within the first few oscillations of the colonization curve in its approach to $\hat{S}$. That is, at t such that E(S(t)) was still considerably (perhaps 25%) lower than the $\hat{S}$ determined by the non-interaction theory just presented, the assumptions underlying that theory ceased to be justified. The logical question now is: whither S?

There is independent evidence that islands where normal amounts of interaction are occurring are in equilibrium. Most convincing is that untreated islands of similar area and distance from source have similar numbers of species present (Wilson and Simberloff, 1968). Furthermore, now that interactions have become important on the experimental islands colonization curves have not fluctuated widely and

irregularly but instead have continued relatively constrained oscillation within a narrow band.

Given the large variance of S(t) derived above, it may seem presumptuous to attempt to predict the direction S will now take on the experimental islands, or indeed even to claim from the shapes of the colonization curves alone that S is no longer approaching the non-interactive $\hat{S}$ (even though the tenets of the model no longer apply). There are, however, three reasons for feeling that the colonization curves are destined to equilibrate more enduringly about slightly lower $\hat{S}$'s than those determined by the non-interaction model (and lower than those fractions of the non-interactive $\hat{S}$ already achieved on all islands but E1), and that the descent of S toward this enduring, interaction-determined $\hat{S}$ has already begun.

First, one would expect intuitively that interactions on these Rhizophora islands would reduce the number of species. This would obviously be so for competitors (e.g. - two or more species utilizing the same part of the mangrove tree). As concerns predators, it should be noted that many of these subsist largely on transients no matter which species are on the island and whatever the sizes of their populations. A prime example is the orb-weaving spiders. Several species were consistently among the earliest colonists and all observed webs were laden with flies and veliid bugs

(none of which ever breed on these islands but all of which are abundant as transients). Even after the islands were colonized by sizable populations of potential prey species the orb-weavers continued to utilize the same transient prey almost exclusively. Ants, which are probably active predators of such relatively defenseless insects as psocopterans and thrips when these abound, are nevertheless apparently able to build up populations in the absence of high densities of these prey, and many species have been seen repeatedly carrying bits of detritus from about mangrove roots even on untreated islands.

Second, on all islands but E1 and E2, the colonization curve at the final regular monitoring was higher than (or equal to, for E9) the pre-defaunation S. As will be explained below, since E1 is the most distant island it would be expected to take longest to achieve any given fraction of the non-interactive $\hat{S}$ (and may not reach nearly as high a fraction as the other islands before interactions become important, for reasons given on p.143). Conversely, E2 as the nearest island should rise to any given fraction of the non-interactive $\hat{S}$ sooner than the other islands, and furthermore interactions might be expected to become significant earlier on near islands since any given species would be expected to colonize near islands first. Apparently a peak was reached on E2 near the penultimate monitoring period,

and this will be used here instead of the final monitoring period.

From the first column in Table 1, then, we have four positive numbers and one 0 (no difference), not counting E1. We cannot calculate the probability of no change, but even though none of the other four figures in itself can indicate a trend (because of the high variance of the colonization curve) if we assume that all four pre-defaunation $\hat{S}$'s were randomly taken from the same class of oscillations about the same $\hat{C}$'s as were final (or penultimate, for E2) S's, the probability of having four positive and no negative numbers is clearly

$$\binom{4}{4}\left(\frac{1}{2}\right)^4 = .0625$$

This indicates, though not conclusively, that the fraction of the non-interactive $\hat{S}$ achieved at the end of regular monitorings was systematically slightly higher than the presumably more enduring $\hat{S}$ found before defaunation.

Finally, identical reasoning using the last column of Table 1 (with E1 now included; since interactions are permitted by increasing population sizes on the other islands, at least some interaction ought to occur among the (few) species on E1) allows the inference that S has been decreasing systematically since the end of regular monitoring. Presumably it is approaching a more enduring $\hat{S}$ determined partly

TABLE 1. Changes in numbers of species present (a) from pre-defaunation to last regular census, and (b) from last regular census to final monitoring

Island	ΔS Pre-Defaunation to Last Regular Census	ΔS Last Regular Census to Final Monitoring
E1	-3	-9
E2	-9 (+1)*	0 (-10)*
E3	+3	-2
ST2	+1	-2
E7	+8	-7
E9	0	-9

*Penultimate (not last) regular census

by interactions, and on all islands but E1 this should be closely similar to the similarly determined pre-defaunation $\hat{S}$. Despite the fact that no single decline is significant because of the high variance of the colonization curve, the probability of 6 decreases and no increases is

$$\binom{6}{6}\left(\frac{1}{2}\right)^6 = .016$$

This strongly implies a systematic decline.

The estimated S both before defaunation and after the regular monitorings, given in Graphs 3-5, includes as an estimate of the number of unseen colonists the mean number of unseen colonists during the last four regular monitorings (p. 95). But both before defaunation and after the regular monitorings more species had large populations than during the periodic censuses, and it seems possible that the probability of not seeing any given species would be correspondingly reduced.

Consequently the estimates of the number of unseen colonists before and after the experiment were, if anything, overestimates. A suitable correction would increase the numbers in the first column of Table 1 and decrease those in the second column, which would strengthen the above conclusions about the relationship of the non-interactive $\hat{S}$ to a more lasting $\hat{S}$ determined partly by interaction.

Looked at another way, the observed data seem to indicate that, no matter what our pre-conceived notions of the relative numerical importance of competitive interactions vs. symbiotic ones, on these islands, at least, competition and other interactions tending to reduce the number of species in a community predominate over those symbiotic relationships which tend in a relatively stable community to raise the number of co-existing species through more effective partitioning of the environment or greater diversity of niches.

Although we can thus predict that on all islands but the most distant (E1) the colonization curve will first rise according to the non-interaction model to a large fraction of $\hat{S} = \sum_{\forall\alpha} \frac{i_\alpha}{i_\alpha + e_\alpha}$, slightly above the original, interactive $\hat{S}$, then decline gradually to this more enduring $\hat{S}$, information on interaction in general is insufficient to permit a predictive stochastic model for later colonization, as stated earlier. Planned later monitorings may yield empirical evidence on the colonization process.

This discussion has neglected the effects of evolution; it is assumed that evolutionary events, including speciation, play a minor role over any conceivable experimental time periods. A general expected trend might be a gradual rise in $\hat{S}$ as many of the colonists evolve together so as to divide more effectively the available microhabitats (Wilson and

Taylor, 1967). Present knowledge of evolutionary rates cannot eliminate a short-term effect, and it should be noted that the large, distant islands posited on p. 128 would probably be exactly those where evolution would occur fastest. The islands in the Keys defaunation are too unstable for long-term changes to be predicted and all are too near (and hence have too much invasion) for their populations to become genetically isolated from those of the source area, much less specifically distinct.

We still must examine how this S curve, whose general characteristics have just been determined, varies with island distance from source (area and other physical island characteristics remaining constant). Since this variable is dependent on the immigration and extinction rates on islands of differing distances, the several rates will now be treated together.

The expected value of the extinction curve at any time t can be calculated easily from the $E(S_\alpha(t))$. For if we let $Ex_\alpha(t)$ be the contribution of species α to the island extinction rate at time t, then

$$E(Ex_\alpha(t)) = E(S_\alpha(t))e_\alpha = \frac{i_\alpha e_\alpha}{i_\alpha + e_\alpha}\left(1-e^{-(i_\alpha+e_\alpha)t}\right)$$

And the expected value of the island extinction rate, since we are assuming species independence, is clearly

$$E(Ex(t)) = \sum_{\alpha=1}^{P} \frac{i_\alpha e_\alpha}{i_\alpha + e_\alpha} \left(1-e^{-(i_\alpha+e_\alpha)t}\right)$$

The "expected" extinction curve, therefore, has exactly the form of the "expected" colonization curve, with each of the P components a constant proportion (e_α) of the corresponding component of the colonization curve. This constant proportion is a reflection of the lack of interaction among species.

Similarly, if I_α (t) is the contribution of species α to the immigration rate at time t,

$$E(I_\alpha(t)) = (1-E(S_\alpha(t)))i_\alpha = i_\alpha - \frac{i_\alpha^2}{i_\alpha + e_\alpha} \left(1-e^{-(i_\alpha+e_\alpha)t}\right)$$

and the "expected" immigration rate is

$$E(I(t)) = \sum_{\alpha=1}^{P} i_\alpha - \frac{i_\alpha^2}{i_\alpha + e_\alpha} \left(1-e^{-(i_\alpha+e_\alpha)t}\right)$$

which is simply a constant ($\sum_{\forall\alpha} i_\alpha$) minus a curve of the form of the "expected" colonization curve, with each of the P components a constant proportion (i_α) of the corresponding component of the colonization curve.

The variances of the extinction and immigration rate curves can be derived similarly to that of the colonization curve, by finding the variance for each species α and then summing, since the species are assumed independent. They are:

$$\text{var}(Ex(t)) = \sum_{\alpha=1}^{P} E(Ex_\alpha(t)) \cdot \left[e_\alpha\left(1-\frac{i_\alpha}{G}\right)\left(1-e^{-Gt}\right)\right]$$

$$\text{and} \quad \text{var}\,(I(t)) = \sum_{\alpha=1}^{P} E(I_\alpha(t)) \cdot \left[\frac{i_\alpha^2}{G}\left(1-e^{-Gt}\right)\right]$$

where $G = i_\alpha + e_\alpha$

For $0 \leq t \leq 150$, the range over which the non-interaction model may hold, and for distributions and values of i_α and e_α of the order of those derived later for insertion into a simulation, these variances are very large fractions of the expected values of Ex(t) and I(t).

The expected colonization rate $(\frac{dS}{dt})$ at time t can be derived either directly by differentiation of the "expected" colonization curve or by subtraction of the expected extinction rate from the expected immigration rate. It is

$$C(t) = \frac{dS}{dt}\Big|_t = \sum_{\alpha=1}^{P} i_\alpha\left(e^{-(i_\alpha+e_\alpha)t}\right)$$

This treatment is valid only so long as the Bossert-Holland model accurately portrays extinction. I have shown that on all but the most distant island this condition held until a large fraction of the non-interactive $\hat{S}$ was achieved. Beyond this point I and Ex may fluctuate in an as yet unpredictable manner - it is impossible to deduce "expected" curves because of the paucity of quantitative information on interaction. Of course, that an equilibrium $\hat{S}$ is achieved

implies that at least from that point on I and Ex are approximately equal, however much they would cross and recross on a real island. Furthermore, since the decline from the large fraction of the non-interactive $\hat{S}$ to a longer lasting equilibrium $\hat{S}$ takes place gradually, I and Ex cannot differ greatly for an extended period, Ex obviously being slightly larger on the average than I until the decline is completed. Although the decline is slight in absolute terms as well as gradual, there is no mathematical necessity for the I and Ex rates during the decline and after the enduring equilibrium is reached to resemble those obtaining before the decline. Since the contribution to both I and Ex rates of their joint major component, the transients, should be unaffected by the vagaries of the colonization curve, however, it is impossible for the I and Ex rates after interactions become important to differ greatly in absolute numerical terms from those before interactions are significant.

How these interdependent characteristics vary with distance of island from source remains to be explained. For the initial part of colonization while S rises to a large fraction of the non-interactive $\hat{S}$ this is a simple matter. Beyond this point, when interactions become effective, it is much more difficult.

Concerning ourselves only with the initial colonization, then, as island distance increases the i_α should all decrease,

while the e_α remain constant. This should produce a lower $\hat{S}$ since:

i) At any given time there will be fewer transients present.

ii) When a more persistent colonist is extinguished, replacement by another, similar species takes longer.

Mathematically the decrease in $\hat{S}$ is determined by equation 11:

$$\hat{S} = \lim_{t \to \infty} E(S(t)) = \sum_{\alpha=1}^{P} \frac{i_\alpha}{i_\alpha + e_\alpha}$$

Since every term in the sum decreases (all i_α decrease) the sum itself is reduced.

It should also take longer to achieve any given fraction of the (lower) equilibrium $\hat{S}$ as distance increases. Biologically this can be explained by the longer time necessary for that component (of the given fraction of $\hat{S}$) composed of "good" colonists(not obligate transients) to arrive. From equation (10) we find that for every species α the expected time t necessary to reach any given fraction x of the $\lim_{t \to \infty} E(S_\alpha(t))$ $(= \frac{i_\alpha}{i_\alpha + e_\alpha})$ is $t_x = \frac{\ln(1-x)}{-(i_\alpha + e_\alpha)}$ which obviously increases as i_α decreases with greater distance. Since this relationship

holds for every species α, the expected time necessary to reach any given fraction of the non-interactive $\hat{S}$ increases with decreasing distance, from equation (13). Although there is no simple general equation relating the fraction and the expected time necessary to achieve that fraction, a numerical solution is easily gotten for any set of i_α and e_α.

Once interactions become important the effects of distance on colonization characteristics are not so clear. Since it has been shown earlier that the more enduring S determined by interaction is only slightly less than the large fraction of the non-interaction $\hat{S}$ achieved on a real island, while the non-interaction $\hat{S}$ varies greatly with distance (see simulation), it is apparent that the long-term $\hat{S}$ will still be lower as distance from source increases. So will immigration and extinction rates, because of the decreased $i_{t_0}(\alpha)$ and the existence of an equilibrium. A more detailed description is not possible with the present lack of sufficient quantitative data on interactions.

Graph 2 depicts these effects of distance.

THE SIMULATION

In order first to verify that the previously described tenets of the non-interaction model would produce colonization curves with the characteristics already derived, and

second to examine numerically the effects of increasing distance of island from source area, that fraction of the colonization process adequately portrayed by the non-interaction model was simulated on the TACT on-line computer of Harvard University with programs written by Dr. W. H. Bossert.

Time was divided into twenty 18-day periods, and the data from the series 1 islands was examined to give distributions of $e_{18\ day}(\alpha)$ and $i_{18\ day}(\alpha)$ which were in reasonable accord first with the observed 18-day immigration and extinction rates on E2 over the last few monitoring periods, and second with the apparent distribution of persistence times on small islands among the species of Keys mangrove animals.

It is important to realize that the only parameters used in the simulation were the $e_{t_0}(\alpha)$ and $i_{t_0}(\alpha)$, and that these were <u>not</u> chosen directly to produce colonization curves of any shape or height. Rather, the simulated colonization curves are the product of but three factors:

i) the non-interaction model described earlier

ii) $i_{18\ day}(\alpha)$ and $e_{18\ day}(\alpha)$ which were consistent with the observed 18-day immigration and extinction rates on E2 after a large fraction of the non-interaction $\hat{S}$ had been achieved.

iii) a distribution of the $e_{18\ day}(\alpha)$ in rough agreement with the observed distribution of "staying" ability among species in the Keys pool

This distribution of persistence times was not, of course, nicely partitioned into a few well-defined classes of animals. The imprecision in estimating $e_{18\ day}(\alpha)$ for individual species α was so great that no major loss of accuracy was incurred by dividing the 300 species of the simulated pool into four groups, the species within each group all having identical $e_{18\ day}(\alpha)$, rather than assigning to each species a unique species extinction rate.

Factor (ii) may not seem independent of the colonization curves, but it should be recalled that it is the difference between the immigration and extinction curves, not their shapes or numerical values, which determines the colonization curve. Since the $i_{18\ day}(\alpha)$ and $e_{18\ day}(\alpha)$ were chosen to approximate the Ex(t) and I(t) near an equilibrium (that is, when $I(t) \approx Ex(t)$), there is obviously no dependence of the chosen invasion and species extinction rates on the observed colonization curves. Put another way, the $i_{18\ day}(\alpha)$ and $e_{18\ day}(\alpha)$ were chosen to give appropriate numerical values of I(t) and Ex(t) near equilibrium, and these numerical values do not determine the colonization curve.

Although observational data can indicate a distribution

of the $e_{t_0}(\alpha)$, no such inferences can be drawn about the distribution of $i_{t_0}(\alpha)$. So long as $\sum_{\alpha=1}^{P} i_{18\ day}(\alpha)$ is slightly larger than the observed number of immigrations between two monitoring periods 18 days apart the distribution of the $i_{18\ day}(\alpha)$ fits the data. In the absence of concrete evidence on this distribution alone and on the joint distribution of the $i_{t_0}(\alpha)$ and $e_{t_0}(\alpha)$ (i.e. - on the correlation between dispersal and "staying" abilities) the distribution of the $i_{18\ day}(\alpha)$ was taken to be uniform. Undoubtedly it is not uniform in nature, but the assumption of uniformity probably does not alter the results qualitatively. Holland (1968) has shown that the main differences in S(t) among positively correlated, negatively correlated, and uncorrelated invasion and species extinction rates involve the size and frequency of the fluctuations about the E(S(t)) curve, but he was dealing with t very large and we have seen that under these conditions the non-interaction model is invalid.

A second apparent difficulty, that the observed immigration and extinction rates are gross underestimates of the true rates (discussed on p. 146) is circumvented by using 18-day periods in the simulation; the observed 18-day I and Ex rates are consequently the appropriate ones to consider. Ideally, good estimates of the true I and Ex rates (that is, those which would be obtained if continuous

observation were possible) would be used to concoct reasonable $i_{1\ day}(\alpha)$ and $e_{1\ day}(\alpha)$, which in turn would be used in a simulation with 1-day periods. A close fit of the resulting colonization curves to the experimental curve would indicate that the estimates of the I and Ex rates were reasonably accurate. The inability to estimate I and Ex to closer than a factor of 2 or 3, perhaps, and the expense of performing such 1-day simulations did not justify this attempt. Better direct estimates of I and Ex rates may be obtainable, perhaps through the constant presence for a week of a team of investigators on an island.

Nevertheless, similarity of the simulated 18-day colonization curves in shape, if not height, to those of the Keys experiment would constitute strong evidence for the validity of the non-interaction model for early colonization of these islands. Similarity in height would be more difficult to interpret because of lack of information on the joint distribution of the e_α and i_α, or indeed on the distribution of the i_α alone.

Storage considerations and computational expense necessitated the use of 300 species in the simulations instead of the 600-700 estimated in the Keys mangrove species pool. The relative proportions of the $e_{18\ day}(\alpha)$ were held constant, however, so that comparisons with the experimental data were still possible.

The $e_{18\ day}(\alpha)$ and $i_{18\ day}(\alpha)$ chosen for the simulation are shown in Table 4, along with the set of lower $i_{18\ day}(\alpha)$ chosen to simulate increasing distance. Figure 3 shows, in the upper section, the E(S(t)) curve with a 95% confidence band (discussed below) and the $\hat{S}$ determined by the $i_{t_0}(\alpha)$ and $e_{t_0}(\alpha)$. The lower section depicts the curves E(I(t)) and E(Ex(t)), the latter rising. Figures 4 and 5 portray actual stochastic colonizations - the upper sections show the curves S(t), while the lower sections include the 18-day immigration and extinction rates (# events in the interval/18). I(t) is highlighted by "o" at its vertices. Figures 6, 7, and 8 correspond to Figures 3, 4 and 5, respectively, except that the $i_{18\ day}(\alpha)$ were uniformly lowered as just described.

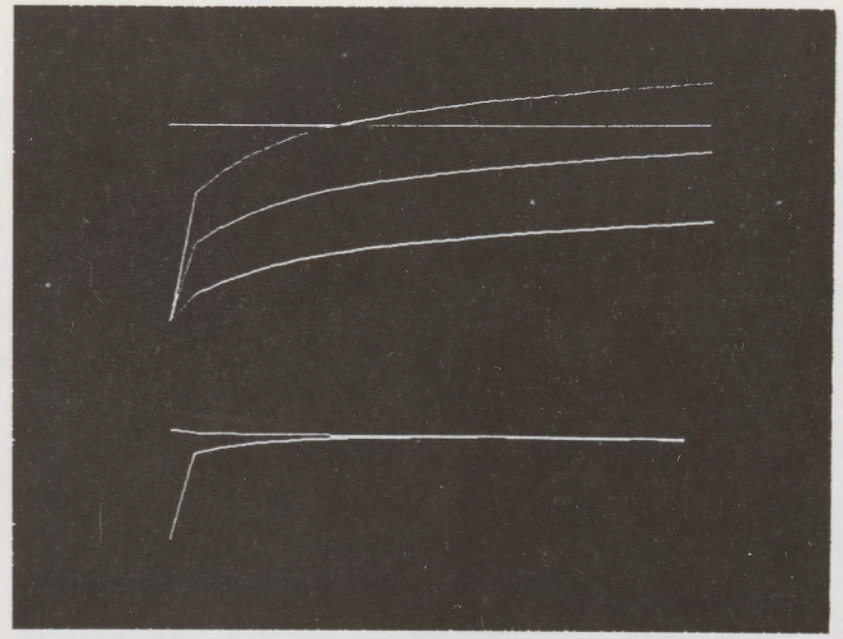
The 95% confidence bands must be interpreted as follows. If we pick a time t <u>in advance</u> at which we will look at S, then in 95% of a number of separate runs S(t) will be within the confidence interval. For at any given point t, $S(t) = \sum_{\alpha=1}^{P} S_\alpha(t)$, where the S_α are independent and are uniformly bounded by, say, 1.1 Since $\sigma_P = (\sum_{\alpha=1}^{P} \text{var } S_\alpha(t))^{1/2}$ increases without bound for any t as $P \longrightarrow \infty$, the Lindeberg theorem holds and the central limit theorem may be applied. Since P = 300 for the simulations the normal approximation should be very close at all t.

TABLE 4. Invasion and species extinction rates used in simulation

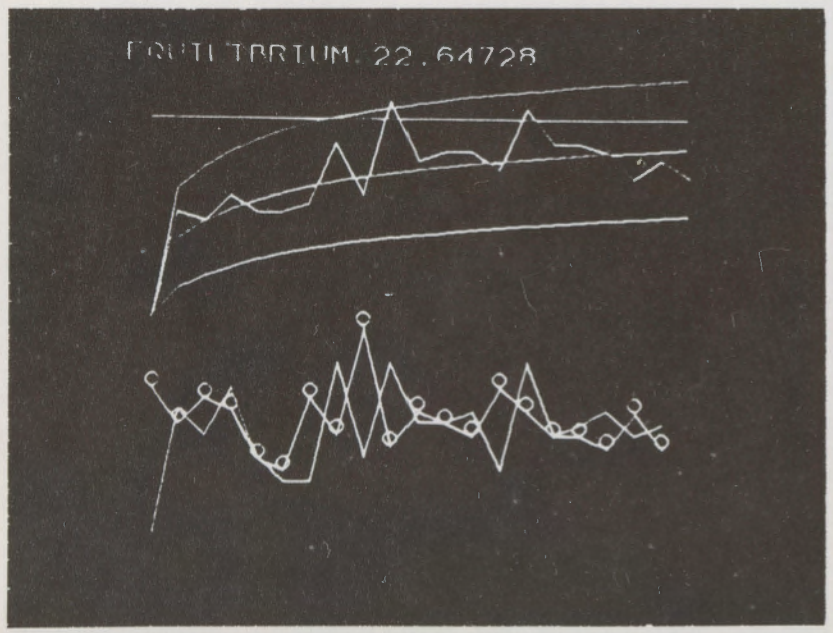
Figures	$i_{18\ day}(\alpha)$	$e_{18\ day}(\alpha)$ (same for all figures)			
1-3	.030, all α				
4-6	.018, all α	# (α):	6	16	63	215
7-9	.030, all α	$e_{18\ day}(\alpha)$:	.004	.060	.300	.995
10	.018, all α					

Figure 3: "Expected" near island colonization, immigration, and extinction curves, with 95% confidence interval and non-interactive equilibrium

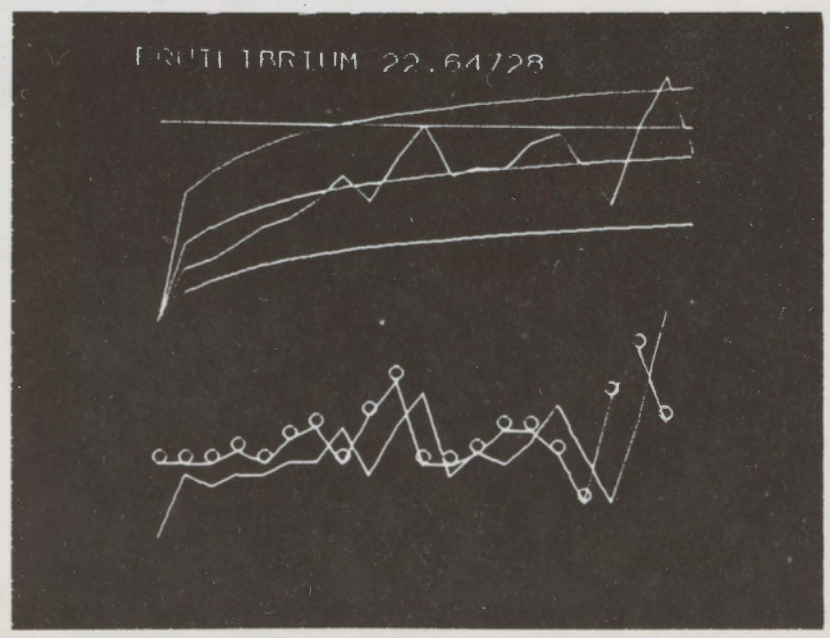
Figures 4-5: Stochastic near island colonization curves (see text)



3



4

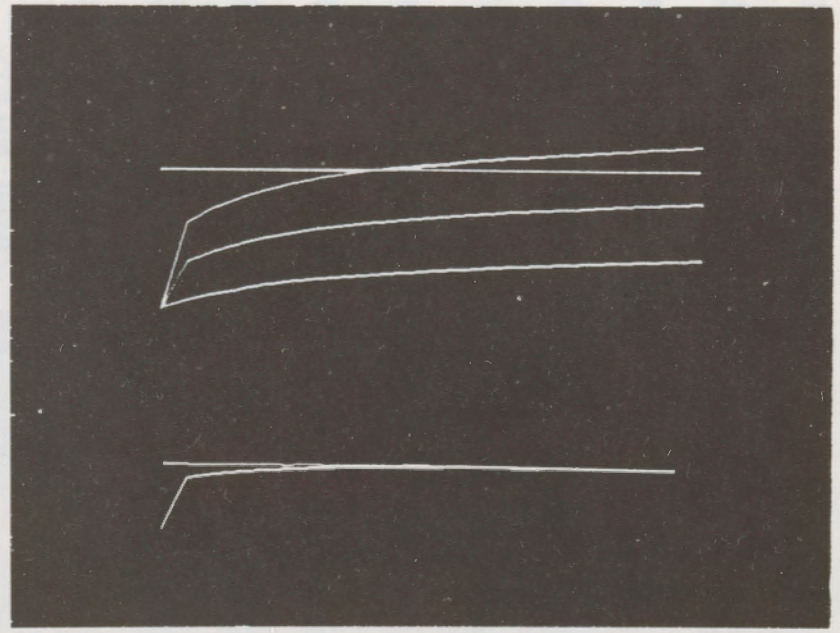


5

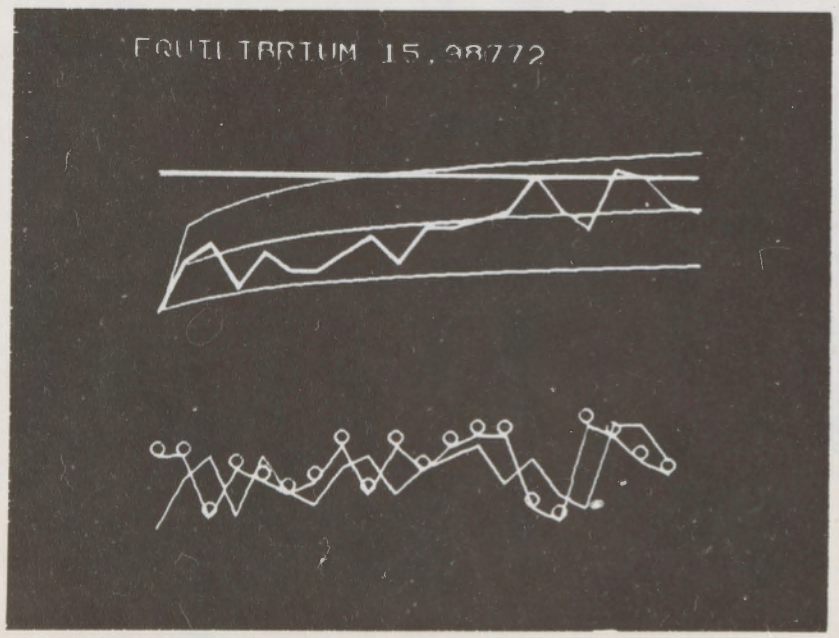
1488

Figure 6: "Expected" far island colonization, immigration, and extinction curves, with 95% confidence interval and non-interactive equilibrium

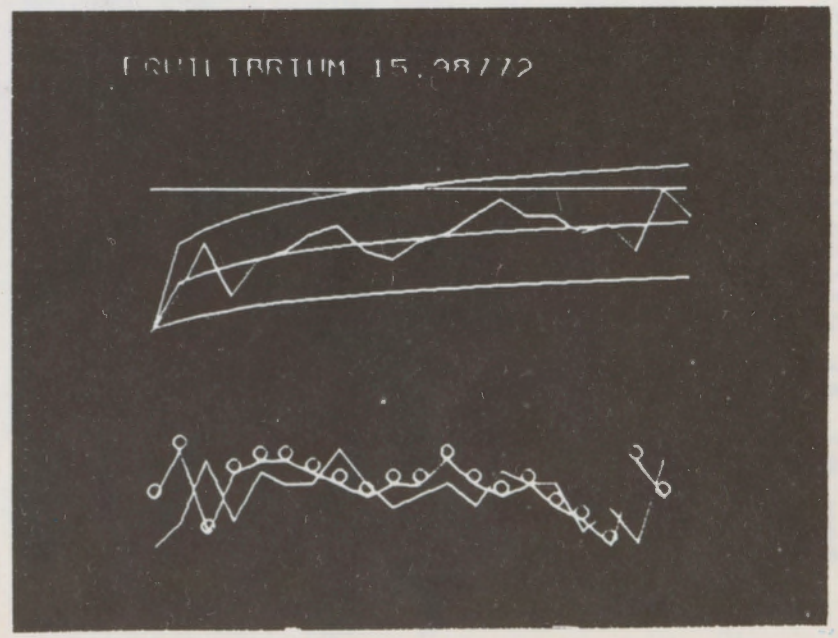
Figures 7-8: Stochastic far island colonization curves (see text)



6



7



8

189

Because the S(t) are related stochastically it is not expected that for any single run S(t) should be inside the confidence interval 95% of the time. In fact, once S(t) goes outside the interval, the probability that S(t+1) is outside the interval is much greater than 5%.

Little need be said about the immigration and extinction curves. The "expected" curves of Figures 3 and 6 demonstrate the properties outlined on p. 179. The curves produced by the simulations appear similar in form to those of the experimental islands (which have not been pictured because of their inability to indicate true immigration and extinction curve shapes and values), but their huge variance renders such comparisons not very meaningful. Furthermore, as was discussed earlier, observed or simulated 18-day immigration and extinction rates are exceedingly poor indicators of the true rates which would be found through daily observation.

The most important implication of the simulated colonization curves is that the general equation for S vs. t cannot be intuited from a few experimental islands. This would be predicted in advance, of course, by the high variance of S(t). In addition, we see graphic evidence for the previously predicted effects of distance on the non-interaction segment of insular colonization. The equilibrium $\hat{S}$, indicated in Figures 4 and 7, is higher on the nearer island. The

"expected" curve on the near island reached 87% of its (higher) equilibrium value at the end of 20 periods (360 days), while on the far island it rose to but 77% of the (lower) equilibrium. On the near island the simulated curves reached the equilibrium value for the first time at 9 and 10 periods, respectively, while on the far island the corresponding values are 14 and 19 periods. Although the sample size is too small to apply appropriate non-parametric tests the implication is clear. It must be remembered, however, that certainly by 20 periods on the defaunated Florida islands interactions had become important and neither the non-interaction $\hat{S}$'s nor the "expected" colonization curves would be valid.

The experimental colonization curves from series 1 islands, particularly E2, can be compared to these simulated curves as follows. The "expected" colonization curve and equilibrium $\hat{S}$ can simply be multiplied by 2 to yield the appropriate curve and $\hat{S}$ for a real island, since the simulations were performed with 300 species instead of the approximately 600 species believed present in the Keys pool, but with the relative proportions of the various estimated $e_{18\ day}$ (α)'s remaining unchanged. This follows directly from equations 4-6. The width of the confidence interval must be multiplied by 2 also; since the variance is multiplied by 2 (equation (7)), σ is multiplied by $\sqrt{2}$. Then $1.96\ \sigma_{600}\sqrt{600} =$

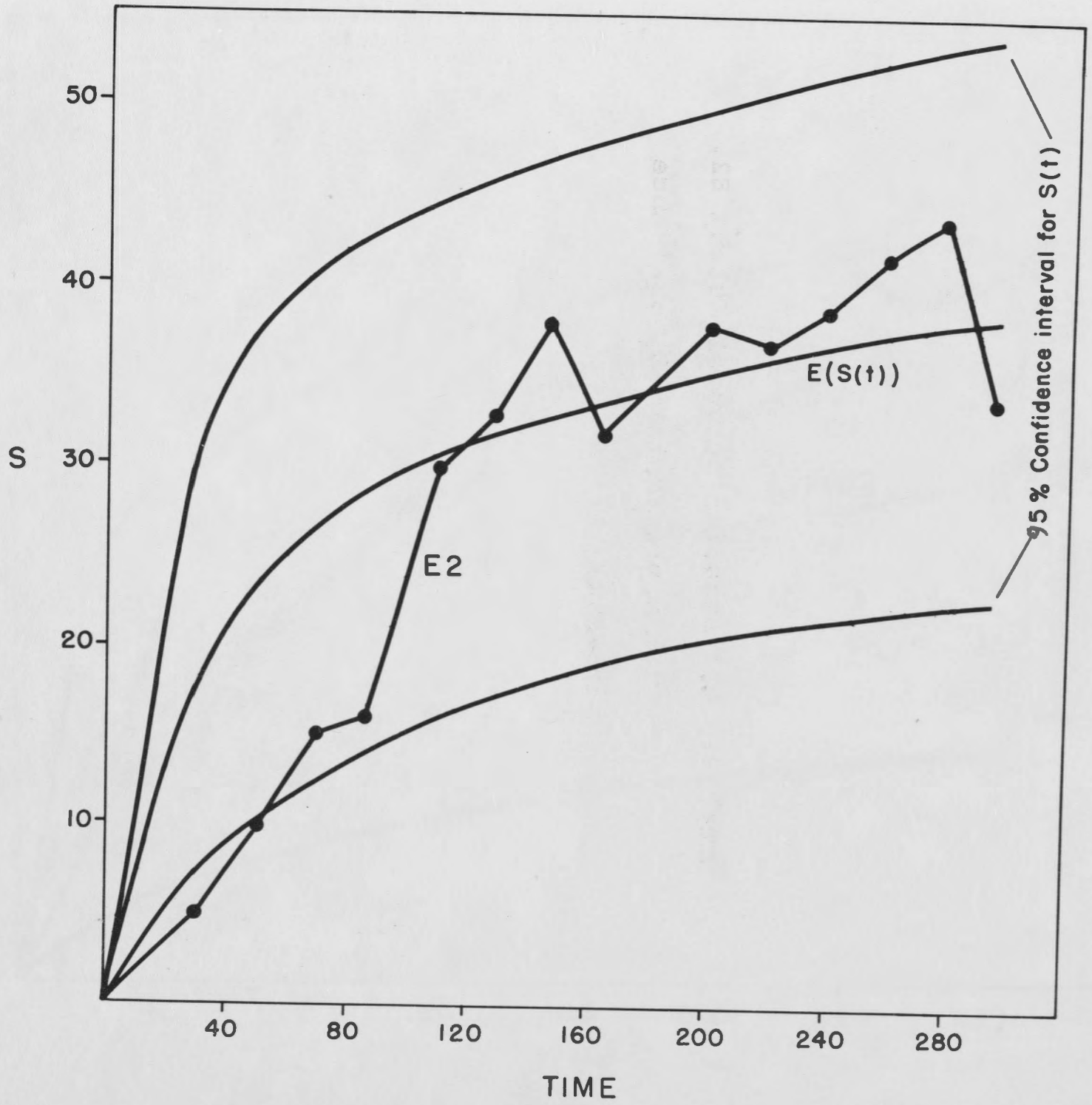
$2 \times 1.96\ \sigma_{300}\sqrt{300}.$

In Graph 6 the colonization curve for E2 has been superimposed on the appropriate near island curves. Both in absolute height and size and frequency of oscillation the similarity to the simulated curves in Figures 2 and 3 is striking. It must be emphasized that there exist other joint distributions of $i_{18\ day}(\alpha)$ and $e_{18\ day}(\alpha)$ which give approximately the same "expected" colonization curve and confidence interval, and that the I and Ex rates used to choose the $i_{18\ day}(\alpha)$ and $e_{18\ day}(\alpha)$ were observed 18-day rates, the inaccuracies of which have been discussed. Nevertheless, the close fit of the simulations to the experimental data supports the validity of the model.

The colonization curves of E3 and ST2 are fitted to the far island confidence interval in Graph 7. Although the $i_{18\ day}(\alpha)$ were not chosen to produce immigration rates similar to those on these two islands, but rather simply to contrast with the near island simulation, the experimental curves seem to fit reasonably well into the confidence interval. It seems likely that a slightly higher $i_{18\ day}(\alpha)$ would have produced an E(S(t)) curve very similar to the E3 and ST2 colonization curves, and that the far island simulation parameters are appropriate to an island with distance intermediate between those of E1 and E3.

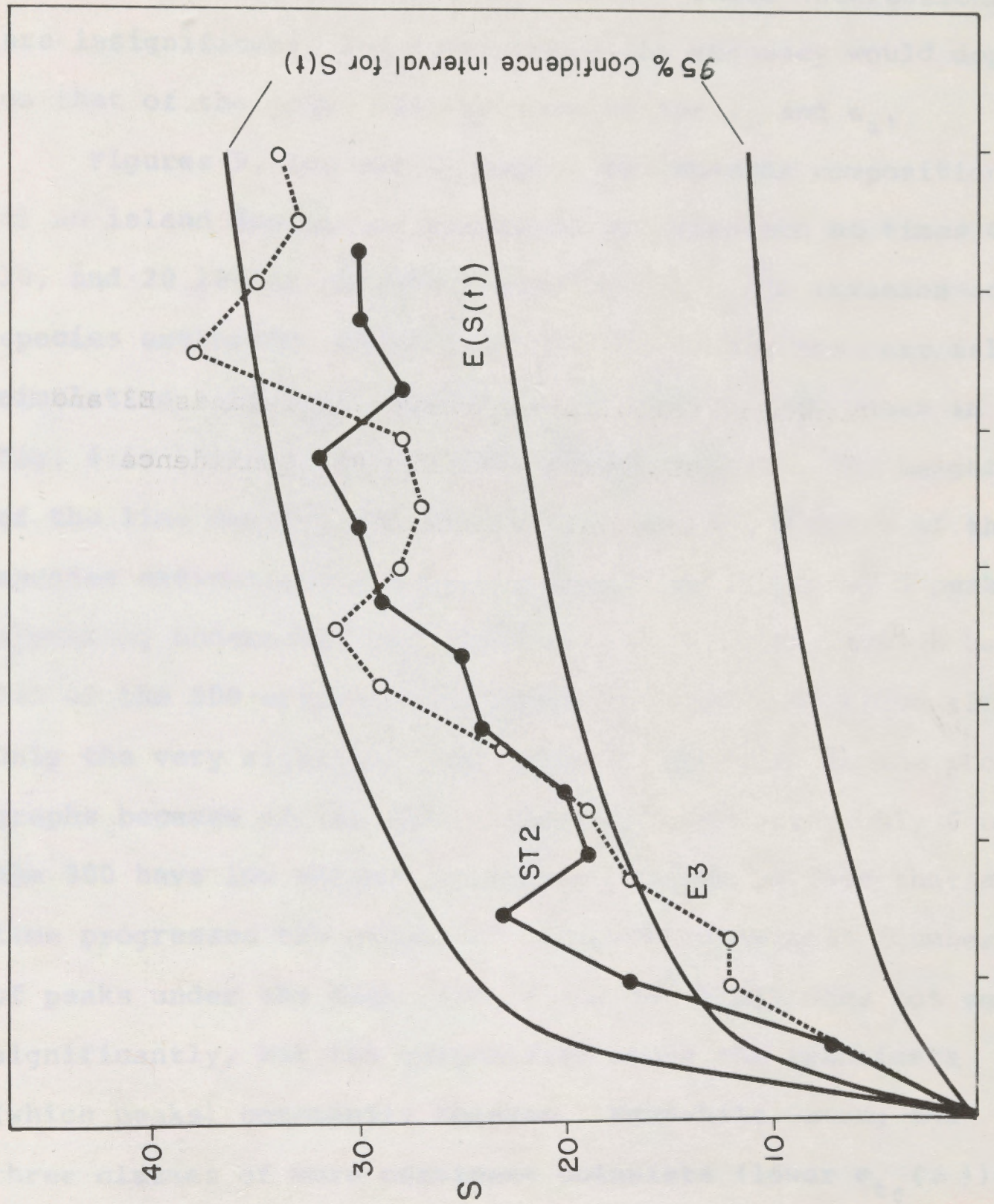
The simulations incidentally provided a means, not

Graph 6: Colonization curve of Island E2, with approximate 95% confidence interval


50
40
30
20
10
S
E(S(t))
95 % Confidence interval for S(t)
E2
40
80
120
160
200
240
280
TIME

CGI 153

Graph 7: Colonization curves of Islands E3 and ST2, with possible 95% confidence interval (see text)


95% Confidence interval for S(t)
E(S(t))
ST2
E3
S
10
20
30
40
40
80
120
160
200
240
280
TIME

pursued, for examining species composition on an island and hence expected degree of species overlap between two identical islands. Again, this treatment would be valid only during the early part of colonization, while interactions are insignificant, and furthermore its accuracy would depend on that of the joint distribution of the i_α and e_α.

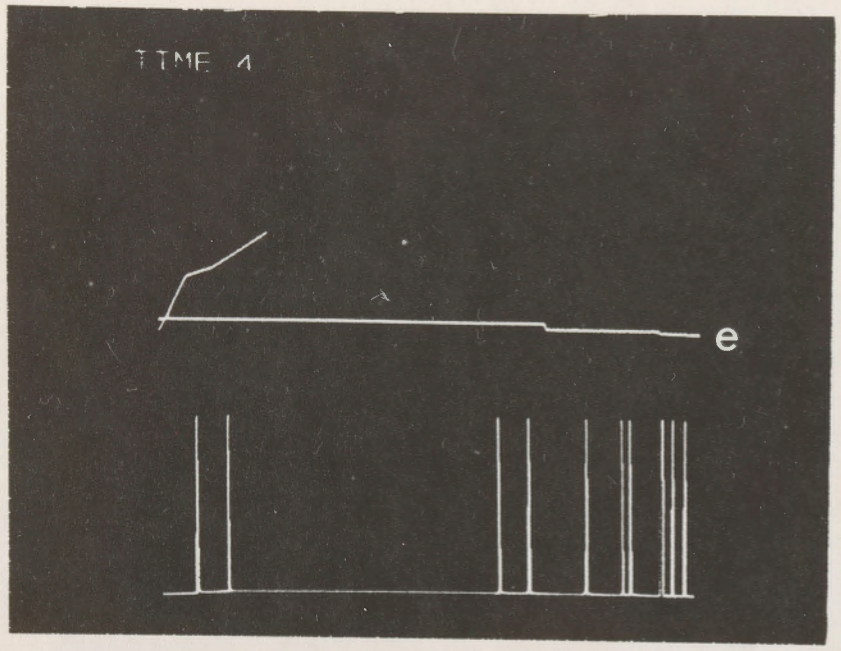
Figures 9, 10, and 11 depict the species composition of an island during one simulated colonization at times 4, 10, and 20 18-day periods, respectively. The invasion and species extinction rates used were those for the near island simulation - in fact, the specific colonization shown in Fig. 4 is the one used in this demonstration. The height of the line denoted "e" in the figures is a measure of the species extinction rate of a species (indicated by a peak) appearing underneath it. Most of the "e" line is high because 215 of the 300 species have identical high extinction rates. Only the very right hand end (almost invisible in the photographs because of its small length) is low since only 6 of the 300 have low extinction rates. It can be seen that as time progresses the number of obligate transients (number of peaks under the high part of the "e" line) does not vary significantly, but the composition among the transients (which peaks) constantly changes. Meanwhile, among the three classes of more permanent colonists (lower $e_{t_0}(\alpha)$) the number of peaks increases with time and, as one would

expect, the further the peak is to the right (lower the $e_{t_0}(\alpha)$ of the species represented by the peak) the longer it tends to persist. The closeness of the rightmost peaks obscures their number, since the oscilloscope is unable to portray 300 peaks distinctly in the short space provided - peaks overlay one another.

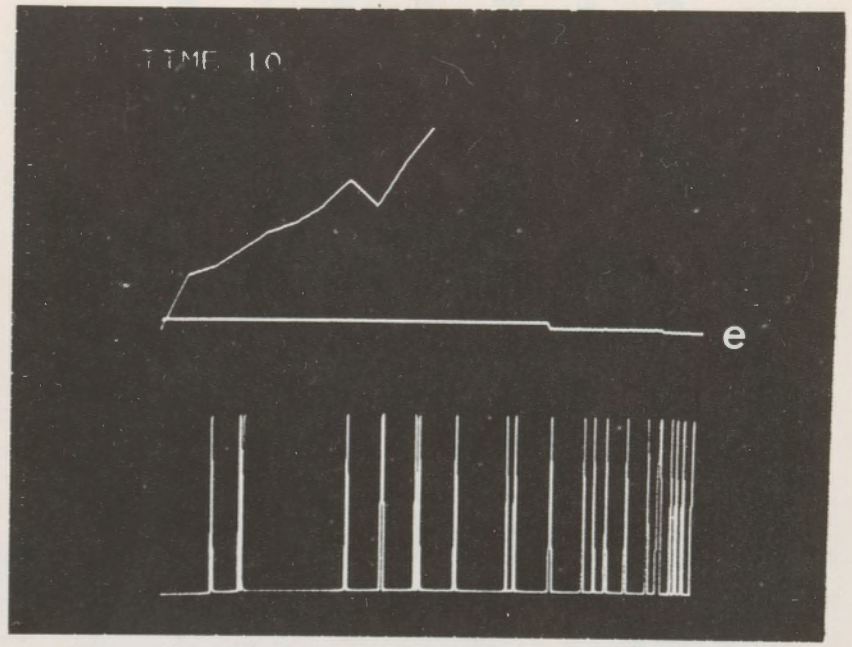
Figure 12 demonstrates the same phenomena. The "e" line has the same meaning as in Fig. 9-11, and the height of the stepped line underneath the "e" line measures the probability that a species with $e_{t_0}(\alpha)$ of the "e" line just above it is present at the time indicated. It is evident that the obligate transients at all times have the lowest probability of presence, and that the increase in the probability of presence with time is greatest for species with lowest $e_{t_0}(\alpha)$.

Figures 9-11: Changes in species composition during one stochastic insular colonization

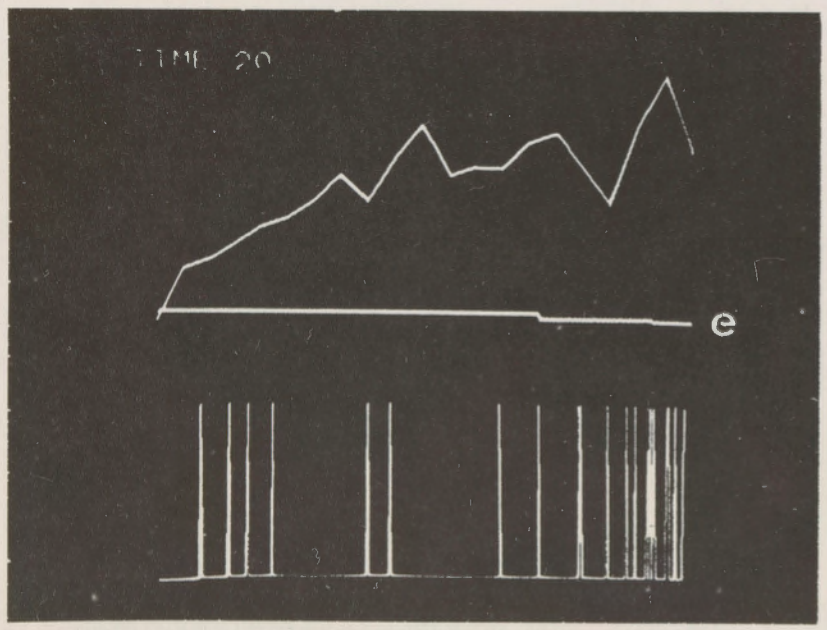
Figure 12: Change with time of relative probability of presence for various classes of colonists (see text)


TIME 4
e

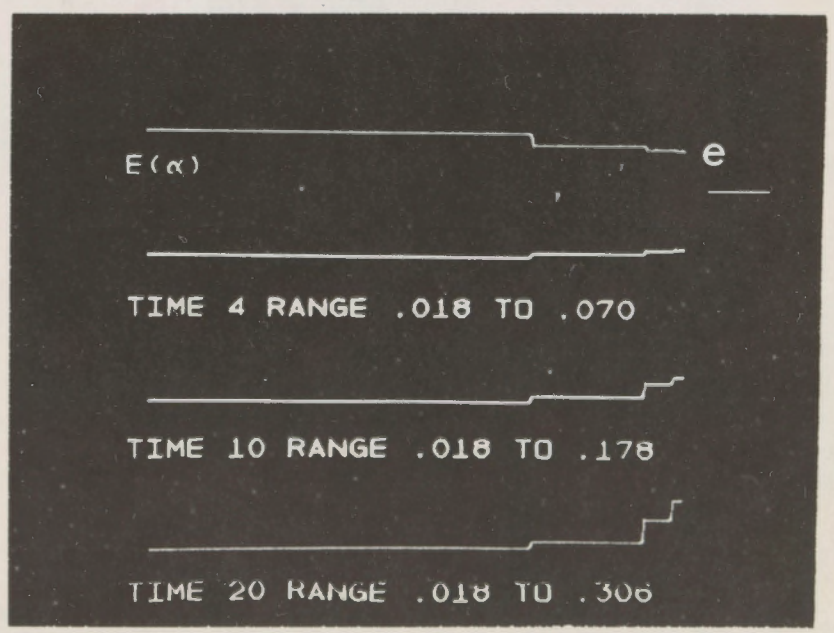
9


TIME 10
e

10


TIME 20
e

11


E(α)
e
TIME 4 RANGE .018 TO .070
TIME 10 RANGE .018 TO .178
TIME 20 RANGE .018 TO .306

12

197

ACKNOWLEDGMENTS

The author expresses his thanks to Dr. William H. Bossert for programming the model described herein and for generous advice on all aspects of this work, and to Dr. E. O. Wilson for a careful reading of the manuscript and numerous suggestions. Computing time for the simulation of island defaunation and recolonization was provided through grant SD-265 of the Advanced Research Projects Agency of the United States Department of Defense.

REFERENCES

Bossert, W. H. 1968. Project TACT. Memorandum 85, Dept. Appl. Math. Harvard Univ.

Holland, P. W. 1968. Some properties of a biogeography model. Memorandum NS-107, Dept. Stat. Harvard Univ. 10 pp.

MacArthur, R. H. and E. O. Wilson. 1963. An equilibrium theory of insular zoogeography. Evolution 17: 373-387.

MacArthur, R. H. and E. O. Wilson. 1967. The theory of island biogeography. Princeton University Press, Princeton. 203 pp.

Simberloff, D. and E. O. Wilson. 1968. Experimental zoogeography of islands. II. The colonization of empty islands. In press.

Wilson, E. O. and D. Simberloff. 1968. Experimental zoogeography of islands. I. Defaunation and monitoring techniques. In press.

Wilson, E. O. and R. W. Taylor. 1967. An estimate of the potential evolutionary increase in species density in the Polynesian ant fauna. Evolution 21: 1-10.