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GROUP ADHERENCE IN THE COMMON TERN¹

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In a preceding contribution (Austin, 1940; 153) it was postulated that colonies of Common Terns (*Sterna hirundo* Linnaeus) breeding on Cape Cod, Massachusetts, form a distinct, concrete group of individuals which is self-sustaining and relatively free from association with other groups during the nesting season. The very small interchange of membership between this and other groups never occurs on the breeding grounds, but only during migration or on the wintering grounds.

An additional decade of field work and study in this area has yielded data which not only further substantiate the concept of the Cape Cod group of terns, but also show some of the reasons for the persistence of this phenomenon. It suggests that while kinship is an important causative factor, as in similar associations of other forms, it is supplemented by long-continued alliance of the component individuals, and increases in effect with age.

Prerequisite to the cohesion of the Cape's tern colonies into a discrete group is the habit of colonial nesting, which in turn is actuated mainly by two major behavior traits, site tenacity and group adherence. The two function concurrently, each enhancing the accomplishment of the other. Site tenacity is based on a tern's attachment to specific terrain. Group adherence is the outcome of the attachment of terns to one another. Site tenacity has already been discussed in detail (Austin, 1946) but its bearing on the establishment and persistence of the Cape aggregation was not stressed.

The purpose of this contribution is to revise and delineate the concept of the Cape Cod group of tern colonies in the light of more recently acquired data, to evaluate the phenomenon of group adherence, and to show its role in the formation and maintenance of the Cape society. The extensive bandings and returns on which these conclusions are based were obtained during 20 consecutive years of work in the Cape Cod colonies, 1929 through 1948. Printing costs forbid their publication in detail. The files of this station show the following totals:

Adults banded	47,409
Chicks banded	165,610
Returns & recoveries, breeding grounds	$31,\!867$
Repeats, breeding grounds	4,800
Recoveries, wintering grounds	292
-	
Total	249,686

¹Contribution number 45 from the Austin Ornithological Research Station.

THE CAPE COD GROUP OF TERNS

The Cape Cod tern colonies are located within a circle about 30 miles in diameter. Its center is on the south shore of Massachusetts Bay midway between the Cape Cod Canal and the Atlantic Ocean. At the four corners of a square inside this circle are the Tern Island, Jeremy's Point, Plymouth, and Ram Island rookeries. That Ram Island is an integral part of the Cape group is contrary to an opinion expressed in 1940. Subsequent field work has demonstrated regular and extensive interchange of its individuals with those of other Cape colonies. Indeed, when the Tern Island colony was disrupted in 1944, one-fourth of its population renested temporarily at Ram Island.

Within this perimeter 13 other smaller nesting sites have been used for varying periods by colonies of from 50 to 3000 pairs of terns. Always about 1000 birds nest in small flocks of a few pairs in widely scattered places. For the last two decades, despite constant shifting of populations between the sites within the circle, the total population of the Cape group has remained approximately 25,000 terns. The lows in the population have always occurred the third and fourth years following seasons of abnormally low chick yields. This indicates that the population is maintained by its own reproduction rather than by accretions from other colonies.

The best proof of the postulated isolation of the Cape group of terns is supplied by an analysis of the 31,867 returns taken from 1933 through 1948. An adequate sample of ten percent of the group's population was trapped for the first time in 1933, and larger samples have been handled every successive season since except in 1934. The average annual sampling is 20 percent, one fifth of the population.

These takes reveal that a small number of terns raised in colonies elsewhere appear regularly in the Cape territory, and become integral members of the group. These so-called "foreign recoveries" are listed in the following table:

> RECOVERIES IN THE CAPE COD COLONIES OF TERNS BANDED ELSEWHERE, THROUGH 1948.

																- D -		
																	nded	
	1933	'35	'36	'37	'38	'39	'40	'41	'42	'43	'44	'45	'46	'47	'48	Adt.	Juv.	T1.
Penikese Island	1		2	3	9	19	23	20	22	18	$\overline{21}$	10	- <u>8</u>		12	31	141	179
	-	-				10								4				114
Weepecket Island		5	- 2	9	11	11	12	15	23	17	13	5	5	5	3	42	94	136
Machias Seal Is., Me.							1		1								2	2
Petit Monan Is., Me.											1						ĩ	ī
Stratton Is., Me.											-			2			ŝ	5
Bumkin Is., Me														4				4
														1			1	1
Moriches Inlet, N. Y							1		1	5	4		2		1	1	13	14
Cartwright Is., N.Y.							1					1					2	2
Tuckers Is., N. J.															1		1	1
Brant Beach, N. J.							1	1									2	2
Charity Is., Mich.							1	1									2	2
Black River Is. Mich.							-	- î	5	1					-		- 7	7
								-	្ម	-								
West Pipe Is., Mich.									1								1	1
Oak Is., Mich									1								1	1
Scarescrow Is., Mich.							1		1								2	2
Leach Lake, Minn.					1												1	1
Ah Gwah Ching, Minn.								1									1	ī
Total	1	5	4	12	21	30	41	39	55	41	39	16	15	12	17	74	274	348

These 348 foreign recoveries are 1.1 percent of the returns taken. The remaining 98.9 percent were all banded originally within the Cape territory. The average annual capture of these foreign birds is 23.5 individuals for the 15-year period. As the annual sample is roughly one-fifth of the total population, this indicates an average of 117 foreign-raised birds present at any one time among the 25,000 Cape terns. But 77 of the 348 foreign returns were made by 48 individual birds retrapped from a second to a seventh season after their first appearance. Thus the foreign recoveries represent only 271 individuals, an average of 18 annually, reducing to 90 the probable number of foreign birds present at any one time, or 0.036 percent of the group population.

This total is so small that, while it may be of importance genetically, it has little distributional significance, and the circumstance cannot be considered a major behavior trait. Nevertheless the presence of these foreign birds requires explanation. How and why they have overcome the impelling urge of site-tenacity will be suggested later. A breakdown of the totals into regional sources as follows:

Vineyard region:		
Penikese Island	172	
Weepecket Island	136	
	308	88.5 percent
From the north:		
Maine	6	1.7 percent
From the south:		
New York	16	
New Jersey	3	
	19	5.5 percent
From the west:		
Michigan	13	
Minnesota	2	
	15	4.3 percent

shows that an overwhelming proportion of these foreigners comes from the nearest adjoining colonies to the south, which is only to be expected, and will be discussed in detail later. But distance is evidently not a factor of moment, for the next nearest source of terns, the New Hampshire and the Maine colonies to the north, whose birds should theoretically pass by Cape territory in migration, show the lowest percentage of incidence, and are surpassed not only by the more distant southern colonies on the Atlantic Coast, but by those in the Great Lakes region.

So far as is known, the Great Lakes birds follow a flyway up and down the Mississippi valley, and do not come in contact with the Atlantic coast individuals until both reach the vicinity of their common wintering grounds in the Caribbean and southward. Latitudinal migration between the Atlantic and Great Lakes regions has been limited to a single occurrence (Lincoln, 1927; 27) which may well be regarded as accidental. The logical explanation for the appearance of these western birds is that it is the result of their pairing with Cape birds on the wintering grounds, and accompanying the new mate back to the breeding grounds. When remating occurs in the Cape colonies the nesting site used is the one most frequently occupied by one of the pair. Thus site tenacity is overcome in these instances by faithfulness to a new mate.

When the Cape's total tern population for the year has been completed by the arrival of the last migrants from the wintering grounds, apparently no further change occurs in it during the remainder of the breeding season. Although terns frequently shift from one colony to another within the area before laying, and later for renesting, no tern trapped breeding in the Cape group's territory has ever been taken nesting outside it the same season, and vice versa.

THE VINEYARD GROUP OF TERNS

It is postulated that a group of tern colonies duplicating the Cape Cod group occupies the area south of the Cape from the Elizabeth Islands to Nantucket, with its geographical center at Martha's Vineyard. This group had three large terneries, on Muskeget, Penikese, and Weepecket Islands, and the usual quota of smaller rookeries where terns still breed scattered along the shores of Martha's Vineyard, Nantucket, and the Elizabeth chain. These terneries are so close to the Cape group geographically that they might seem to form part of it. Weepecket and Penikese are nearer to Ram Island than the latter is to Tern Island and Plymouth. Yet the banding evidence shows no such close affinity of Weepecket and Penikese terns to Ram Island as the birds from the Cape rookeries do.

The nearest Vineyard colony to the Cape's territory was, until its final dispersal in 1940 (Crowell; 1946), on the Weepecket Islands, off Naushon Island, seven miles southeast of Ram Island. Next in proximity, five miles farther south, is Penikese. Then 22 miles to the eastward are the Muskeget Islands, formerly occupied by one of New England's largest tern colonies, which in recent years has been largely displaced by gulls. Ten miles east of Muskeget, and 25 miles south of Tern Island, are the few scattered rookeries on Nantucket Island.

The terns on Muskeget were never banded in quantity, nor has any attention ever been paid to the small satellite colonies on the Nantucket and Martha's Vineyard beaches. The Weepecket and Penikese terns, however, have been banded in some numbers. Terns nested for at least 40 years on the Weepeckets until they were dispossessed by Herring Gulls ten years ago (Crowell; idem). The average population through 1934 was 3500 birds. Thereafter it diminished rapidly until the final nesting in 1940. In 1934 the colony yielded 1135 chicks, 586 in 1939, and in 1940 only eight. Altogether 1057 adults and 6005 chicks were banded at Weepecket before its destruction.

Penikese Island has domiciled a colony averaging 5000 individuals for many years. It has experienced the seasonal variations in size, and the usual mishaps which occur from time to time in all large rookeries. Some years it has matured no chicks. Various workers have banded a total of 991 adults and 17,539 chicks there. The numbers of these birds taken in the Cape terneries has never increased when the Penikese colony was known to be smaller than usual. In 1938, when the Cape group's population was at an unprecedented low, two days were spent trapping adults at Penikese in a search for the missing Cape birds. Not one of the 616 adults taken had been banded in a Cape colony. Casual trapping the following year by the resident warden yielded similarly insignificant results. However, in early June 1950, 531 adults were trapped there, of which 12 were returns: seven from Penikese itself, two from Ram Island, and one each from Tern, Bird, and Weepecket Islands. AUSTIN, Group Adherence in the Common Tern

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The most compelling reason for considering the Vineyard and Cape colonies a single rather than separate groups is their geographical closeness. It is difficult to accept the fact that proximity of nesting sites has but small influence on an interchange of individuals. An examination of the banding evidence, however, shows that distances up to at least 30 miles have a negligible influence on tern behavior. The air-line, tern-flight distances between Weepecket, Penikese, and the major Cape terneries are shown in the following table:

DISTANCES IN MILES BETWEEN COLONIES

	Weepecket	Penikese	Ram	Bird	Tern	Plymouth
Weepecket		9	7	$9\frac{1}{2}$	44	28
Penikese	9		$11\frac{1}{2}$	16	53	35
Ram	7	$11\frac{1}{2}$		5	38	23
Bird	$9\frac{1}{2}$	16	5		35	19
Tern	44	53	38	35		36
Plymouth	28	35	23	19	36	

Weepecket and Penikese birds would be expected on geographical grounds to show their closest affinities to Ram and Bird Islands, which are four times as close to their customary nesting sites as the next nearest Cape colony. However, an analysis of the Penikese and Weepecket recoveries as follows:

Banded at:		R	Recovered at:					
	Ram Is.	Bird Is.	Other Cape Sites	Total				
Penikese Is.	28	18	96 (67.5%)	142				
Weepecket Is.	22	11	60 (64.9%)	93				

shows that only one-third were taken at the nearest sites. These recoveries suggest that the Weepecket colony, although closer to Cape territory than Penikese, has a slightly less affinity with the Cape group.

The banding evidence is unfortunately one-sided. Although both adults and chicks were banded rather extensively at Weepecket before its destruction, and chicks were banded in wholesale quantities some years at Penikese, the combined totals are only a small fraction of the totals banded in the Cape colonies. Likewise the sampling of the adult population at neither of those sites has approached the thoroughness and adequacy of the Cape sampling. The percentage of banded birds present in the Cape colonies is many times higher than at Weepecket and Penikese. These important variables can be minimized by comparing the returns as percentages of the total banded birds available from each site.

The 142 individual recoveries of Penikese birds are 2.84 percent of its estimated 5000 population, and 0.008 percent of the total banded. The 93 Weepecket terns recovered are 2.66 percent of the peak population there in 1935, and 0.01 percent of the total banded. This gives a truer picture, showing that as percentages of the banded birds available, more Weepecket than Penikese birds have appeared in the Cape colonies. However, the Weepecket birds were dispersed in 1940, while the occupancy of Penikese has continued over the years. Hence a higher percentage of Weepecket birds should appear elswhere.

A further breakdown of the Weepecket and Penikese recoveries in

the Cape territory is given in the following table, with a set of similar Tern Island recovery figures for comparison. These figures are all percentages, based on the numbers of banded birds available from each source of origin:

RECOVERY PERCENTAGES OF TERNS BANDED AT THE WEEPECKET, PENIKESE, AND

	TERN ISI	AND COLONIES,	rhrough 1948	,,
		WEEPECKET RECO	VERIES	
Banded as:	Ram Isl.	Bird Isl.	Plymouth	Entire Cape
Adults	.014	.0057	.0038	
Chicks	.0023	.0023	.0022	
Total	.004	.0028	.0024	.008
		PENIKESE RECOV	ERIES	
Banded as:	Ram Isl.	Bird Isl.	Plymouth	Entire Cape
Adults	.004	.003	.004	
Chicks	.001	.001	.0012	
Total	.0013	.001	.0019	.009
	1	TERN ISLAND RECO	OVERIES	
Banded as:	Ram Isl.	Bird Isl.	Plymouth	Entire Cape
Adults	.0043	.0093	.014	
Chicks	.004	.0008	.0026	
Total	.0012	.0026	.005	.164

This table shows even more clearly the irrelevancy of geographical proximity to choice of site. While twice as many Weepecket birds went to Ram Island as to Bird Island, a mere $2\frac{1}{2}$ miles farther away, almost equal percentages of them relocated at Bird Island, $9\frac{1}{2}$ miles away, and at Plymouth, 28 miles distant. The percentages of Penikese birds taken at Ram Island, $11\frac{1}{2}$ miles, and at Bird Island, 16 miles distant, are smaller than at Plymouth, 35 miles away. Also, almost exactly the same percentages of birds came to Ram from Tern Island, 38 miles distant, as from nearby Penikese, while a far higher percentage of Tern Island emigres went 36 miles to Plymouth.

The dissociation is more apparent when data undistorted by variables are selected. Two-thirds of the chicks banded at Weepecket were marked in the 1930, 1931, 1933, and 1934 seasons (Crowell; idem), when the colony was at its peak production. The recoveries in the Cape are from this selected group, in percents of the total banded, are as follows:

Ram Isl.	Bird Isl.	Plymouth	Entire Cape
.0017	.00024	.001	.014

These recoveries show beyond question that geographical proximity has no effect on the selection of new breeding sites.

The 308 recoveries of Weepecket and Penikese birds in Cape territory comprise less than one percent of the 31,178 returns and recoveries taken in the Cape colonies from 1933 through 1948. As Penikese terns furnish 0.5 percent, Weepecket birds 0.4 percent, the relationship of both colonies to the Cape group is almost equal. This contrasts markedly with the seasonal interchange of memberships between the Cape colonies themselves, which is rarely less than five percent (Austin; 1949).

The 76 members of the dispersed Weepecket colony recovered in the

Cape colonies since 1938 represents so small a fraction of the probable survivors that the remainder must have relocated elsewhere in the Vineyard vicinity where no adult trapping has yet been done to discover them. This is what terns have been found to do under similar circumstances in the Cape group.

The principal reason for assigning the Weepecket and Penikese terns to the postulated Vineyard group in the absence of positive banding evidence is the negative evidence against their holding close membership in the Cape group. There exists between them and the Cape colonies no such bond as unites the latter into a unit. The small interchange of memberships which has occurred between them is simply the logical result of environmental changes rather than of a tie between the birds themselves.

Other corroboratory data are available, but the foregoing seem sufficient to indicate strongly that the Weepecket and Penikese colonies are not an integral part of the Cape group, but rather are part of another similar association adjoining it to the south. The evidence, however, is not conclusive, and additional banding data from the Vineyard colonies may modify the postulate.

GROUP ADHERENCE

A predominant trend in all colonial nestings is the annual return of the same groups of individuals to the sites each had occupied before. The implication is that site tenacity is wholly responsible, which is not entirely true among the Cape Cod terns. Although the group always nests within the same loosely defined perimeters, the degree to which site tenacity is effective is in direct ratio to the size of the association or unit concerned, and to the comparative amount of territory each unit occupies.

Each colony uses only a part of the group's territory, and each pair of birds holds only a few square feet within its colony's boundaries. The Cape group as a whole, it has been shown above, consists 98.9 percent of birds raised or banded here. In its component colonies, which are smaller units, the corresponding percentage drops to 75.4. Of individual birds, only 56.8 percent return to the territory each occupied the previous season (Austin; 1949, 12). If site tenacity alone determined where the birds nested, the size of the unit would not matter, and all these percentages would be about equal. Hence there exists a second influence which increases in potency as the size of the units grows larger. This is group adherence.

Apparently there exist within tern colonies, especially large ones, associations or clans of from a few to even 100 or more birds. Such societies may persist for two or more seasons. The organizations are rather loose, yet some of them appear to be maintained quite as consistently as are the colonies themselves. They follow the general behavior pattern as consistently as does the colony as a whole, but some acts, performed in unison by the members of such an association, are not duplicated simultaneously by the remainder of the colony. Attention was first drawn to this during adult trapping at Tern Island.

It was observed repeatedly that the serial band numbers of the returns taken on a given day were too nearly consecutive to be a coincidence. Reference to the station's records which show the part of each site trapped each day, revealed that the series of bands in question had been applied one or more years previously in the same restricted locality. At first it was thought that site tenacity was responsible for this grouping. But later, when it was found that small groups of Tern Island birds, likewise wearing consecutive numbers, were trapped renesting compactly at Bird Island and Plymouth, it became evident some additional factor existed.

Every season some unknown condition prevails temporarily over both site tenacity and group adherence to cause a moderate amount of impermanent shifting of breeding sites. This is shown by data obtained from Tern Island birds during three seasons when the colony was 1000 birds smaller than usual, and one when it was 3000 birds smaller. Of the Tern Island birds recovered at other sites those years, more than one-half of those recovered subsequently had returned again to Tern Island.

From 1932 through 1943, coincident with maximum populations at Tern Island, there were large nestings on North Point, one mile away. This colony was always started each year by an overflow of Tern Island birds, which was occasionally augmented later each season by renesting individuals from other colonies. No terns have nested on North Point since 1943. Of the birds which formerly nested there, 10 at most have been taken since then elsewhere than at Tern Island.

There have been seasons when an entire colony has failed to occupy its customary site. There was no nesting at Plymouth in 1943 and 1944. The larger part of that colony repaired to Tern Island and raised its occupancy to a peak of 18,000 birds. In 1945, however, the usual 4000 birds relocated at Plymouth, and only 16 of their fellow members were retaken at Tern Island.

The behavior pattern of renesting shows that when only a few birds are involved, they tend to use a different part of the same site. In a marsh bordering Tern Island is a small elevated islet 1200 square feet in extent, 100 feet away from the main colony. Almost all the 50-odd pairs nesting on this islet were trapped and color-banded for three consecutive years. Shortly before the colony returned the fourth year, a severe storm buried the islet under a mass of wreckage. The evicted birds, easily identified by their colored bands, did not scatter over the large island, but nested closely together on a small, nearby section of it. At Plymouth in 1947 rats destroyed all the eggs and chicks in the outer part of the point where nesting, as always, had been earliest and heaviest. The two dunes at the extreme tip were trapped before their clutches were destroyed. When these birds renested, most of them located in a body at the opposite end of the colony.

When large numbers are frustrated, they usually emigrate in a body to nest together elsewhere (Austin; 1940, 165: and 1942, 17: and 1946, 25). Rarely have fewer than 25 percent of these renesting individuals recaptured following seasons failed to rejoin their original colonies the ensuing year. Conspicuous examples of this followed the wanton wreckage of the Billingsgate colony by picnickers in 1929, and the complete dispersal of the Tern Island colony by rat predation late in June 1933. The only notable exception is the failure of one-half of the Tern Vol. XXII 1951

Island colony to return after its debacle in 1944 (Austin; 1946).

More indicative of the existence of group adherence and its influence in determining the membership of a colony are the involved findings at Little Sipson, a small island about four acres in extent in Pleasant Bay, three miles from Tern Island. Occupied for the preceding decade by only a few pairs of terns, 500 birds nested there in 1935, and 400 in 1936. Since then only a few pairs have used the site. It was well sampled the last two years of its peak occupancy as follows:

А	dults banded	Returns taken
1935	93	14
1936	163	49

Of the 14 returns taken in 1935, 11 or 78.6 percent had been banded at Tern Island. Ten of them, or 71.3 percent, had been banded as chicks in 1932 and 1933, and, returning for their first or second nesting in 1935, accompanied Tern Island adults to a site with which they had no previous contact. Three of these 14 birds were retaken at Little Sipson in 1936, one at Tern Island. Since 1936, four of the 14 have been trapped at Tern Island, and none elsewhere. Of the 93 adults banded at Little Sipson in 1935, 21 were retrapped there in 1936, none elsewhere. All but two of the 22 of these 93 birds retaken since 1936 were renesting on Tern Island. Of the 49 returns taken at Little Sipson in 1936, 24 or 48.8 percent had been taken there in 1935. Of the remaining 25 Little Sipson 1936 returns not trapped there in 1935, 17 or 68 percent had been banded at Tern Island. Of all the 212 adults taken at Little Sipson in 1936, 54 were taken in subsequent years. Of these 45, or 83.4 percent, were breeding at Tern Island. Since all the foregoing percentages meet the requirements of a major behavior trait, the incident represents far more than the erratic doings of a few individuals.

Obviously this temporary colony at Little Sipson consisted essentially of a portion of the Tern Island colony which returned to its original site in 1937. The transient separation is accounted for by the peak populations at Tern Island in 1935 and 1936, with a resulting reduction in the amount of nesting territory available. A duplicating overflow of Tern Island birds went to North Point at the same time. The presence at Little Sipson in 1935 of the 10 Tern Island chicks nesting for the first time suggests that group adherence may begin to function very early in the life of the Common Tern.

Ever since a back-log of banded adults varying from 20 to 60 percent was established in the Cape colonies 15 years ago, the ratio of returns has averaged four of birds banded as adults to one banded as chicks. The ratio is invariably highest when Tern Island birds are involved, because adult banding has been far more comprehensive there than elsewhere, the only marked exception is the recovery of Weepecket birds at Ram Island, seven banded as adults for each one as a chick. This is evidence that the bond which united the Weepecket birds into a persistent colony tended to keep groups of them together when they were compelled to use a new nesting site. Also it shows that group adherence is at times of more value than site tenacity in preserving the species. In all probability group adherence is strongest during the nesting season because then is the only time Common Terns consort closely together in large numbers. Several other behavior traits function actively only for limited periods. A better evaluation of the trait results from knowing as far as possible how dormant it becomes during the winter months, and to what extent, if at all, it modifies the species' northward and southward migrations. It may be possible at least to learn some of the end results of its activity during the breeding months.

GROUP ADHERENCE ON THE WINTERING GROUNDS

The literature contains comparatively few observations on the wintering ground distribution and behavior of the many thousands of Common Terns that breed in North America. They only reliable data available are the recoveries of banded birds:

w	INTERING GROUP	ND RECOVERIES OF CAPE	COD TERNS
Locality	Adul	ts Juvena	ls Totals
WEST INDIES			
Bahamas	0	1	1
Cuba	2	1	3
Jamaica	0	1	1
Haiti	8	33	41
Porto Rico	9	51	60
Virgin Island		1 2 2 6 3	2 2 2
Barbadoes	0	2	2
Guadeloupe	0	2	
Martinique	5	6	11
Grenada	1		4
Trinidad	4	56	60
CENTRAL AME	CRICA		
San Salvado		1	1
Panama	0	2	2
SOUTH AMERI WEST COAST Peru	CA,	2	3
SOUTH AMERIA NORTH COAS Aruba	ST 0	1	1
Colombia	03	3	3
Venezuela	3	33	36
SOUTH AMERI EAST COAST	•		
British Guia		14	19
Dutch Guian		0	1
French Guia		8	13
Brazil	13	13	26
TOTALS	58	(19.9%) 234	(80.1%) 292

The wintering range of the Common Tern is extensive. It includes the West Indies, Central America, the entire Caribbean coast line, the east coast of South America south to Patagonia, and the west coast at least to Peru. With an even dispersal of the species there would be no large concentrations in any one locality, such as the banding recoveries show. Most of the people likely to come in contact with terns in their

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wintering area probably know nothing of the import of a bird band, and are unable to comprehend the directions on the band concerning reporting. With few exceptions all the recoveries are reported as found dead, or killed for some unspecified reason. So the relative number of recoveries in each country does not necessarily mirror the actual dispersal of the species.

Of greatest importance is the gross inadequacy of the sampling, which is too small and insufficiently diversified to eliminate even minor variables. That 80.1 percent of the recoveries were banded as chicks, of which 74 percent were recovered the first winter after banding, does not indicate the relative number of young and old birds present, but reflects instead the higher susceptibility of inexperienced juvenals to accident and capture. These deficiencies suggest that, at most, all the recoveries can do is to indicate trends. They cannot make the existence of a behavior trait factual as do the adequate samplings obtained during the nesting season.

The disproportionate recovery of adults and young raises the question of how the latter make their way southward. Since they have no previous knowledge through experience of where they are to winter, never before having travelled the intervening territory, their first journey to the species' customary wintering grounds can be effected by only two means: first, either an inherited instinct, or directions received in an unknown manner from their elders on the breeding grounds; or second, some degree of guidance in transit. For the latter, which is the more likely explanation, there are three possible sources. Guidance could be obtained: (1) from their parents, (2) from continued association with other adults in the unit, large or small, of which both the young birds and their parents are members, or (3) from contact with terns from other units using the same flyway.

It is not known how long parents continue association with their progeny. In August, when many terns exhibit the post-nuptial wandering previous to migration characteristic of many other species, adults are occasionally seen feeding well-grown young of the year miles from the nearest ternery. If, as is likely, they are parents and their chicks, they represent the longest time after hatching such contact can be indicated to have continued. Nevertheless the possibility of parental guidance to the wintering ground cannot be discarded even though, as will be shown later, it could not have accomplished the collection of simultaneous recoveries on the wintering grounds without the help of group adherence.

During their southward migration terns usually string out along the shorelines during daylight hours. While they do not travel in compact flocks, large groups of them containing both adults and young of the year are often seen resting together on points and sandbars. These observations are not inconsistent with the opinion that most juvenals are guided to their winter sites by some degree of continuous contact with their summertime associates. An instance was shown of young birds being led to unfamiliar territory by their older affiliates when the Little Sipson colony was discussed above.

No banding evidence shows continued association of adults and young

from the same colony on the wintering ground, but the Cape recoveries give adequate proof that young from the same colony remain together during their first year. Of the 234 juvenals recovered, 112 or 47.8 percent were taken in 33 groups of two to ten as the following table shows:

SIMULTANEOUS WINTERING GROUND RECOVERIES OF CAPE COD TERNS BANDED AS JUVENALS

					0	40		
Haiti 1928—4 1933—3 1934—4 1935—3 1938—2 1940—3 1945—2 1946—5 1947—3	Porto Rico 1931— 3 1933— 3 1934—10 1935— 4 1938— 4 1942— 3 1945— 3 1946— 2		Martinique 1926—2 1932—2 Grenada 1944—2 Trinidad 1927—4 1929—3 1933—2 1939—5			19 19 19 19 19 8 6 9 19 19 F 6	nezuela 128—2 133—2 135—2 135—2 135—3 137—3 137—3 139—4 rench uiana 134—4	Peru 1934—2
			ç	Summa	rat	17	or r	
			~	ummu	, y			
Groups of:		2	3	4	5	7	10	Totals:
No. of grou No. of bird		$\frac{11}{22}$	10 30	$\frac{7}{28}$	$\frac{3}{15}$	$\frac{1}{7}$	$1 \\ 10$	33 groups 112 birds

BANDED AS ADULTS

HAITI	2 banded in 1947, recovered in 1947
PORTO RICO	2 banded in 1936, recovered in 1936
BRAZIL	2 banded in 1936, recovered in 1939

Thirty-five of these simultaneous recoveries, or almost one-third of them, were banded on the same day in the Tern Island colony as follows:

> TERN ISLAND CHICKS BANDED THE SAME DAY AND RECOVERED TOGETHER ON THE WINTERING GROUNDS

Date Banded	Place Recovered	Place Recovered Date Recovered				
9 July 1928	Haiti "	27 Sep. 1928 3 Oct. 1928				
6 July 1933	Trinidad "	15 July 1934 22 Aug. 1934				
24 June 1934 "	Porto Rico "	7 Sep. 1934 18 Sep. 1934 12 Oct. 1934				
24 June 1934 "	Venezuela "	15 Nov. 1934 5 Dec. 1934 9 Dec. 1934				
26 June 1934 "	Venezuela "	7 Dec. 1934 9 Dec. 1934 25 Dec. 1934				
10 July 1934	Peru "	1 Mar. 1940 "				
13 July 1934 "	Haiti "	5 Oct. 1934 20 Oct. 1934				

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18 July 1934 "	Porto Rico "	29 Sep. 1934 5 Oct. 1934 13 Oct. 1934 19 Oct. 1934
1 July 1935	Porto Rico	28 Sep. 1935 27 Oct. 1935
26 June 1939 "	Trinidad "	1 Mar. 1940 9 June 1940
29 June 1939 "	Venezuela "	16 Nov. 1939 "
11 July 1939 "	Venezuela	9 Nov. 1939 16 Nov. 1939
7 July 1940	Haiti	6 Oct. 1940 7 Oct. 1940
5 July 1946	Haiti "	16 Oct. 1946 3 Dec. 1946
18 July 1946	Haiti "	29 Oct. 1946 8 Nov. 1946

This table reveals that Tern Island chicks banded on the same day were retaken in one group of four, three groups of three, and eleven groups of two, at the same place on the wintering grounds, twice on the same day, otherwise within a few weeks of each other. One pair was taken in Trinidad the following summer, when the older birds were back on the breeding grounds. The pair taken in Peru had remained together for three years.

That young of the year usually remain south instead of returning northward their first summer is verified by many June, July, and August wintering ground recoveries of year old birds. Fourteen such Tern Island chicks, banded the same season but not on the same day, were recovered together as follows:

SIMULTANEOUS SUMMER RECOVERIES OF TERN ISLAND CHICKS ON THE WINTERING GROUNDS

Birds	Summer	Place	Summer
in Group	Banded	Recovered	Recovered
3	1929	Trinidad	1930
4	1934	French Guiana	1935
3	1937	British Guiana	1938
5 4	1937 1939	Trinidad	1938

These simultaneous recoveries are too numerous to be disregarded as fortuitous. They suggest that group adherence may originate in family relationship.

The colonies of Common Terns which nest along the Atlantic Coast from the Florida Keys to Labrador use the same migration route and wintering grounds. They do not migrate compactly in groups as aligned on the breeding grounds, but in smaller flocks. The initial descent of the large colonies onto their nesting sites on their return from the wintering grounds is usually made by at least a majority of their memberships, as has been observed by many workers in tern colonies (Palmer; 1941, 39). Usually the birds collect on nearby beaches before repairing to the nesting area, but at Tern Island the colony gathers together off shore. This behavior must be motivated by group adherence, for it indicates that site tenacity alone does not bring about the final alignments. Were it not for these two behavior traits, especially group adherence, there would be a much more frequent interchange of memberships between the Cape group and other groups along the Atlantic Coast.

From whatever standpoint group adherence is studied, the conclusion is always the ultimate inference that kinship plays a role in its development and perpetuation, exactly as it is known to do in some other animal aggregations. There is no credible evidence at hand to indicate that family influence does not control to a considerable extent the group behavior of individual terns, be it parent-offspring, sibling, or an even more distant relationship. Certainly it offers the most logical explanation for most of the occurrences recounted herein, particularly the alignment of individuals on the wintering grounds.

COLONIAL INTERRELATIONSHIPS

Tern colonies are never static, but vary continually in size and composition. Terns have nested at 17 different sites in the Cape area in the last two decades. Several of these sites, Billingsgate, Egg Island, and Nauset Point in particular, have washed away. Others have become equally untenable because of ecological changes. Tern Island itself, the nucleus and mainstay of the Cape group, has been maintained as a breeding site only by extensive annual reclamation work.

As various colonies have broken up, their members have been found nesting with other flocks within the circle of the group's tenure. These displaced birds usually join one of the larger colonies. Most of the Billingsgate and Egg Island birds went to Tern Island and Plymouth. Tern Island refugees have moved to Plymouth, Bird Island, and Ram Island at various times. Such emigrees are seldom found in the smaller colonies. The trend has been constantly toward coalescence of the smaller colonies with the larger ones. This is advantageous to the maintenance of the species, for reproductive success is much greater in the larger colonies.

Until 1930 most investigations of breeding terns were carried on in the largest colonies, such as Tern Island on the Cape, Muskeget, Penikese, and Weepecket in the Vineyard area, Cobb Island in Virginia, and those in the Great Lakes. Very little attention was paid to the smaller colonies, or to their relationship with the large ones, as has been done comprehensively since then on the Cape. However, a study of the literature, and personal reports from workers in other areas show that elsewhere, as in the Cape group, most large tern colonies have one or several smaller satellites near them, with which they probably form similar self-contained, self-perpetuating groups. In inland fresh-water lakes these groups are frequently separated so far from the nearest other set of colonies that there is little question of their unity. In others, as in the Maine-New Hampshire coastal region, and along the shores of New Jersey, Maryland, and Virginia, no probable line can be drawn between them, if one exists, without banding evidence. Vol. XXII 1951

The recent history of other important colonies shows them as variable and unstable as the Cape colonies have been. The terneries on Cobb Island have shifted with the changing environment many times in the last half century. When the former larger rookery on Gull Island off Long Island was evicted by Army occupation in 1898, the birds apparently relocated in the nearby area. They formed several new large colonies off Long Island, each with its complement of smaller ones, usually on sites where terns are known to have nested before.

It appears that when relatively large colonies are dispossessed, either for a season or permanently, they relocate as a group in the same general area. While site tenacity is responsible to some extent for this behavior, group adherence is predominantly accountable for the maintenance of the species under such adverse conditions.

SUMMARY

The Cape Cod colonies of breeding Common Terns form a distinct, self-perpetuating group, free from association with other colonies during the nesting season. Similar groups appear to exist elsewhere.

Membership in such a group is not determined by the geographical proximity of colonies to one another, but is engendered by two behavior traits, site tenacity and group adherence. The former implies the attachment of terns to specific territory, the latter the attachment of terns to each other.

Group adherence functions throughout the whole life of the species. even on the wintering grounds. Probably originating in kinship, it tends to coalesce terns into progressively larger units in which reproductive success is greater.

Group adherence maintains these societies for concerted action when site tenacity ceases to function because of ecological or other environmental changes. Hence it is essential to the welfare of the species,

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