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COLOR VARIATION IN THE SOFT PARTS AND DOWN OF ROYAL TERN CHICKS

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BENT (1921) calls attention to the remarkable and extensive variation in the down color of Royal Terns, *Sterna* (= *Thalasseus*)¹ *maxima* and to the less extensive variation in its close relative, *S. sandvicensis*, but this variation has never been quantified. As the first part of a study on the adaptive nature of social behavior and plumage variation of Royal Terns, we undertook to quantify the variation in chick down and soft part colors to determine its extent and whether it was continuous or truly polymorphic (*sensu* Ford, 1940; Huxley, 1955). We collected our data in a large Royal Tern colony on Fisherman's Island, Cape Charles, Virginia (now Fisherman's Island National Wildlife Refuge.)

MATERIALS AND METHODS

As a basis for future studies on the inheritance of chick down color in Royal Terns, an arbitrarily chosen number of chicks (400), all between ca. 10 and 20 days of age, were captured at random in July 1967 and colorbanded for individual recognition according to a computer-generated scheme (Buckley and Hancock, 1968). After banding, each chick was scored for 10 characters of down color pattern and color of the soft parts (i.e. bill, legs, and feet; Table 1). The birds were not scored against graphic standards, but each bird was evaluated individually for each character. We feel that error from subjective variability was held to a minimum, as only one observer (PAB) scored birds. The color plate (frontispiece) depicts all variable ranks, in different hypothetical combinations.

Each bird's data were punched onto an IBM card and, using a canned program (RANKO) for the CDC 1604 digital computer at the Cornell University Computing Center, nonparametric analyses of the data were done, computing Kendall's rank correlation coefficient (*tau*) and a measure of concordance or multiple correlation (*W*). The formulae used in writing the program are from Kendall (1962); for evaluation of these statistics, see Siegel (1956). The usual level of significance ($P \leq 0.05$) was adopted before evaluation of the statistics computed.

¹ We follow Moynihan (1959) and European workers in a broad generic concept in the Laridae.



Frontispiece: Royal Tern chicks showing hypothetical combinations of all classes of all variables. Painted from color slides and motion pictures of living chicks. See Table 1 and text for details.

TABLE 1
 VARIABLES SCORED AND ANALYZED FROM DATA OBTAINED IN 1967 STUDY

Variable	Classes	Categories
Bill color	Three	<ul style="list-style-type: none"> 0 = pinkish 1 = yellow/orange 2 = greenish
Bill tip	Two	<ul style="list-style-type: none"> 0 = no tip 1 = tip present
Foot/leg color	Four	<ul style="list-style-type: none"> 0 = pink 1 = yellow/orange 2 = greenish 3 = black
Dorsal ground color Throat ground color Pileum ground color	Four	<ul style="list-style-type: none"> 0 = white 1 = light beige 2 = moderate beige 3 = dark beige
Dorsal spotting extent Throat spotting extent Pileum spotting extent Wing spotting extent	Five	<ul style="list-style-type: none"> 0 = none 1 = trace 2 = light 3 = moderately extensive 4 = heavy

Figures 1, 2, and 3 show the intraclass percentage distributions of all variables measured in the field. Figure 4 is a frequency distribution histogram of cumulative pigmentation scores: class 0 includes all-white birds with pink legs and bills, and class 26 includes the darkest birds found in 1967, which usually had greenish bills, black legs, dark beige ground color and heavy black superficial markings on back, pileum, throat, and wings. The same classes appear in Figure 5, but individual bird scores exclude soft part ranks and show only plumage score distributions. Table 1 lists the ranks for all the field characters scored. Table 2 is a Kendall rank correlation matrix for the ten field-recorded variables, with 95 per cent confidence limits for *tau*. Table 3 compares the variability of ground color and of superficial spotting.

RESULTS

Bill color as a variable was uncorrelated with any other variable; most (85 per cent) bills were either orange-yellow (similar, but not identical to adults), or more pink, almost pigmentless. But green bills, the third class, were significantly associated with green legs ($\chi^2 = 66.85$; 1 df; ≤ 0.001), confirming field impressions. The age when bills become (adult) orange is not known. Leg color was also uncorrelated with any other variable. About 40 per cent each had either yellow-orange or black legs, but it is unknown by what age all attain (adult) black legs. The time of this change certainly varies, for we have noted birds still retaining yellowish legs the spring after hatching. Chamberlain (1939) rightly noted that many birds had blotched, two-color legs. However, all such birds we have examined (many more than the 400 in this study) had legs partly black, and partly one of the other leg colors in our rankings (see frontispiece). If more than half the leg (by inspection) was black, it was

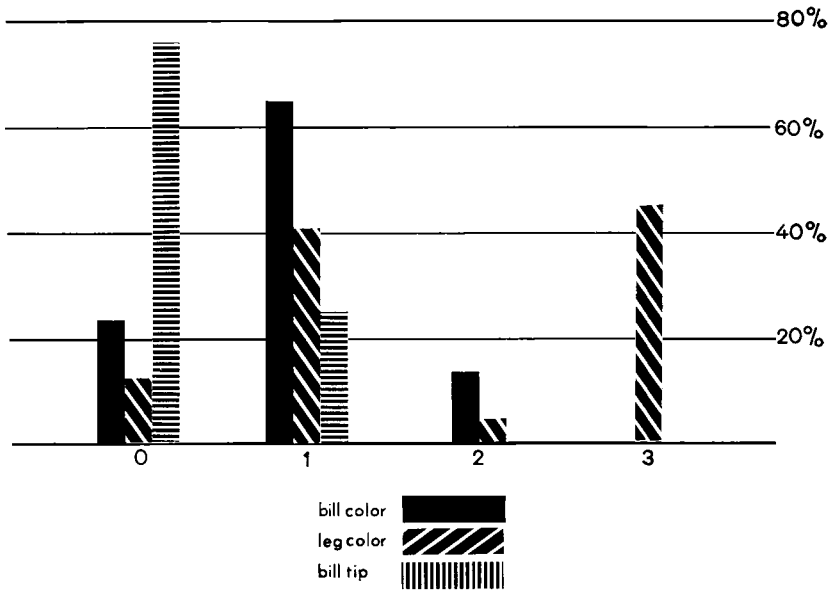


Figure 1. Frequency distribution histograms for soft parts classes.

scored black; if less than half black, it was scored the appropriate other color. A decision was made in each case, and for all practical purposes both a bird's legs were the same color. While the foregoing was a less than desirable scoring procedure, leg-color complexity forced its adoption. Nevertheless leg coloration can be considered polymorphic if one divides birds into those hatched black-legged and those assuming this color at some later age.

The presence of a dusky bill tip was uncorrelated with the other two soft parts variables, but showed a high and consistent correlation with the four superficial spotting variables. Seemingly a dusky bill tip was either present (77 per cent) or absent (23 per cent) and was thus dimorphic, but possible variation in the extent of tip pigmentation was not investigated quantitatively in 1967, nor was age-dependent variation in tip pigmentation.

Ground color, whatever its intensity, was generally constant over the entire body (excluding the usually white breast and abdomen), and white predominated. The percentage distribution histograms for ground color in the three body areas measured (Figure 2) show the following characteristics: class 0 (white) is most frequent in the three body areas, class 2 (moderate beige) is next frequent, class 1 (light beige) is third, and class 3 (dark beige) is least frequent. The null hypothesis of no overall difference *between* classes, considering all three components in each class,

TABLE 2
 KENDALL RANK CORRELATION MATRIX AND 95 PER CENT CONFIDENCE INTERVALS FOR THE 10 FIELD-RECORDED CHARACTERS

	Bill tip	Leg color	Dorsal ground color	Throat ground color	Pileum ground color	Dorsal spotting extent	Throat spotting extent	Pileum spotting extent	Wing spotting extent
Bill color	<i>-.15</i>	<i>-.01</i>	<i>-.24</i>	<i>-.21</i>	<i>-.25</i>	<i>-.11</i>	<i>-.16</i>	<i>-.08</i>	<i>-.09</i>
	<i>-.02¹</i>	<i>-.13</i>	<i>-.11</i>	<i>-.07</i>	<i>-.12</i>	<i>.03</i>	<i>-.02</i>	<i>.06</i>	<i>.05</i>
Bill tip	<i>.12</i>	<i>.26</i>	<i>.03</i>	<i>.07</i>	<i>.02</i>	<i>.16</i>	<i>.12</i>	<i>.19</i>	<i>.18</i>
		<i>-.12</i>	<i>-.02</i>	<i>.08</i>	<i>.02</i>	<i>.19</i>	<i>.26</i>	<i>.24</i>	<i>.28</i>
		<i>.02</i>	<i>.12</i>	<i>.22</i>	<i>.15</i>	<i>.33</i>	<i>.30</i>	<i>.38</i>	<i>.41</i>
Leg color		<i>.15</i>	<i>.25</i>	<i>.35</i>	<i>.29</i>	<i>.45</i>	<i>.51</i>	<i>.50</i>	<i>.53</i>
		<i>-.17</i>	<i>-.04</i>	<i>-.17</i>	<i>-.22</i>	<i>-.19</i>	<i>-.17</i>	<i>-.19</i>	<i>-.05</i>
		<i>-.04</i>	<i>.10</i>	<i>-.03</i>	<i>-.09</i>	<i>-.05</i>	<i>-.03</i>	<i>-.05</i>	<i>.09</i>
Dorsal ground color			<i>.58</i>	<i>.69</i>	<i>.64</i>	<i>.08</i>	<i>-.06</i>	<i>-.02</i>	<i>.23</i>
			<i>.78</i>	<i>.75</i>	<i>.75</i>	<i>.22</i>	<i>.08</i>	<i>.12</i>	<i>.17</i>
Throat ground color				<i>.83</i>	<i>.83</i>	<i>.35</i>	<i>.22</i>	<i>.25</i>	<i>.30</i>
				<i>.59</i>	<i>.59</i>	<i>.14</i>	<i>.00</i>	<i>.08</i>	<i>.12</i>
				<i>.71</i>	<i>.71</i>	<i>.28</i>	<i>.13</i>	<i>.21</i>	<i>.26</i>
Pileum ground color				<i>.79</i>	<i>.79</i>	<i>.41</i>	<i>.27</i>	<i>.34</i>	<i>.39</i>
						<i>.09</i>	<i>-.03</i>	<i>.04</i>	<i>.04</i>
Dorsal spotting extent						<i>.23</i>	<i>.10</i>	<i>.18</i>	<i>.18</i>
						<i>.36</i>	<i>.24</i>	<i>.31</i>	<i>.31</i>
Throat spotting extent							<i>.22</i>	<i>.51</i>	<i>.44</i>
							<i>.36</i>	<i>.63</i>	<i>.57</i>
Pileum spotting extent							<i>.48</i>	<i>.72</i>	<i>.67</i>
								<i>.27</i>	<i>.32</i>
								<i>.41</i>	<i>.45</i>
								<i>.53</i>	<i>.56</i>
									<i>.45</i>
									<i>.57</i>
									<i>.68</i>

¹ Figures in italics are calculated *tau* values.

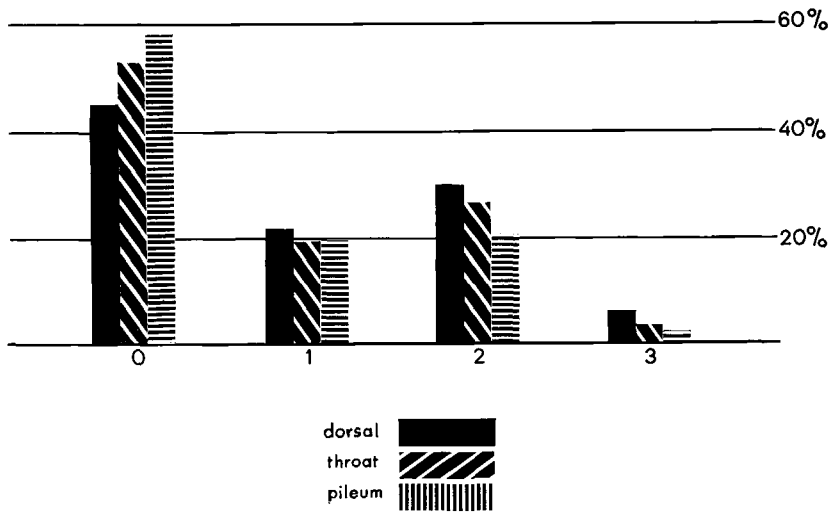


Figure 2. Frequency distribution histograms for ground color classes.

is rejected at the 0.0017 level (Friedman two-way analysis of variance by ranks: $\chi_r^2 = 9.0$; $n = 3$, $k = 4$; see Siegel, 1956: 166-172 for details). Similar analysis of the difference *within* classes fails to reject the null hypothesis of no difference. Thus considering all four color classes, the differences between peaks within each color class are not significant. One can therefore legitimately conclude that ground color is effectively the same over all areas of the body, where measured, this interpretation of these data being supported by high ground color correlation values between the three areas where it was measured, and by the concordance value for all ground colors (see below).

Dorsal ground color is slightly but significantly correlated with dorsal and wing spotting; throat ground color is slightly but significantly correlated with dorsal, pileum, and wing spotting (but not with throat spotting); and pileum ground color is also slightly but significantly correlated with dorsal, pileum, and wing spotting. But, as the lower confidence limits in all these cases approach zero, these correlations may not have much biological significance. Otherwise ground color variables were significantly correlated only inter se, and had a concordance value of 0.71 ($P \leq 0.001$). Continuous variation between all classes of ground color rules out any polymorphism, while supporting polygenic control. Direct genetic evidence is, of course, lacking at this stage.

Superficial spotting categories were significantly correlated inter se and had a concordance value of 0.53 ($P \leq 0.001$), but aside from the

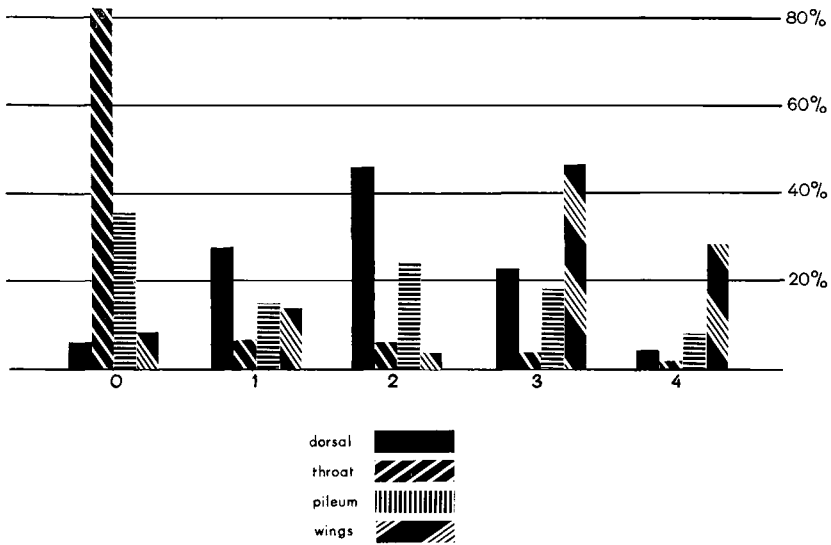


Figure 3. Frequency distribution histograms for superficial spotting classes.

weak correlations with certain ground color variables (mentioned above) they were strongly correlated only with a pigmented bill tip, discussed earlier.

The frequency distribution histograms for spotting (Figure 3) show remarkable variability: the most frequent color class in one spotting area is not necessarily the most frequent in any other area, and quite unlike ground color, no overall trends are noticeable. Indeed, similar analysis of variance by ranks *between* classes yields $\chi_r^2 = 3.2$; $n = 4$, $k = 5$; $P = 0.60$, and *within* classes yields $\chi_r^2 = 2.04$; $n = 5$, $k = 4$; $P = 0.60$. In neither case is the null hypothesis of no difference rejected, and one must treat all the variability in the Figure 3 histograms as random. Thus one can say confidently that polymorphism for overall spotting also does not exist, and in fact the data make it seem quite likely that different selective pressures act on spotting in each of the four body areas examined. The extent of variation suggests polygenic control for spotting.

Ground color and superficial spotting are compared in Table 3. Whatever its hue, ground color was generally the same over the entire body (except the white breast and abdomen), reflected in the high ground color concordance value of 0.71. Spotting *hue* was constant if any spotting at all was shown, but the *extent* of spotting spread over the body varied from individual to individual; this was reflected in the lower spotting concordance value of 0.53 (vs. 0.71 for ground color). If only a trace

TABLE 3
COMPARISON OF VARIATION IN GROUND COLOR AND SUPERFICIAL SPOTTING OF
CHICK DOWN

	Ground color	Superficial spotting
Population variability	Continuous, from white to dark beige	Continuous, from unspotted to heavy spotted
Uniformity of color	Constant over entire body ¹ of each individual	Dark brown or black in every spotted bird
Size of spots		Always small, but aggregation occurs if bird is heavily spotted.
Location of pigmented areas	Back, pileum, throat, wings	If few spots present, always only on lower back and rump; if more present, then also on pileum and wings; rarely is throat spotted, and then only when back and pileum heavily spotted.
Relationship between ground color and superficial spotting	Very slight between certain areas (see text and Table 2)	

¹ Except breast and belly: always white and unspotted.

of spotting was present, it was confined to the lower back and rump. Birds with more dorsal spotting usually had a spotted pileum as well. Rarely was the throat spotted, and then only when the back and pileum were heavily spotted. Wing spotting variation was puzzling and possibly more complex than our scoring system could show. It needs further study and little weight should be placed on its class distributions.

The cumulative pigmentation distribution curves (Figures 4 and 5) make essentially invalid statistical assumptions: summing the scores for all variables on a given bird gives equivalent weight to each rank within each category, even if some characters have only two possible ranks and others four or five. Thus bill tip presence or absence is accorded the same weight or significance in computing a bird's total score as is any one of the four ground color ranks. Nonetheless we feel that a frequency distribution histogram of summed bird scores is a good way to depict what was evident in the field: extremes of overall lightness and darkness were in the minority, most birds being in between. It is analogous if not directly comparable to the "hybird index" method of character scoring used by Sibley (1954 et seq.) and his students. Figure 5, where soft parts are excluded, shows a shift to the lighter end and this too reflects general field impressions that, while both light and dark extremes of plumage were rare,

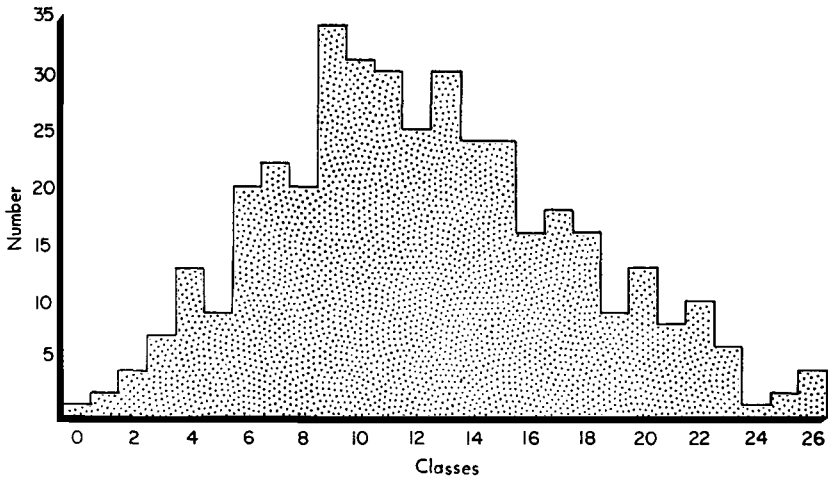


Figure 4. Frequency distribution histogram for total pigmentation scores (both soft parts and plumage included).

lighter birds outnumbered darker birds. Statistical analysis of curve deviations from symmetry are probably invalid because of the rank-weight inequalities discussed above.

The identification of all pigments is uncertain, but previous work (e.g. Fox and Vevers, 1960) suggests that the beige ground color is probably due to phaeomelanin, and the color of the superficial spotting and bill tip to eumelanin. Chemical extraction and analyses of the actual pigments are necessary before firmer statements can be made.

DISCUSSION

The data presented here demonstrate: (1) that color variation in downy Royal Tern chicks is extensive, perhaps the most extensive ever reported in any species of bird, and (2) that—while certain soft part characters (black or not black legs; presence or absence of dusky bill tip) may be polymorphic if the definition of the term is stretched—down ground color, superficial spotting extent, and the overall color of Royal Tern chicks are certainly continuously variable and hence not polymorphic. Variation overall is continuous and unimodal (Figures 4 and 5). Another measure of the lack of continuous variation, a definitional prerequisite for genetic polymorphism, is the concordance value for all 10 scored characters taken together for all 400 birds: W is 0.23, significant only at the 0.85 level, and therefore rejected. We have no data on the sexual distribution of variation in Royal Tern chicks, as none were sexed. But a similar study of the Brown Noddy (*Anous stolidus*) revealed no sex-

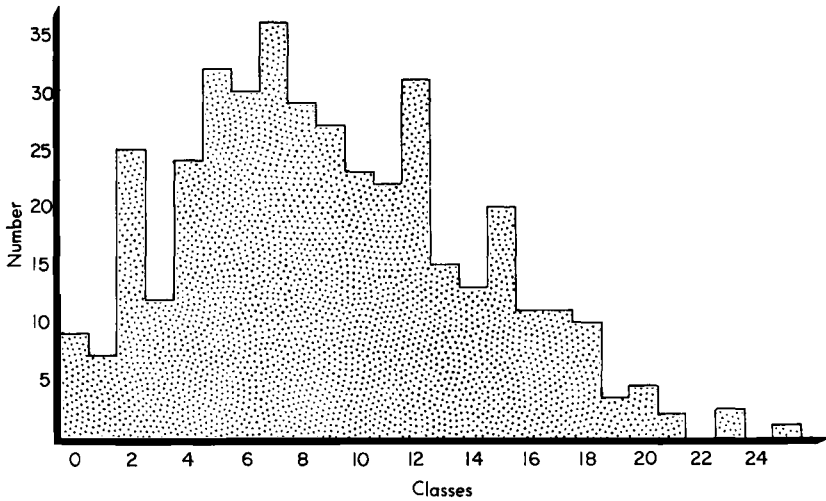


Figure 5. Frequency distribution histogram for total plumage pigmentation scores (soft parts excluded).

related variation (Dorward and Ashmole, 1963), and we have no reasons to expect it in Royal Terns.

Two unanswered questions remain: (1) Why do lighter chicks predominate and (2) why does any chick color variation occur at all in an open-nesting, colonial, precocial species? No concrete data are available to answer the first question, but we suggest that thermoregulatory problems in the very hot nesting environment may limit the percentage of darker chicks. Ground color class distributions support this interpretation, but spotting, especially dorsal spotting class distributions do not. Perhaps superficial spotting is not as critical in temperature regulation as ground color, but this is speculative. Additional support for this explanation of lighter bird predominance would be a further shift towards the lighter end of the curve, and/or a truncation of the darker end, in colonies with a warmer average daytime temperature in the breeding months. This should be investigated.

In answer to the second question, the great morphological variation itself seems related to some unusual aspects of the species' breeding biology. Briefly, Royal Terns nest in dense colonies; we found average densities at Fisherman's Island of 6-9 nests per square meter, comparable to the figure for *S. m. albidorsalis*, the little-known African race (de Naurois, 1959; Dragesco, 1961). The species nests on exposed islets usually free from mammalian predators (Kale et al., 1965) and quickly

deserts these sites when predators reach them, which should obviate the need for the cryptic coloration and behavior typical of many of the other members of the Laridae. Once this selective pressure was relaxed, latent down and soft part color variation could have been selected for, to supplement the parents' voice identification of their own chicks in the dense creches characteristic of this species.

The evolution of creche behavior and its probable cofactor in Royal Tern breeding biology, a single-egg clutch, will be discussed at length elsewhere. Briefly, the following seem to be some of the selective advantages of creche behavior: (1) it capitalizes on a chick's tendency to wander from its nest site; (2) it increases the speed with which a returning parent locates its chick; (3) by reducing the amount of time a parent must spend shepherding a chick it consequently allows more time for foraging; (4) a tightly packed, rapidly moving, alarm call-giving creche is a target toward which protective parents can easily orient to drive off threatening predators; and (5) the usual flock advantage conferred on each member of a densely packed, rapidly moving group when confronted by any predator.

We believe that once in a creche, a chick is discriminated from others by vocal means, the parent identifying the chick and the chick responding to and identifying the parent. But we also think that voice alone is not enough. We have often seen the following approximate sequence of events: an adult arriving with a fish calls loudly; a chick answers from somewhere in the creche; the chick emerges from the creche, reaches the adult, and lunges at the proffered fish, calling as it does so; the adult suddenly pecks at the chick, or quickly flies off with the fish still in its bill, only to repeat the whole process somewhere else at the edge of the creche. Clearly the chick in the creche must first be attracted to its parent's vocalizations and approach the sound; the parent must then recognize the chick vocally and finally visually before feeding it. Thus a triple safety mechanism ensures that each pair feeds only its offspring. The system does break down sometimes, but not often, and for extraneous reasons. Experimental analysis of the precise nature of the discrimination and recognition has not yet been done for Royals, but Hutchison et al. (1968) show that enough variability of the right sorts exists in the closely related (and at least in the U. S., creche-forming) Sandwich Tern to serve as a basis for individual vocal recognition in that species.

Unstudied in detail and seemingly so far unreported anywhere in the literature is the extensive variation that persists into juvenal plumage in Royal Terns. Because of the difficulty in obtaining flying juveniles for similar scoring of the variation, we have not yet quantified or even

described it. But it is almost as extensive as that present in downy chicks, and also includes soft part colors. Quite probably different selective pressures affect juvenal plumage, and we know only imperfectly the relationship between the overall color of a downy chick and its overall color as a juvenile. In general terms, it is as one might expect: very light, unspotted chicks become very light gray juveniles, not too dissimilar from first winter immatures; darker, heavily spotted downy chicks become dark, heavily mottled juveniles, with all possible intermediates, despite Escalante's (1968) description of a "typical" juvenile. (Others have made the same assessment before him; none to date seems aware of the lack of a uniform juvenal plumage in this species).

Ashmole and Tovar (1968) show that U. S.-breeding Royal Terns wintering in Peru were still feeding young well into late winter and early spring. We have seen the same behavior in the southeastern U. S. and in Puerto Rico, also into late winter and early spring. Ashmole and Tovar postulate that it takes young Royals an extraordinarily long time to acquire the skills needed to fish successfully, and while so learning the adults must continue to feed them. We have repeatedly heard parent-young antiphonal calling under these conditions, and hypothesize that here, as in the creche, plumage differences reinforce vocal differences in individual recognition. By the time immature (= first winter, first basic) plumage is achieved, little or no individual plumage variation remains, but parent-young antiphonal calling is still common. Presumably at that late stage of association, voice is sufficient for individual recognition. Indeed, this prolonged period of having to learn its parents' particular voices may well prepare the young Royal Tern for identifying its own mate in a 4,000-10,000 member breeding colony, and its experience as a creche member could well encourage the exceptionally high nesting densities characteristic of the species.

Finally it should be noted that despite numerous literature references to chick color variation in many species besides those already mentioned, including *Sterna nilotica* (Witherby et al., 1941), *S. paradisaea* (Bergman, 1955), *S. dougallii* (Bent, 1921), *S. albifrons* (Tomkins, 1959), and *S. fuscata* (Bent, 1921), we have not attempted any comparisons with other species because with one exception even reasonably accurate qualitative descriptions of the variation are lacking, and the term "polymorphism" is used frequently and uncritically. The exception concerns a *Sterna caspia* colony in San Francisco Bay, Calif., that has been examined for chick color variability by DeGroot (1931), Miller (1943), and recently by Chaniot (pers. comm.). While Chaniot's scoring methods differ somewhat from ours, his results are comparable and should be published soon.

We hope that his study and ours will stimulate detailed descriptions of chick color variation in a variety of sternines.

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SUMMARY

Four hundred Downy Royal Tern chicks were color banded and rank-scored for plumage and soft part characters showing unusual color variation. Nonparametric statistical analyses of these data suggest the presence of four distinct systems of pigmentation, and multifactorial inheritance probably operates in each group, although no genetic studies have yet been made. Bill color and leg color are essentially uncorrelated with each other or with other variables. Pigmented bill tip is correlated only with superficial spotting on the down; one may possibly consider dusky bill tip presence/absence, and black/not black leg color at hatching the only polymorphisms present; but bill color is continuously variable from green to pink. Down ground color varies continuously from white to dark beige, but is essentially uniform over the body of a given bird and is not correlated with any other variable. Any superficial spotting present is always dark brown or black, but the extent of spread over the body varies continuously from bird to bird; the spotting in these areas is correlated inter se and only with a pigmented bill tip. Cumulative scores for plumage characters and plumage plus soft parts characters are distributed unimodally, but are higher at the white or lighter end, possibly in response to thermoregulatory pressures. It is suggested that chick down color variation is probably the result of relaxed selection for crypsis. The relationship between this variation and Royal Terns' creche behavior is discussed briefly in the light of four other unusual aspects of this species' breeding biology: single egg clutches, specialized feeding behavior, extended parental care, and extensive variation in juvenal plumage.

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