# NOTES ON COLOR VARIATION IN DOWNY CASPIAN TERNS

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Variation in the color of the downy plumage is known to occur in many species of terns. Descriptions of the downy young which indicate polymorphism or considerable individual variation in down color can be found in the literature for at least the following species: *Gelochelidon nilotica* (Witherby et al. 1949; Bannerman 1962), *Hydroprogne caspia* (Bergman 1955), *Sterna hirundo* (Bent 1947; Witherby et al. 1949), *S. paradisaea* (Bergman 1955), *S. forsteri* (Bent 1947), *S. dougallii* (Bent 1947; Witherby et al. 1949), *S. aleutica* (Bent 1947), *S. fuscata* (Murphy 1936; Bent 1947; Witherby et al. 1949), *S. albifrons* (Murphy 1936; Tomkins 1959), *Thalasseus maximus* (Chamberlain 1939; Bent 1947), *T. sandvicensis* (Witherby et al. 1949; Bannerman 1962), and *Anous stolidus* (Watson 1908; Murphy 1936; Dorward and Ashmole 1963). Species apparently monomorphic include *Chlidonias* spp. (Witherby et al. 1949), *Anous tenuirostris* (Cullen and Ashmore 1963), and *Gygis alba* (Dorward 1963). The degree of color variation and the extent to which different color forms or morphs intergrade with each other appear to vary from species to species.

Despite the widespread occurrence of color variation in tern chicks, few species have been described carefully, and relatively little is known concerning the ecological significance of this variation. This paper deals with the color variation, the frequencies of the various color types, and possible selective pressures influencing these frequencies in downy Caspian Terns (*Hydroprogne caspia*) at a breeding colony in the south end of San Francisco Bay, California.

## HISTORY AND DESCRIPTION OF THE COLONY

The first known breeding record of the Caspian Tern in San Francisco Bay is a set of eggs collected in 1916, presumably in the south arm of the bay (Grinnell and Miller 1944). In 1922 a small colony of seven pairs was found in the southern end of the bay, and in 1923 two pairs nested again at the same location. Apparently no young were raised at this site in either year or in later years. In 1924 Caspian Terns were discovered nesting at a new site (the present one) some two miles distant. This colony increased in size during the next seven seasons, and 287 nests were counted in 1931 (DeGroot 1931). On 21 May 1943 there were 378 occupied nests (Miller 1943). The terns have apparently nested at this same site in every breeding season since then, with the numbers staying approximately the same or declining somewhat. I visted the colony on 22 July 1964, 2 July 1965, 14 May 1966, and 16 July 1966, and counted 119, 138, 299, and 98 occupied nests, respectively—the number varying through the breeding season.

The colony is situated on a narrow dike between two hypersaline evaporation ponds of the Leslie Salt Company about ½–¾ mi. NW of the KGO transmitter on Dumbarten Bridge, Alameda County, California. There is no vegetation in the immediate vicinity of the nesting area, and apparently there never has been any (see photographs in DeGroot 1931 and Miller 1943). The colony still consists of two segments separated by a gap of about 10 yards, as noted by earlier authors.

The dike was constructed in 1916 (Leslie Salt Company, letter), eight years before the terns were first found nesting on it. Therefore, as of 1964, the terns had nested there for at least 41 years (no more than 49). If Caspian Terns first breed when they are three years old (Ludwig 1965), the colony was on the order of 14–16 successive generations old in 1964.

## DESCRIPTION OF COLOR VARIATION

As early as 1926 it was noted that there were "two distinct color phases" of downy young (DeGroot 1931), a brownish phase and a whitish phase. In 1943 Miller found a slight predominance of the darker phase and a small number of chicks which were intermediate in character.

On the 22 July 1964 trip the downy chicks under approximately 10 days of age were classified into three color classes: light, intermediate, and dark. Judging by the voucher

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TABLE 1.  Color categories of downy Caspian Terns.

| Code | General description | Reference specimen |
|---|---|---|
| **Dorsal ground color** | | |
| 1,–,– | nearly white | no specimen |
| | to very faint gray | MVZ 101423 |
| | or very faint buff | MVZ 88381 |
| 2,–,– | light buff | MVZ 88380 |
| | to medium buff | MVZ 156035 |
| 3,–,– | dark buff | MVZ 88382 |
| | to brownish | MVZ 101422 |
| | and darker | no specimen |
| **Dorsal spotting** | | |
| –,1,– | faint wisps of | MVZ 88380 |
| | blackish on back | MVZ 88381 |
| –,2,– | moderate blackish | MVZ 91705 |
| | spotting | MVZ 88383 |
| –,3,– | heavier spotting, | MVZ 91706 |
| | spots almost confluent and more extreme | |
| **Throat color** | | |
| –,–,0 | pure white | no specimen |
| –,–,1 | very faint gray | MVZ 88381 |
| | | MVZ 91705 |
| –,–,2 | moderate gray | MVZ 88383 |
| | | MVZ 156035 |
| –,–,3 | darker gray, generally extending further ventrally | MVZ 89929 |

specimens collected by Miller, this classification does not differ essentially from his. These three classes do not, however, adequately express the variability observed. On the three following trips each chick was rated on three variables and the score expressed as a three-digit numeral (e.g., 2,2,1) referring to dorsal ground color, degree of dorsal spotting, and throat color, respectively. The categories are defined in table 1. Reference specimens are in the Museum of Vertebrate Zoology. This classification, while adequate for use in the field, still does not express the total variation. There is variation in the extent of the ground color laterally and onto the ventral surface, and there are at least two components to the ground color, a grayish component due to pigment in the basal portion of the down feather and a brownish component in the distal portion. The dorsal spots do not appear to vary in hue, but mainly in density. When a series of specimens can be compared closely, the categories of table 1 grade smoothly into each other and do not represent discrete morphs.

There is also variation in the color of the legs, as noted by Miller (1943), which has also been reported for chicks of the Royal Tern, *Thalasseus maximus* (Chamberlain 1939), but I did not collect consistent field data on this character. The leg color of

Caspian Tern chicks at this colony varies from bright orangish through graded intermediates to dark gray, and although leg color changes with age, differences can be discerned in both newly hatched chicks and chicks well into the juvenal plumage. This color variation can be seen in a limited way in dried study skins. Judging from one specimen in which the two layers of the interdigital web were separated when fresh, chicks with dark legs also have orangish pigment on the inside, but it is masked by more superficial black pigment.

Dr. Robert K. Selander made spectrophotometric analyses of the dorsal ground color of three chicks for me on a Bausch and Lomb Spectronic 505 analyzer. These three chicks represented the light, intermediate, and dark categories of table 1, and were selected for a minimal amount of gray in the basal portion of the down feathers. The analyses were made on a small area on the dorsal surface of the head where there is minimal obfuscation due to spotting. The spectral analyses of light reflected from this region are shown in figure 1, together with the constants Y (per cent brightness), $\lambda_d$ (dominant wave-length), and $P_e$ (per cent excitation purity), as defined by the Committee on Colorimetry (1963). From the light specimen to the dark specimen there is a marked increase in the excitation purity, a decrease in brightness, and a slight shift in dominant wave-length to the red, which can also be discerned when comparing chicks to Munsell color standards (Munsell 1943). In the Munsell re-notation system, the colors of these three chicks would be designated as follows: light, 2.5 Y 7/2; intermediate, 10 YR 6.1/2.3; dark, 10 YR 4.5/2.5 (interpolated from tables in Nickerson 1946).

RESULTS

Table 2 shows the frequencies of various color combinations in the colony in 1965 and 1966. The partitioning of this spectrum into light, intermediate, and dark categories is arbitrary, but probably approximates the classes used in 1964 and by Miller in 1943, except that the breadth of the intermediate class may be slightly narrower (Miller, pers. comm.). Miller's intermediate specimen MVZ 88383 might be classified more critically as 1½, 2½, 2.

As can be seen in table 2, the different types of color variation are not strictly correlated, and they recombine rather freely. However, many possible combinations were not observed. In table 3 Spearman Rank Correlation Coefficients ($r_s$), corrected for ties (Siegel 1956), have been computed for the three vari-
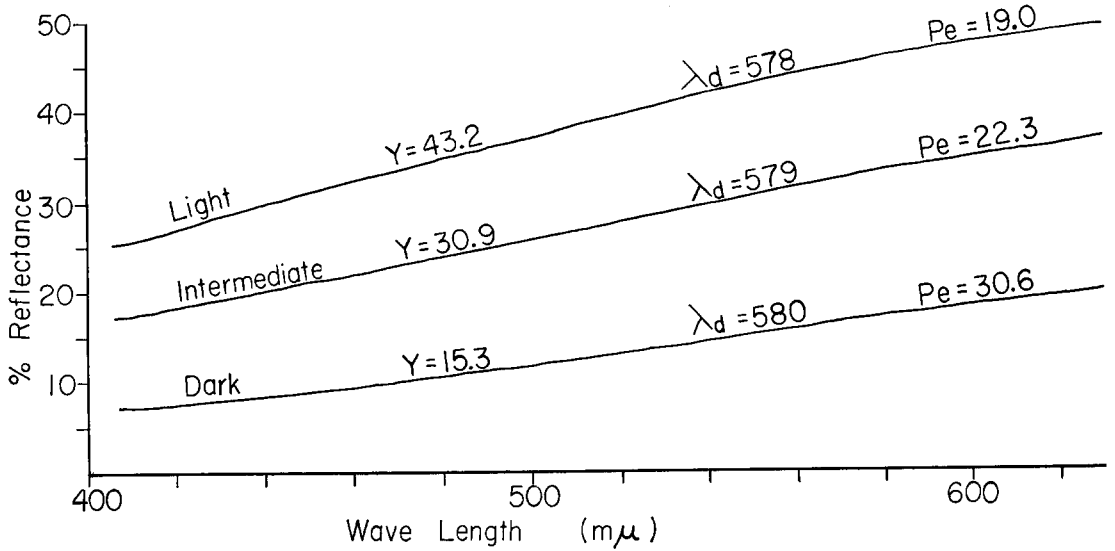
FIGURE 1. Spectrophotometric reflectance curves for ground color of light, intermediate, and dark Caspian Tern chicks.

ables taken in pairs, along with their probabilities under the null hypothesis of "no correlation." All character-pairs show a weak positive correlation with $P$ values $< 0.05$.

To test for relation between leg color and the other three color variables, the 13 available museum specimens were ranked on leg color from the most orange to the most black, and correlation coefficients were computed

TABLE 3. Spearman Rank Correlation Coefficients between pairs of characters of downy Caspian Terns.

| Character-pairs | $r_s$ | $P$ |
|---|---|---|
| Ground color vs. dorsal spotting | + 0.249 | < 0.01 |
| Ground color vs. throat color | + 0.205 | < 0.02 |
| Dorsal spotting vs. throat color | + 0.452 | < 0.001 |

with the other three variables (table 4). The values of $r_s$ in tables 3 and 4 cannot be compared directly with each other in magnitude because sample sizes and precision of ranking differ, and because the museum specimens are a selected sample rather than a population sample. Nevertheless, it can be seen within each table that throat color, leg color, and dorsal spotting show a greater degree of correlation with each other than with ground color. The former three colors all involve increasing amounts of black pigment, and their mutual correlation suggests that they may have overlapping or linked genetic control.

Examination of museum specimens from this colony shows that no color variant is restricted to either sex. However, the possibility

TABLE 2. Frequency distribution of various color combinations of downy Caspian Terns.

|  | No. chicks | | |
|---|---|---|---|
| Code | 2 July 1965 | 14 May 1966 | 16 July 1966 |
| **Light** | | | |
| 1,1,0 | 4 | 2 | 1 |
| 1,1,1 | 9 | 4 | 5 |
| 1,1,2 | 1 | 1 | 0 |
| 1,1,3 | 1 | 0 | 1 |
| 1,2,1 | 4 | 1 | 3 |
| 1,2,2 | 3 | 4 | 2 |
| 1,3,2 | 0 | 1 | 0 |
| **Intermediate** | | | |
| 2,1,0 | 6 | 1 | 1 |
| 2,1,1 | 11 | 7 | 5 |
| 2,1,2 | 2 | 4 | 4 |
| **Dark** | | | |
| 2,2,1 | 5 | 9 | 3 |
| 2,2,2 | 8 | 6 | 5 |
| 2,3,1 | 0 | 1 | 0 |
| 2,3,2 | 1 | 2 | 1 |
| 3,2,1 | 1 | 0 | 2 |
| 3,2,2 | 5 | 1 | 2 |
| 3,2,3 | 0 | 1 | 0 |
| **Totals** | 61 | 45 | 35 |

TABLE 4. Spearman Rank Correlation Coefficients between leg color and three other color variables of downy Caspian Terns.

| Character-pairs | $r_s$ | $P$ |
|---|---|---|
| Ground color vs. leg color | + 0.359 | < 0.20 |
| Dorsal spotting vs. leg color | + 0.554 | < 0.05 |
| Throat color vs. leg color | + 0.592 | < 0.05 |

TABLE 5. Percentages of light, intermediate and dark Caspian Tern chicks observed on five dates.

| Class | May 1943 ($n = 110$) | July 1964 ($n = 42$) | July 1965 ($n = 61$) | May 1966 ($n = 35$) | July 1966 ($n = 45$) |
|---|---|---|---|---|---|
| Light | 36.4 | 35.7 | 36.1 | 28.9 | 34.3 |
| Intermediate | 7.3 | 31.0 | 31.1 | 26.7 | 28.6 |
| Dark | 56.4 | 33.4 | 32.8 | 44.4 | 37.1 |

that color variants differ in frequency between the sexes remains to be tested.

Table 5 shows the relative frequencies of the light, intermediate, and dark classes of chicks for five different dates. When the numbers of chicks in each class are compared for all five dates taken together, the null-hypothesis of "no difference in frequency between dates" must be rejected at the 0.05 level ($\chi^2 = 23.92$, $P < 0.01$, $df = 8$). However, when Miller's data for 1943 are omitted and the last four dates are taken together, the null-hypothesis must be accepted ($\chi^2 = 1.80$, $P > 0.90$, $df = 6$). Thus, between 1943 and 1964 there has been a marked increase in the frequency of the intermediate class at the expense of the dark class. If one were to expand the boundaries of the intermediate class in table 2 to include the 1,2,- and/or 2,2,- categories, this would only accentuate the increase in intermediates, and, therefore, the differences cannot be explained reasonably on the basis of differing classifications. Nor can the difference be explained as a change in frequency between the early part of the breeding season and the late, since there is no significant difference between the frequencies of May 1966 and July 1966 ($\chi^2 = 0.46$, $P > 0.70$, $df = 2$).

## DISCUSSION

Assuming that there has been an historical change in the proportions of color variants in this colony, one may then ask what selective pressures have brought this about. Protective coloration is a very plausible possibility. Miller (1943) and I agree that the lightest and darkest chicks are more extreme in coloration than the predominant soil color within the colony. Approximately five per cent of the soil within the nesting area is covered with a consolidated, white, or creamy white, deposit of guano which apparently has accumulated over many years. The lightest chicks and chicks with a very faint buffy color match these deposits very closely. About 15 per cent of the soil in the colony is dark brown (darker than the darkest chicks), apparently due to the accumulated chitin of dead brine flies.

These areas are mainly scattered along the waterlines and margins of the dike where very few tern nests are placed, and they are covered periodically when the water level in the ponds is raised. There are a few very small areas of reddish brown soil. The remaining 80 per cent of the soil is a buffy tan color of varying shades and variously spotted with guano. The largest part of this is strikingly similar to the dorsal ground color of the intermediate chicks. (Color photographs of live chicks against their natural background and of a graded series of museum specimens against a series of background colors have been taken.) The major part of the soil surface is of such a texture that under the bright summer sun, a fine shadow pattern is produced which is similar to the dorsal spotting of the chicks.

The only potential predators which have been noted around the colony in the breeding season are immature Ring-billed Gulls (*Larus delawarensis*) and California Gulls (*Larus californicus*) (Miller, unpubl. MS). During several of my visits to the colony, gulls appeared to be attracted to the colony during the disturbance, approached unattended chicks and eggs, but were driven away by adult terns. Where California Gulls and Caspian Terns nest together, the gulls are known to devour the terns' eggs (Twomey 1948). In addition to summering, non-breeding gulls, Barn Owls (*Tyto alba*), Short-eared Owls (*Asio flammeus*), Red-tailed Hawks (*Buteo jamaicensis*), Peregrine Falcons (*Falco peregrinus*), Sparrow Hawks (*Falco sparverius*), and White-tailed Kites (*Elanus leucurus*) probably occur in the vicinity while the terns are breeding and may prey upon the chicks. Caspian Terns themselves have been reported to attack and, in some cases, kill the downy chicks of Gull-billed Terns (Pemberton 1927), Ring-billed Gulls (Lewis 1925) and their own species (Bent 1947). If there is predation pressure, or if indeed Caspian Terns do kill young of their own species with any regularity, it is probable that cryptically colored chicks would be less vulnerable.

Human visitation may also have a selective effect. As one walks through the colony, many

chicks crouch and freeze, particularly very small chicks or those that have been recently fed and are laden with fish. These crouching chicks are easily passed over, even by someone attempting to census them thoroughly. When approached closely, or handled, they generally attempt to run away and are not easily quieted. Many waddle to the water and swim out onto the ponds. Many others desert their nest sites and run ahead of the observer down the dike, particularly older birds coming into juvenal plumage. Many of the chicks that take to the water can later be seen swimming back to the dike. However, chicks that leave their nest sites undoubtedly suffer greater mortality than those that do not. It may be, therefore, that an observer walking down the dike examining nests or banding chicks displaces a greater proportion of contrastingly colored chicks from their nest areas and passes by a greater proportion of cryptically colored chicks.

Bergman (1955) found geographic variation in the frequency of the color phases of the chicks of Caspian Terns and Arctic Terns (Sterna paradisaea) and attributed it to protective coloration. In the Baltic region, about 90 per cent of the Caspian Terns nest upon flat stone surfaces which become whitewashed with guano (see photos in Bergman 1953), and in this region chicks of the white phase predominate. In North America, however, they nest more frequently on sand or gravel areas where guano accumulation is less pronounced, and there is a lower proportion of white chicks and a higher proportion of "gray," "light yellowish white," and "brownish" chicks. Chicks of the Arctic Tern show geographical variation in the ratio of color phases within the Baltic region. On the southern coast of Finland this species nests mostly upon sandy and gravelly beaches of a predominately gray color, and the gray phase is more frequent. On the southwestern and western coasts of Finland these terns tend to nest in rocky areas with dark, low vegetation, and the brownish phase is more frequent.

If protective coloration has been the selective basis for the increase in intermediate colored chicks at this San Francisco Bay colony, the question remains as to why this has been accompanied by a decrease in dark chicks. As mentioned above, the areal extent of soil matching the darkest chicks is much less than that matching the light and intermediate chicks. A further untested possibility is that chicks of different colors differ in their thermoregulatory capacities. Insolation is strong during the breeding season, and there

is no shade available in the colony except beneath adult terns. Dark chicks may succumb to overheating more quickly when unattended, particularly during disturbances by observers.

Another possibility for the increase in diversity of color types at this colony is that it may facilitate individual recognition of the chicks. I have no observations which would suggest that adults can recognize their own chicks by their color, or that chicks can recognize their nest mates, or that any disadvantage would accrue if broods were mixed, and this study remains to be done.

Places where many tern species nest, such as lake shores, sand bars, and islands, are unstable habitats, subject to change or destruction from changes in water level, erosion, or plant succession. The "life expectancy" of a suitable nesting area may be rather short, and shifts of colonies may be necessary every hundred generations or so. Thus, tern populations may be faced with selection pressures which periodically change directions, and gene frequencies may seldom come into equilibrium or reach fixation. Chick polymorphism may be a result of and adaptation to the necessity of frequently changing colony sites. It is possible that in the next decades, land development in southern San Francisco Bay may destroy this colony or force a change in breeding areas. In the latter event, it would be of interest to study changes in frequencies of color types in the new location.

## SUMMARY

Caspian Terns have nested at a single location in southern San Francisco Bay since sometime between 1916 and 1924. In 1964 the downy young were censused and classified into light, intermediate, and dark classes similar to those of Miller (1943). In 1965 and 1966 the downy young were classified on the basis of three variables: dorsal ground color, dorsal spotting, and throat color. An additional variable, leg color, was studied only in a small sample. The first three variables recombine freely, but there is a weak, significant correlation between all pairs of variables. Since Miller's census in 1943, there has been a marked increase in the frequency of chicks of intermediate coloring and a corresponding decrease in the frequency of dark chicks. Intermediate chicks more closely resemble the predominant soil color of the nesting area than do the extreme types. It is suggested that cryptically colored chicks are less vulnerable to attacks by predators or other

Caspian Terns, or are less frequently dissociated from their nest sites by human visitors.

## ACKNOWLEDGMENTS

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