

ASSORTATIVE MATING AND SEXUAL DIMORPHISM IN THE COMMON TERN

MALCOLM C. COULTER¹

ABSTRACT.—Although male and female Common Terns (*Sterna hirundo*) are almost identical in plumage and in most external body measurements, males have longer, deeper, and wider bills than do females. Two patterns in the size relationships between mates are demonstrated. First, males tend to have larger bills than their mates. This may be explained by random mating, given the sexual dimorphism observed. Second, Common Terns mate assortatively according to bill size. This pattern may result if there is either a year-to-year component or an age component of bill size variation and if first-breeding birds return to the colony after experienced breeders have already established pairbonds and most birds retain their mates from year to year. Received 11 Jan. 1985, accepted 30 Aug. 1985.

Mating patterns may contribute significantly to the genetic structure of bird populations. When similar individuals tend to mate with each other (i.e., mating is positively assortative), progeny are more homozygous, and phenotypic variability in the population may be greater than when mating is either random or disassortative (Falconer 1981, Halliday 1978, Partridge 1983; but see Lande 1977). Positive assortative mating based on the color morphs has been demonstrated for white and blue morphs of the Snow Goose (*Chen caerulescens*) (Cooke et al. 1976). This involved discrimination according to a discrete variable (i.e., distinct blue and white morphs). It is more difficult to demonstrate mating patterns according to continuous variables, particularly in wild populations. Recently, Boag and Grant (1978) presented evidence that Medium Ground Finches (*Geospiza fortis*) mate assortatively according to bill size and tarsus length. In this paper I examine assortative mating and mating pattern according to size in the Common Tern (*Sterna hirundo*). Sexual dimorphism has not been demonstrated for Common Terns, although in two early works it was suggested that females tend to be slightly smaller than males (Coues 1903, Ridgeway 1919). I examine sexual dimorphism and ask whether the observed mating patterns may be due to random mating alone, given the sexual dimorphism observed.

METHODS

I caught Common Terns, including both members of 61 pairs, on Great Gull Island, Long Island Sound, New York, in 1978, 1979, and 1980. For each individual, I measured wing length to the nearest mm. I also measured tarsus and middle toe length as well as culmen

¹ Savannah River Ecology Lab., P.O. Drawer E, Aiken, South Carolina 29802.

TABLE 1
BODY MEASUREMENTS OF COMMON TERNS CAUGHT ON GREAT GULL ISLAND IN 1978 AND 1979

Body measurement	Sex	N	Mean	Standard deviation	Range	Probability of a difference between the sexes ^a
Weight (g)	Female	55	117.0	7.88	102.8–134.7	NS ^b
	Male	50	117.1	7.02	104.1–138.5	
Wing (mm)	Female	55	268.1	5.08	258.0–284.5	NS
	Male	50	268.1	5.88	258.0–280.0	
Tail (mm) ^c	Female	30	148.4	7.53	132.0–169.0	NS
	Male	26	250.6	5.74	133.0–161.5	
Tarsus (mm)	Female	55	24.1	0.90	22.30–25.98	NS
	Male	50	24.0	0.76	22.55–26.06	
Middle toe (mm)	Female	55	24.0	1.24	20.85–26.45	NS
	Male	50	24.4	1.31	21.11–27.05	
Bill length (mm)	Female	55	34.7	1.50	30.95–37.85	<0.001
	Male	50	37.0	1.42	34.32–41.00	
Bill depth (mm)	Female	55	8.0	0.48	6.85–9.27	<0.001
	Male	50	8.4	0.34	7.54–9.19	
Bill width (mm)	Female	55	5.4	0.51	4.42–7.54	<0.05
	Male	50	5.6	0.48	4.55–6.91	

^a *t*-test.

^b *P* < 0.10.

^c Data from 1979 only.

length, depth, and width with either of two calipers. One caliper measured in metric to the nearest 0.05 mm; the other measured in English measurements to the nearest 0.001 in., from which the measurements were converted to the metric equivalents. I weighed birds to the nearest 0.1 g. In 1979 and 1980, I also measured tail length to the nearest mm. Through the efforts of the Great Gull Island Project, all of the birds were color-banded previously. Their sexes were determined by observing behavior during copulation. I examined the measurements for sexual dimorphism and assortative mating by relative size. Among the measurements I took, mating patterns were only discernible according to the bill measurements. In this paper I discuss only the patterns according to culmen length, but the same trends held for all culmen measurements (Table 3). In order to distinguish whether the observed mating pattern was due to random mating or to some other factor, I ran 25 simulations. In each simulation I paired the 61 females with the 61 males. I compared the mating patterns according to the body measurements in these random matings with the field data.

RESULTS

Sexual Dimorphism.—Adult male and female terns are not morphologically distinct. Plumages are similar, and measurements for most body parts are not statistically different (Table 1). Averages for bill measure-

TABLE 2
STANDARDIZED COEFFICIENTS OF THE DISCRIMINANT FUNCTION FOR SEPARATING THE SEXES OF COMMON TERNS OF GREAT GULL ISLAND, LONG ISLAND SOUND, NEW YORK, IN 1978

Body parts included	Standardized coefficients for three functions		
	A	B	C
Bill length	-0.912	-0.947	-0.904
Bill depth	-0.396	-0.451	-0.418
Bill width	-0.013	0.082	0.144
Weight		0.360	0.352
Wing length			0.082
Tarsus			-0.225
Middle toe			0.074
Accuracy of determination ^a	72%	80%	80%

^a Percent of cases for which sex is correctly determined.

ments were different, although there were overlaps: 70% for culmen length, 91% for culmen depth, and 99% for culmen width. Based on these three measurements, one can accurately determine sex 72% of the time using discriminant function analysis (Table 2). If weight, a measure of body size, is included in the analysis the accuracy of statistical prediction increases to 80%. The discriminant function is $D = 0.4647$ (Bill length) + 0.3895 (Bill depth) - 0.1349 (Bill width) - 0.0485 (Weight) - 17.1862 , where culmen length, depth, and width are in mm; weight is in g; and $D < 0.00$ for females and >0.00 for males. Accuracy is not increased further by including additional body measurements. For a given body size, males have larger bills than females. These findings are not surprising: a combination of head and bill length is sufficient to determine sex in a number of species of gulls (Larinae) (Coulson et al. 1983).

Mating Pattern.—Within pairs of Common Terns, there was no tendency for individuals of one sex to be larger than those of the other sex, except in bill size (Table 3). In 60 of 61 pairs, males had longer bills than their mates (Sign Test, $P < 0.005$). In the exceptional pair, the female's bill was 0.11 mm longer than her mate's bill, a difference within measurement error. The average difference in bill length was $2.60 \text{ mm} \pm 1.48$ (SD). At the same time, mating was assortative: males with longer bills tended to mate with long-billed females, and short-billed males tended to mate with short-billed females. The correlation coefficient between males and females of individual pairs was $r = 0.46$ ($N = 61$, $P < 0.05$) (Fig. 1). Correlation coefficients for other body parts between mates were not significant. Assortative mating according to bill length and whether

TABLE 3
BILL SIZE DIFFERENCES BETWEEN SEXES WITHIN PAIRS OF COMMON TERNS ON GREAT GULL ISLAND, LONG ISLAND SOUND, NEW YORK

Bill measurement	Males larger than females	Males and females the same size	Females larger than males	Probability of a significant difference ^a
Length	60 (98) ^b	0 (0)	1 (2)	≤0.0001
Depth	49 (80)	1 (2)	11 (18)	≤0.001
Width	42 (69)	2 (3)	17 (28)	=0.002

^a Two-tailed sign test.

^b N (%).

males have longer bills than their mates are distinguishable, and I deal with this below.

SIMULATION OF MATING PATTERNS

An observed mating pattern may be due to any of a number of factors: discrimination among potential mates, annual variation in adult size coupled with mating predominantly among cohorts, or even random mating in sexually dimorphic species. Common Terns are sexually dimorphic according to bill size. It is important, therefore, to distinguish whether the observed mating pattern may have been due to random pairing alone, or whether some other factors such as distinguishing among potential mates may also have been involved. To examine the importance of random pairing, I paired, according to a random number table, the 61 members of each sex in 25 simulations. I compared the bill lengths among pairs obtained by this simulation with the measurements of bill lengths for the pairs that I collected in the field. I asked three questions:

- (1) Can random mating alone explain the high proportion of pairs in which males have longer bills? One would expect, given the sexual dimorphism observed, that under random mating alone there would be a large number of pairs in which the males had longer bills than their mates. In 25 random simulations, males had longer bills in an average of 56 pairs (92%). This was not significantly different from the 60 out of 61 pairs observed in nature (Fisher's Exact Test, $P = 0.090$). It is possible that Common Terns choose their mates so that males have longer bills and that only a very large sample size would demonstrate a difference from the 92% of the pairs with males having longer bills that would be expected under random mating. The only exceptional case observed in this study involved birds whose bills were, within measurement error, almost identical. At present, however, random mating is sufficient to explain this pattern.

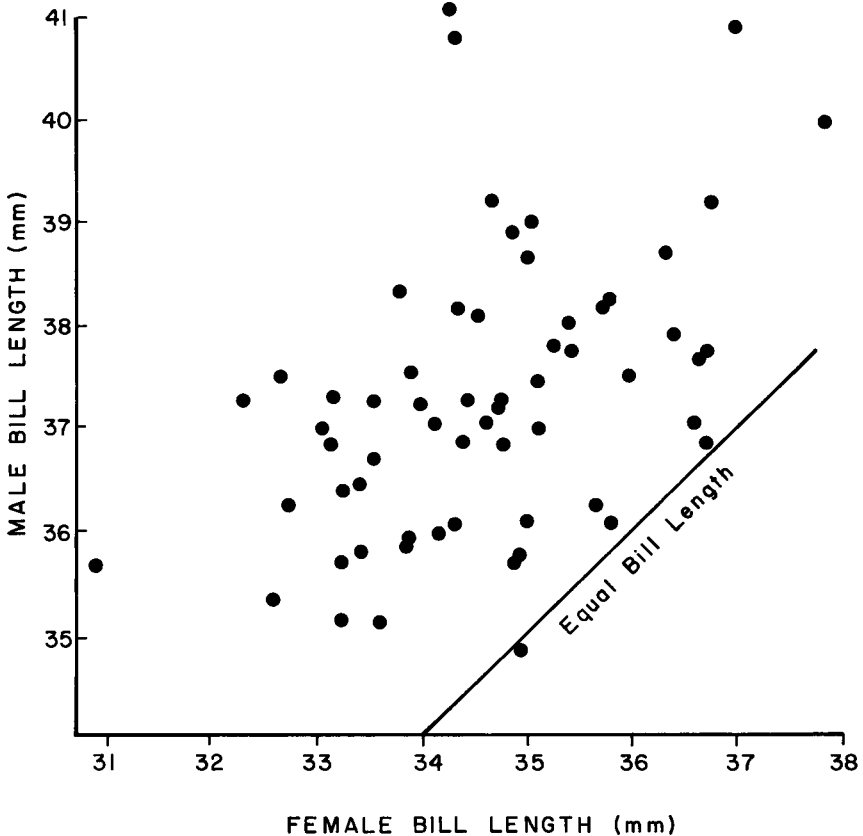


FIG. 1. Relation of culmen lengths of pairs of Common Terns caught on Great Gull Island.

- (2) Can random mating alone explain the assortative mating? The correlation between bill lengths of mates was significant. This indicated that the assortative mating observed was not the result of random pairing. Furthermore, among the 25 random pairings, none was significant (range of correlation coefficients: -0.215 to $+0.298$, $P > 0.05$). Random mating, then, would not lead to a pattern of assortative mating.
- (3) Can the observed pattern of males having longer bills than their mates explain the assortative mating? Among the 25 random trials, when I considered only those pairs in which males had longer bills, I found that in all but one of the trials the correlation coefficients were not significantly different from zero ($P > 0.10$); in the one case the coefficient was 0.401 ($P < 0.05$). The average correlation

coefficient (r) for the 25 trials was 0.09, significantly less than the 0.46 observed. Thus, the pattern of males having longer bills than their mates cannot explain the assortative mating.

The results of the simulation indicate that random mating is sufficient to explain the high frequency of pairs in which the males had longer bills than their mates. However, random mating would not lead to the positive assortative mating observed.

DISCUSSION

I have demonstrated two patterns in the size relationships between mates of Common Terns: (1) assortative mating and (2) that males have larger bills than their mates. These patterns seem to be independent from each other and so may be due to different factors. I discuss them separately.

Males have larger bills than their mates.—A difference in bill size between mates has been shown for other members of the Charadriiformes. Among some species of shorebirds, females tend to be larger than males, and in those species examined the females had larger bills in nearly all pairs (Harris 1967, Jehl 1970, Soikkeli 1966). In many gull species, males tend to be larger than females. Harris and Hope-Jones (1969) examined bills in pairs of Herring Gulls (*Larus argentatus*) and Lesser Black-backed Gulls (*L. fuscus*) and found that in almost all pairs the male had the larger bill. All of these species show sexual dimorphism in bill size, and random mating alone may explain the size relationships between mates. Random mating is sufficient to explain this pattern in Common Terns.

Assortative mating according to bill size.—The case for Common Terns described here is the first demonstration of assortative mating according to a nondiscrete character for any Charadriiformes species. Halliday (1978) has suggested that assortative mating according to a nondiscrete character would maintain greater phenotypic variability than would be found under other mating patterns. Lande (1977), however, developed a model that indicated that when mutation and selection are considered for a large population, the mating pattern would have no influence on genetic variability in the population. We can differentiate between these two hypotheses because they predict different shapes of the statistical distribution of the character involved. According to the former approach, one would expect a platykurtic distribution (i.e., the tails of the distribution would have more observations than if the measurements were normally distributed); according to Lande's approach, one would expect a normal distribution, which is what I found ($\gamma_1 = 0.393 \pm 0.330$ (SD), $P > 0.10$; $\gamma_2 = 3.235 \pm 0.661$ (SD), $P > 0.10$).

Nisbet et al. (1984) have shown that Common Terns mate assortatively

according to age. The factors that led to the assortative mating are not apparent. Coulson and Thomas (1983) have demonstrated that Black-legged Kittiwakes (*Rissa tridactyla*) also mate assortatively according to age. First-breeding birds usually pair together because they arrive at the colony late, at which time most of the experienced breeders have already established pairbonds. Many birds retain their mates from year to year. A similar pattern may also exist among Common Terns. At the same time, there may be a year-to-year component of bill size variation. Year-to-year variation in tarsus length has been demonstrated for the Great Tit (*Parus major*) (Garnett 1981). Alternatively, if bills grow slowly after fledging and during the first few years of adult life, then this may impose an age component to bill size variation. Slow growth of adult Herring Gull bills has been demonstrated by Coulson et al. (1981). If, then, there is a tendency for Common Terns to mate assortatively according to age, and if either (1) there is a year-to-year component of bill size variation or (2) there is an age component of bill size variation, then this may explain the assortative mating according to bill size.

ACKNOWLEDGMENTS

I am thankful to the Frank M. Chapman Memorial Fund for a fellowship that supported this study, and I am grateful to Helen Hays for permission to work on Great Gull Island and for providing facilities on the island. I thank the Long Point Bird Observatory and the Savannah River Ecology Laboratory for providing a place to write. Preparation of this manuscript was supported by contract DE-AC09-76SR00-819 between the University of Georgia's Savannah River Ecology Laboratory and the U. S. Department of Energy. A. Brásh, D. Evans, and E. Liebson helped with measurements in the field. J. Novak provided advice on statistics. L. Orebaugh drew the graphics. I thank R. Banks, G. Barrowclough, J. Burger, C. Collins, J. DiCostanzo, J. Farrand, Jr., P. Grant, J. Greenway, H. Hays, M. LeCroy, R. J. O'Connor, R. Payne, A. Poole, T. Price, R. E. Ricklefs, and F. Vuilleumier for discussions and comments on earlier versions of the manuscript. This is contribution number 64 of the Great Gull Island Project.

LITERATURE CITED

- BOAG, P. T. AND P. R. GRANT. 1978. Heritability of external morphology in Darwin's Finches. *Nature* 274:793-794.
- COOKE, F. G., H. FINNEY, AND R. F. ROCKWELL. 1976. Assortative mating in Lesser Snow Geese. *Behav. Genet.* 6:127-140.
- COUES, E. 1903. *Key to North American birds*. Dana Estes, Boston, Massachusetts.
- COULSON, J. C., N. DUNCAN, C. S. THOMAS, AND P. MONAGHAN. 1981. An age-related difference in the bill depth of Herring Gulls *Larus argentatus*. *Ibis* 123:499-502.
- AND C. S. THOMAS. 1983. Mate choice in the Kittiwake Gull. Pp. 361-376 in *Mate choice* (P. Bateson, ed.). Cambridge Univ. Press, Cambridge, England.
- , C. S. THOMAS, J. E. L. BUTTERFIELD, N. DUNCAN, P. MONAGHAN, AND C. SHEDDEN. 1983. The use of head and bill length to sex live gulls Laridae. *Ibis* 125:549-557.
- FALCONER, D. S. 1981. *Introduction to quantitative genetics*. Longman, London, England.

- GARNETT, M. C. 1981. Body size, its heritability and influence on juvenile survival among Great Tits, *Parus major*. *Ibis* 123:31–41.
- HALLIDAY, T. R. 1978. Sexual selection and mate choice. Pp. 180–213 in *Behavioral ecology: an evolutionary approach* (J. R. Krebs and N. B. Davies, eds.). Blackwell, Oxford, England.
- HARRIS, M. P. 1967. The biology of Oystercatchers *Haematopus ostralegus* on Skokholm Island, south Wales. *Ibis* 109:180–193.
- AND P. HOPE-JONES. 1969. Sexual differences in measurements of Herring and Lesser Black-backed gulls. *Br. Birds* 62:129–133.
- JEHL, J. R., JR. 1970. Sexual selection for size differences in two species of sandpipers. *Evolution* 24:311–319.
- LANDE, R. 1977. The influence of the mating system on the maintenance of genetic variability in polygenic characters. *Genetics* 86:485–498.
- NISBET, I. C. T., WINCHELL, J. M., AND A. E. HEISE. 1984. Influence of age on the breeding biology of Common Terns. *Colonial Waterbirds*. 7:117–126.
- PARTRIDGE, L. 1983. Non-random mating and offspring fitness. Pp. 227–255 in *Mate choice* (P. Bateson, ed.). Cambridge Univ. Press, Cambridge.
- RIDGEWAY, R. 1919. *The birds of North and Middle America*. Vol. VIII. U.S. Government Printing Office, Washington, D.C.
- SOIKKELI, M. 1966. On the variation in bill and wing-length of the Dunlin (*Calidris alpina*). *Bird Study* 13:256–269.

GENERAL MEETING

OF THE WORKING GROUP ON GRANIVOROUS BIRDS—INTECOL

On 13 August 1986, during the meeting of the IV International Congress of Ecology, Syracuse, New York, USA, 10–16 August 1986, the General Meeting of the Working Group on Granivorous Birds—INTECOL, will be held.

The theme of the symposium has been tentatively formulated as “The role of granivorous birds in ecosystems.” The following topics will be included: (1) population dynamics, (2) biomass and production rates, (3) energetics, (4) impact of granivorous birds on ecosystems, and (5) pest management.

The symposium will include a review of up-to-date results of international studies on certain granivorous birds and a discussion of the most fruitful directions for further study.

Oral presentations at the symposium will be limited to 15 min. The program of the symposium will be established by 31 December 1985, based on titles and one-page abstracts submitted by that date.

All correspondence including requests for information should be sent to: Chairman of Working Group—Professor Dr. Jan Pinowski, Dept. Vertebrate Ecology, Institute of Ecology/PAS, Dziekanow Lesny, 05-092 Lomianki, Poland.