

Variability and interbreeding of Sandwich Terns and Cayenne Terns in the Virgin Islands, with comments on their systematic relationship

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mating, but sample sizes of yellow-billed birds are small and the sex of yellow-billed individuals unknown. The intermediacy and variability of bill coloration in breeding populations throughout the Caribbean imply extensive interbreeding between the two taxa. Nevertheless, persistence of presumably "pure" phenotypes where the two taxa overlap within the Caribbean suggests a tendency toward assortative mating. In the absence of direct evidence for assortative mating, however, maintaining the two taxa as conspecific seems appropriate.

INTRODUCTION

The North American race of Sandwich Tern (*Sterna sandvicensis acuflyvida*) breeds along the Atlantic and Gulf of Mexico coasts of North America, and on islands in the northern Caribbean Sea; in the southern Caribbean and the Atlantic coast of South America, it is replaced by "Cayenne" Tern (*S. s. eurygnatha*; Gochfeld and Burger 1996, Shealer 1999). The chief distinction between the two taxa is bill coloration. In "Sandwich" Tern (hereinafter referring strictly to *S. s. acuflyvida*), the bill is virtually always black with a yellow tip; most authors describe the bill of Cayenne Tern as being much more

variable, typically pale yellow but often with dark markings, and rarely orange or even reddish (e.g., Junge and Voous 1955, Buckley and Buckley 1984, Malling Olsen and Larsson 1995, Shealer 1999). The two races are virtually identical in plumage, although Cayenne Tern may possess, on average, a slightly longer, shaggier nuchal crest and slightly darker gray upperparts (Malling Olsen and Larsson 1995, Shealer 1999). Populations of Cayenne Tern in southern South America breed during the austral summer and are notably larger in size than northern populations of Sandwich and Cayenne Terns, and may be subspecifically distinct (Voous 1968, Escalante 1973, van Halewijn 1990).

The significance of variability in bill coloration is poorly understood, and few published photographs, drawings, or descriptions illustrating such variability are available (e.g., Junge and Voous 1955, Haverschmidt 1968, Harrison 1987, van Halewijn 1990, Malling Olsen and Larsson 1995, Gantlett 2003). A crucial, unresolved question is whether individuals with phenotypically "intermediate" bill coloration (black with yellow/orange blotches or yellow/orange with black blotches) represent (1) variant phenotypes of Cayenne Tern (e.g., Voous 1983, van Halewijn 1990, French 1991, Sick 1993), (2) intergrades between the two taxa (Junge and Voous 1955), or (3) a mixture of both phenomena. In this paper, I document variability and interbreeding of the two forms at a mixed colony in the Virgin Islands, review previous studies documenting variability of bill coloration within the Caribbean, consider the handful of recent North American records of Cayenne Tern, and discuss the taxonomic implications of variability and interbreeding.

STUDY AREA AND METHODS

The Virgin Islands are an archipelago comprised of several major islands and numerous

ABSTRACT

A mixed colony of 410 breeding pairs of Sandwich Tern (*Sterna sandvicensis acuflyvida*) and Cayenne Tern (*S. s. eurygnatha*) was studied at Dog Island off St. Thomas, U. S. Virgin Islands, during May–July 2003. An estimated 94% of breeders were typical Sandwich Terns (bill black with yellow tip), two (0.24%) were typical Cayenne Terns (bill pure yellow), and the remaining 6% were highly variable intermediates (bill black with yellow/orange blotches or yellow/orange with black blotches). The proportion of Cayenne Terns and intermediate individuals in the Virgin Islands appears to be increasing since the 1980s. Two pure yellow-billed Cayenne Terns, two predominantly (90–95%) yellow/orange-billed intermediate terns, a half-yellow-, half-black-billed intermediate tern, and at least five predominantly black-billed intermediate terns were each mated with a Sandwich Tern, suggesting non-assortative



Figure 1. Mixed colony of Sandwich Tern and Cayenne Tern at Dog Island, 28 May 2003. Photograph by Floyd E. Hayes.

offshore islets on the eastern Puerto Rican Bank (Dammann and Nellis 1992). Sites and numbers of Sandwich/Cayenne Tern breeding colonies in the Virgin Islands vary from year to year among the few islets that possess suitable habitat (Norton 2000; Judy J. Pierce, pers. comm.). I reviewed available ornithological literature to document historic variability of bill coloration in breeding colonies of the Virgin Islands and elsewhere within the range of both taxa in order to assess trends in geographic variation.

From 28 May to 20 July 2003, I visited a large breeding colony of Sandwich and Cayenne Terns at Dog Island, a 12.1-ha islet off southeastern St. Thomas, U. S. Virgin Islands (18° 18' N, 64° 49' W; Dammann and Nellis

1992). I estimated the number of breeding pairs on the islet by counting the number of clutches within the densely packed colony prior to hatching (a few late breeders may have been excluded). With 8 x 42 binoculars, I scanned terns in the colony whose bills were clearly visible to estimate the proportion of adults possessing three bill coloration phenotypes: (1) typical Sandwich Tern (entirely black with yellow tip); (2) intermediate (dark with yellow/orange blotches or yellow/orange with dark blotches); and (3) typical Cayenne Tern (pure yellow without dark markings). To document variability and facilitate identification of individuals, color photographs were taken of as many intermediate and Cayenne Tern phenotypes as possible.

To assess whether assortative mating was occurring between birds based on bill-color phenotypes, a few hours were spent during the morning each day observing terns with pure or predominantly yellow/orange bill coloration and intermediate terns to identify the bill phenotype of their mates. An individual's mate was identified when it: (1) relieved an incubating focal bird or was relieved by an incubating focal bird; (2) delivered food to or received food from a focal bird at a nest; (3) delivered food to a chick under a focal bird or guarded a chick fed by a focal bird; or (4) interacted cooper-

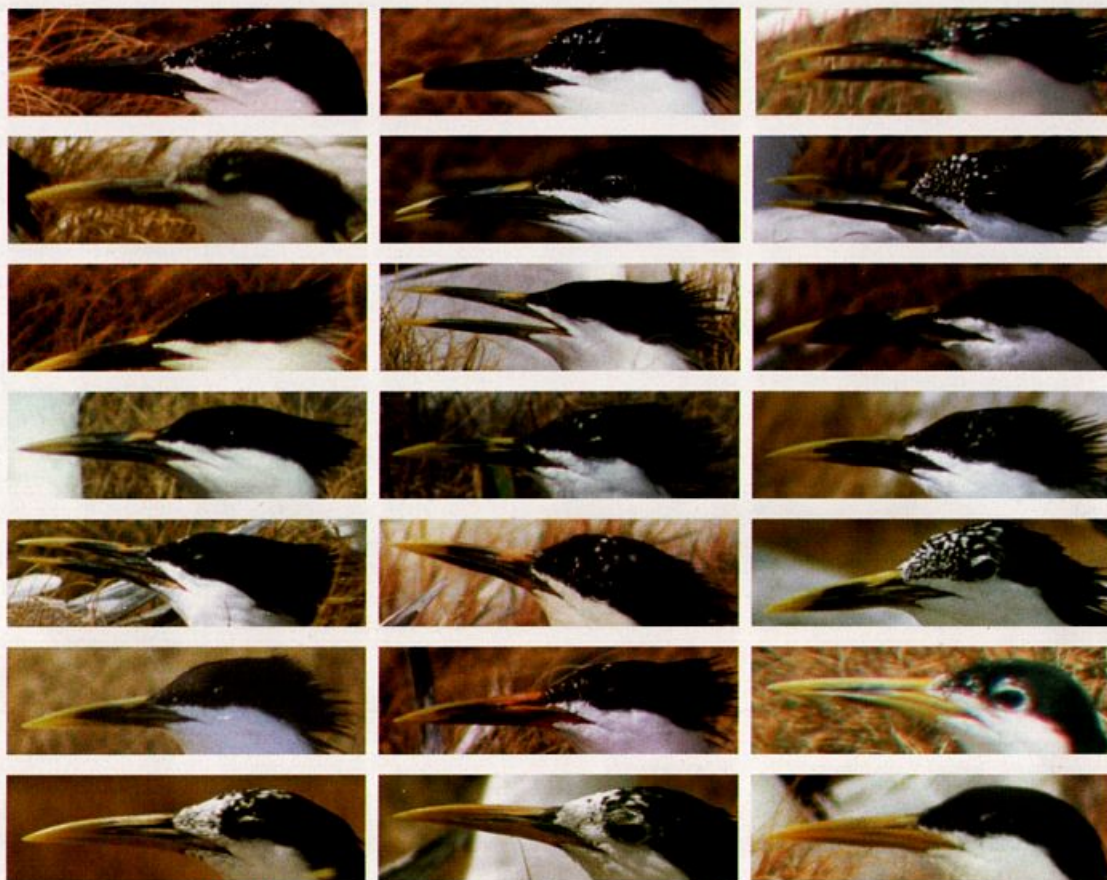


Figure 2 (a–u). Variability of bill coloration ranging from typical Sandwich Tern (top left: image 2 a) to typical Cayenne Tern (bottom right: image 2 u) at Dog Island, 28 May to 26 June 2003. Photographs by Floyd E. Hayes.

atively with a focal bird and an accompanying chick by gently nodding their bills up and down while facing each other (rather than jabbing, which often occurred between neighbors), exchanging a chick between them, or walking together through the colony.

RESULTS

Variability

In the northern Caribbean, small numbers of presumed Sandwich x Cayenne Terns "with varying amounts of yellow in their otherwise black bills" (Norton 1984) were first reported nesting among larger numbers of Sandwich Tern on small cays off St. Thomas (Pelican Cay, 1982–1983; Flat Cay, 1985–1987) and at Anegada (1980–1986) in the Virgin Islands (Norton 1984a, b, 1985a, b, 1986, 1987, 1988). The proportion of intermediate individuals in these colonies varied from <1% to 4%, but was usually <2%, and outnumbered pure yellow-billed Cayenne Terns (Table 1). Small numbers of Cayenne Terns and presumed intergrades were subsequently reported in Sandwich Tern colonies on southwestern Puerto Rico in 1990–1994 (Shealer 1999; Shealer, pers. comm.) and at Cayo Matojo off eastern Puerto Rico in 1984 (Schaffner et al. 1986), where the frequency of intermediate and yellow-

low-billed individuals ranged from <1% in southwestern Puerto Rico to 5% on Cayo Matojo (Table 1).

On 28 May and 1 June, about 410 pairs of Sandwich/Cayenne Terns (based on a nest count each day) and 74 pairs of Royal Tern (*S. maxima*; based on high count each day of incubating adults) were incubating eggs in a tightly packed colony on the islet (Figure 1). About half of the eggs had hatched by 22 June and about three-quarters by 26 June. By 20 July, many fledglings were taking short flights, but several very small chicks, thought to be less than one week old, were present, indicating late breeding or replacement clutches by a few pairs. Scanning of breeding birds on 1 June ($n = 200$) and 22 June ($n = 287$) revealed that 93.7% (22 June) to 94.0% (1 June) of individuals were typical Sandwich Terns (Figure 2 a), although a few birds with slightly excessive yellow markings on the bill may have been overlooked. Two birds (0.24%) were typical Cayenne Terns with pure yellow bills (Figure 2 u). The remaining 6% were highly variable intermediates.

A series of photographs documented at least 19 intermediate individuals within the colony (Figures 2 c–t); however, several other intermediate individuals with predominantly black bills were also present but not photographed. One bird possessed only a

TABLE 1. Geographic variation in proportion (%) of individuals with bill coloration typical of "Sandwich" Tern (black with yellow tip), "intermediate" bill color (blotched black and yellow), and typical "Cayenne" Tern (entirely yellow or orange/red) in mixed breeding colonies in the Caribbean (n = number of breeding pairs).

Region, Colony, and Year	Sandwich	Intermediate	Cayenne	n	Source*
NORTHERN CARIBBEAN (LOCALITIES ARRANGED FROM WEST TO EAST)					
Southwest Puerto Rico (17° 56' N, 67° 05' W)					
1990	>99	<1	0	262	13
1991	>99	<1	<1	341	13
1992	>99	<1	<1	404	13
1993	>99	<1	<1	440	13
1994	>99	<1	<1	473	13
Cayo Matojo, Puerto Rico (18° 20' N, 65° 17' W)					
1984	95	5	<1	123	12
Culebra, Puerto Rico (18° 19' N, 65° 17' W)					
1971, 1983–1984	100	0	0	100+	12
Flat Cay (St. Thomas), Virgin Islands (18° 19' N, 64° 59' W)					
1985	98	2	0	23	7
1987	100	0	0	13	10
Pelican Cay (St. Thomas), Virgin Islands (18° 25' N, 64° 55' W)					
1982	>99	<1	0	442	5
1983	98	2	0	337	5
Dog Island (St. Thomas), Virgin Islands (18° 18' N, 64° 49' W)					
2003	94	6	<1	410	15
Anegada, Virgin Islands (18° 43' N, 64° 19' W)					
1980	98	2	--	27	5
1982	>99	<1	--	65	5
1983	96	4	--	39	5
1984	99?	?	1	370	6
1985	98?	2	?	721	8
1986	99	<1	<1	475	9
Virgin Islands (localities unspecified)					
1988	>99?	?	<1	723	11
SOUTHERN CARIBBEAN (LOCALITIES ARRANGED FROM WEST TO EAST)					
Aruba (12° 30' N, 69° 58' W)					
1984	10	37	53	71	2
1985	8	29	63	70	3
Curaçao (12° 15' N, 68° 45' W)					
1954	21	11	68	?	4
1958 (field observations)	2	43	55	1150	1
1958 (photographs)	12	27	61	96	1
Bonaire (12° 15' N, 68° 45' W)					
1955	25	36	39	?	4
Islas las Aves (11° 58' N, 67° 33' W)					
1956	7	21	71	?	14

*Sources: 1 = Ansingh et al. (1960); 2 = van Halewijn (1985); 3 = van Halewijn (1987); 4 = Junge and Voous (1955); 5 = Norton (1984a); 6 = Norton (1984b); 7 = Norton (1985a); 8 = Norton (1985b); 9 = Norton (1986); 10 = Norton (1987); 11 = Norton (1988); 12 = Schaffner et al. (1986); 13 = Shealer (1999; Shealer, pers. comm.); 14 = van der Werf et al. (1958); 15 = this study.

slight amount of excessive yellow at the base of the upper bill (Figure 2 b), and two had excessive yellow only in the tip of the bill (Figures 2 c–d); seven had yellow or slight orange blotches basally and excessive yellow distally (Figures 2 e–k). Five possessed excessive yellow at the tip of the bill and a narrow yellow line on the upper ridge of the bill, and all but one of these had yellow or slight orange basally (Figures 2 l–p). One bird's bill showed bright orange basally connected to the yellow tip along the upper ridge, with extensive black in the middle (Figure 2 q). In three birds, the bill was about 85–95% yellow (one with advanced head molt was tinged orange), with black blotches in the middle or base of the bill (Figures 2 r–t).

All adults were in alternate plumage, but many breeders were molting feathers on the forehead, especially later in June. As early as 28 May, the entire front half of the crown and face of a Sandwich Tern thought to be a breeder was white. Most adults appeared slightly pinkish on the breast in comparison with nearby Royal Terns, with no apparent differences in intensity between yellow-billed and dark-billed individuals. Predominantly yellow-billed individuals did not appear to have darker mantles or shaggier crests or differ in bill or body size from dark-billed birds.

Soft-part coloration of chicks and juveniles was highly variable and difficult to assess quantitatively. Bill color was pinkish (smaller chicks, relatively rare), yellow (frequent), or gray (a slight majority), often with a darker tip. Leg color was usually gray or black, but sometimes yellow or even pink. None of the juveniles flying on 20 July had attained adult Sandwich Tern bill coloration, and many still had pale legs, including one with pure yellow bill and legs that was fed by a Sandwich Tern.

Interbreeding

Only two copulations were observed during 5–6 hours of observation on 28 May and 1 June combined, and both were between Sandwich Terns; some copulations were probably overlooked, however, because it appeared that birds were made nervous by my presence, especially when approached for photographs. Few feedings or incubation switches took place on 28 May and 1 June, all between Sandwich Terns. No copulations were observed during 22 and 26 June, but feedings and incubation switches were frequent, and only feeding was observed on 20 July.

On 22 June, two pure yellow-billed Cayenne Terns were present at the same time about 20 m apart: one with more advanced head molt was incubating (Figure 2 u), and the other was guarding a chick

(Figure 3). At 12:40, a Sandwich Tern landed beside the yellow-billed tern guarding a chick. No feeding was observed, but the two adults faced each other, nodded their bills up and down, and appeared to be vocalizing while the chick shuttled back and forth between them several times. During the next 15 minutes, the three slowly wandered together about 20 m through a sparsely populated edge of the colony (Figure 3). On two occasions, the Sandwich Tern flew a few meters ahead, turned back to face its presumed mate and offspring, and vocalized; in the first instance, it was joined by its mate and offspring, and in the other, it flew back to them. The chick wandered frequently from one adult to another but spent more time with the Cayenne Tern.

On 22 June, the incubating pure yellow-billed Cayenne Tern (Figure 2 u) departed the colony and later appeared to have been replaced by a predominantly orange/yellow-billed individual with about 5% black on its bill (Figure 2 t); the two were suspected of being mated, but no incubation switches were observed. On 26 June, the pure yellow-billed Cayenne Tern was again incubating when the orange/yellow-billed individual (Figure 2 t) landed nearby at 07:25 and loafed at the edge of the colony until 07:57, when it walked into the colony, interacted cooperatively (bill nodding) with an incubating Sandwich Tern only 0.5 m from the yellow-billed tern, and relieved it after about 30 seconds. The pure yellow-billed tern continued incubating until at least 10:15, when I moved to another part of the colony; at 10:25, I noticed the same yellow-billed tern (based on stage of head molt) landing elsewhere in the colony, so I quickly returned to my original observation point and confirmed that the incubating yellow-billed tern was replaced by a Sandwich Tern, based on its position relative to the orange/yellow-billed individual (Figure 4).

Within 5 m of the incubating yellow-billed and orange/yellow-billed terns, a predominantly yellow-billed individual with about 5% black on the bill (Figure 2 s) was incubating on 26 June when a Sandwich Tern walked up to it at 07:42 and, after about 30 seconds of bill nodding, relieved it of its incubation duties.

On 22 June, an intermediate individual resembling Figure 2 j (orange at base of bill, extensive yellow at tip) flew into the colony with a fish and fed an adult Sandwich Tern. Twice a Sandwich Tern delivered food to another intermediate adult resembling Figure 2 e (slight orange at base of upper bill). In both cases, a chick was present in between the

intermediate tern and its Sandwich Tern mate.

On 26 June, an intermediate tern resembling Figure 2 f (bright yellow patch at base of upper bill) flew into the colony on four occasions and fed a chick under a Sandwich



Figure 3. Adult Sandwich Tern (left) and Cayenne Tern (right) with a chick between them at Dog Island, 22 June 2003.

Photograph by Floyd E. Hayes.

Tern. An intermediate tern resembling Figure 2 c (excessive yellow at tip of bill) fed a chick under a Sandwich Tern. An intermediate tern resembling Figure 2 o (about 50% yellow, with black primarily in mid-bill) was seen interacting cooperatively (bill nodding) with a Sandwich Tern for 2 minutes (uncertain whether a chick was between them), but no feeding was observed. Another intermediate tern resembling Figure 2 e fed a chick under a Sandwich Tern (possibly the same mated pair as observed on 22 June). A Sandwich Tern fed a chick under an intermediate tern resembling Figure 2 h (yellowish patches at base of bill).

DISCUSSION

Variability and interbreeding

The proportion of intermediate and yellow-billed individuals in the breeding population

of the Virgin Islands appears to be increasing since the 1980s, but more data are needed to assess long-term trends. My observations confirm that two phenotypically "pure" yellow-billed Cayenne Terns, two predominantly yellow/orange-billed intermediate terns (with 90–95% yellow/orange bills), a half-yellow-, half-black-billed intermediate tern, and at least five intermediate terns with predominantly black bills were each paired with a typical Sandwich Tern. These observations suggest non-assortative mating, but sample sizes of yellow-billed birds are small and the sex of yellow-billed individuals unknown.

The comment by Gochfeld et al. (1994: 191) that Cayenne Tern "often nests separately" from Sandwich Tern was apparently based on observations in southwestern Puerto Rico, where two pure yellow-billed Cayenne Terns were often seen beside each other among much larger numbers of Sandwich Terns at Media Luna West in 1991, Media Luna East in 1992, and

San Cristobal in 1993 (all colonies within 0.5 km; Table 1); although these individuals were thought to be mated with each other, they may have been incubating in adjacent nests while each was mated with a Sandwich Tern (D. Shealer 1991; Shealer, pers. comm.). In 1991, one Cayenne Tern was thought to be mated with a Sandwich Tern. A few intermediate-appearing birds were also present each year in the colonies, including one (paired with a Sandwich Tern) whose bill was yellow-orange basally, black medially, and yellow distally.

The taxonomic relationship between Sandwich and Cayenne Terns is poorly understood. If any reproductive isolating mechanism exists between the two taxa, it may be based on bill coloration or, perhaps more likely, postural and vocal displays (P. A. Buckley, pers. comm.). However, no behavioral differences between the taxa have been described. As for bill coloration, the crux of the issue is whether individuals with phenotypically "intermediate" bill coloration represent (1) variant (or even normal) phenotypes of Cayenne Tern, (2) the results of interbreeding between the two taxa, or (3) a mixture of both phenomena. A second crucial question is whether individuals indistinguishable from Sandwich Terns nesting in the southern Caribbean and eastern Brazil represent (1) Sandwich Terns or (2) variant Cayenne Tern phenotypes.

Now that interbreeding between extreme phenotypes of the two taxa has been documented in the northern Caribbean, it is not unreasonable to

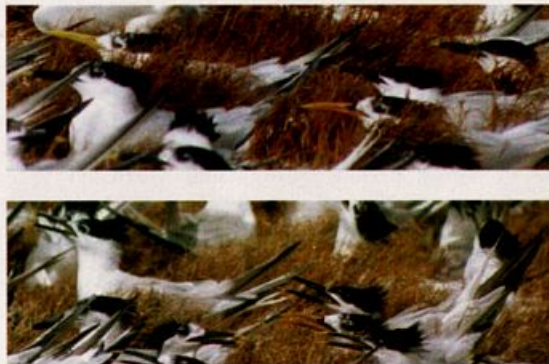


Figure 4. Incubating Cayenne Tern with pure yellow bill (above left; photograph A) and intermediate tern with 95% orange/yellow bill (right; photographs A–B) among Sandwich Terns at Dog Island, 26 June 2003. The intermediate tern at right relieved an incubating Sandwich Tern, and the Cayenne Tern at upper left (photograph A) was relieved by a Sandwich Tern (photograph B). Photographs by Floyd E. Hayes.

TABLE 2. North American records and reports of Cayenne Tern.

Location	Date	Description	Source*
Cape Hatteras, NC	30 May 1983	alternate adult male courting Sandwich Terns	1
Cape Hatteras, NC	1 Sep 1986	no details	5
Cape Hatteras, NC	16 Aug 1988	no details	6
Cape Hatteras, NC	7 Oct 1989	no details	7
Cape Hatteras, NC	23 Sep 1994	basic adult	2, 4
Off Oregon Inlet, NC	31 Jul 1995	basic adult	3
Cape Hatteras, NC	23 Sep 1997	basic adult	4
Long Island, NY	17–18 Jul 2000	basic adult	8
Fort Fisher, NC	5 Apr 2003	alternate adult	9

*Sources: 1 = Buckley and Buckley (1984); 2 = Davis (1995a; photograph currently posted to: <[http://www2.msstate.edu/~sd122/Other bird photos.htm](http://www2.msstate.edu/~sd122/Other%20bird%20photos.htm)>); 3 = Davis (1995b; photograph currently posted to: <<http://www.seabirding.com/images/sate-B13.jpg>>); 4 = Dinsmore and Hass (1997); 5 = LeGrand (1987); 6 = LeGrand (1989); 7 = LeGrand (1990); 8 = Mitra and Buckley (2000); 9 = Davis (2004).

This list does not include possible Cayenne Terns seen and/or photographed in Texas, including one photographed at East Beach, Galveston Island, Texas 4–5 November 2001, with photographs currently posted to: <<http://members.tripod.com/~tbrctern.htm>>.

assume that many or all intermediate individuals there are intergrades. Given that small numbers of Cayenne Terns nest among Sandwich Terns in the northern Caribbean, it seems probable that small numbers of Sandwich Terns nest among Cayenne Terns in the southern Caribbean and perhaps southward into Brazil (see below), where interbreeding would seem just as likely to occur. If so, some or all of those with intermediate bill coloration may represent intergrades.

In the absence of molecular genetic tests or direct observations of mating, interbreeding between two taxa can be inferred phenotypically by an increase in variability and intermediacy in concert where their ranges meet; in contrast, if variability is clinal, the intermediate populations should not exhibit increased variability in any given population along the cline (Schueler and Rising 1976). In the Sandwich/Cayenne Tern complex, an increase in variability and intermediacy in bill coloration where their ranges meet should provide the best phenotypic evidence for interbreeding (as with the hybridization of *Butorides* herons in the same region [Hayes 2002]). To assess whether variability within the two taxa is clinal (in a broad, geographical sense, given the highly disjunct distribution of the terns' breeding colonies) or fits the pattern pre-

dicted for a hybrid zone, the following synthesis of bill color variability is offered.

In southeastern North America, bill coloration of Sandwich Terns varies little. In North Carolina, Buckley and Buckley (1984: 397) reported "incubating Sandwich Terns with yellow rami and, occasionally, faint yellowish blotches along the mandibles." Whether this represents normal variation within Sandwich Terns or introgression of Cayenne Tern alleles remains uncertain, but the observation of an alternate-plumaged Cayenne Tern courting with a Sandwich Tern at Cape Hatteras, North Carolina on 30 May 1983 (Buckley and Buckley 1984) suggests that occasional hybridization may occur. Vagrant crested terns are well known for hybridizing with congeners in colonies distant from their normal breeding range (Malling Olsen and Larsson 1995, Collins 1997, Paul et al. 2003), and because Sandwich Tern colonies are seldom scrutinized for Cayenne Terns, isolated instances of interbreeding may be overlooked. There are eight additional extralimital records of Cayenne Tern along the east coast of North America (Table 2), all probably representing post-breeding dispersal. One individual, photographed and described as "slightly larger than a Sandwich Tern" with a bill "roughly 25% longer than the bills of nearby Sandwich Terns,"

was thought to have been a male from an austral-breeding population (Dinsmore and Hass 1997; Table 2).

Variability clearly increases south of the North American continent. In the northern Caribbean, at least 94% of individuals in colonies appear to be phenotypical Sandwich Terns, up to 6% possess intermediate bill coloration, and fewer than 1% appear to be phenotypical Cayenne Terns (Table 1). Variability is greater in the islands of the southern Caribbean, where seven studies revealed that the majority of individuals have entirely yellow bills (median = 61%, range = 39–71%), a substantial proportion have intermediate bill coloration (median = 29%, range = 11–43%), and a minority resemble Sandwich Terns with black, yellow-tipped bills (median = 10%, range = 2–25%; see Table 1). However, some of the Sandwich-type terns in these colonies have brown-tinged bills, thus the percentage of potentially "pure" Sandwich Terns is probably smaller (A. del Nevo, pers. comm.; R. van Halewijn, pers. comm.).

Variability is also high in populations breeding during the boreal summer along the Brazilian coast of South America. On Dos Papagaios Island off Macaé, Brazil, Sick and Leão (1965: 507) reported that all nesting birds in a colony of boreal-summer breeders "had light lemon-colored bills, although occasionally a touch of black was present on the sides of the bills," but noted one individual nearby with a black basal half of the bill. More than half of boreal-summer-breeding Cayenne Terns at three colonies in central Brazil possessed a pure yellow bill, about 1.5% of birds from Ilha Escalvada, Espírito Santo, Brazil, resembled Sandwich Tern, and the remaining birds were intermediate (Marcio Efe, pers. comm.). An unpublished photograph by Cesar Musso from the latter colony in June 2002 revealed an incubating individual resembling a Sandwich Tern and several individuals with intermediate bill coloration among predominantly yellow-billed birds; another photograph from the same colony reveals a similar tern with slightly more yellow at the tip and base of the bill (Efe et al. 2000).

Variability decreases in southern South America, where breeding Cayenne Terns are predominantly yellow-billed with an apparently higher proportion of individuals with orange-red bills (Voous 1968, Escalante 1970). A series of photographs supplied by Flavio Quintana and Pablo Yorio from a colony at Punta Leon, Chubut, Argentina, in November 2000 revealed that 93% of individuals had a completely yellow or yellow-orange bill and only 7% of individuals ($n = 70$) had dark markings on the bill. These figures mirror those of the Virgin

Islands, but despite many years of research at Cayenne Tern colonies (e.g., Yorio et al. 1998), none resembling a Sandwich Tern has ever been documented (F. Quintana and P. Yorio, pers. comm.). As pointed out by van Halewijn (1990: 131, translated from Dutch), "a population of purely yellow-billed birds does not exist."

The identity of intermediate and dark-billed terns breeding in the southern Caribbean and Brazil has been disputed. Several authorities regarded all such individuals, including those indistinguishable from Sandwich Terns, as variant phenotypes of Cayenne Tern (e.g., Voous 1983, van Halewijn 1990, French 1991, Sick 1993). Buckley and Buckley (1984) suggested that intermediate and dark-billed terns nesting as far south as Argentina might result from introgression of Sandwich Tern alleles. Sandwich Terns clearly migrate southward along the east coast of South America. The southernmost band recovery (of an individual banded in Mississippi) is from Rio Grande do Norte, northeast Brazilian coast (Sick 1979), and there are several sight records of immatures (one with a leg band) and adults associating with substantially larger, alternate-plumaged Cayenne Terns in Buenos Aires Province, Argentina, from November-January (e.g., Narosky and Di Giacomo 1993, Jaramillo 2000). Mixed pairs potentially could occur during the austral breeding season, if boreal-breeding Sandwich Terns were to mingle with local austral-breeding Cayenne Terns, lingering to breed rather than returning to the Northern Hemisphere. Although Gochfeld and Burger (1996) reported mixed pairs in Patagonia, no details were provided.

In the absence of molecular data, the increased intermediacy and variability of bill coloration in the Caribbean, where the ranges of the two forms meet, do suggest extensive interbreeding, as initially interpreted by Junge and Voous (1955). But because no individuals resembling Sandwich Tern have been documented nesting in Patagonia despite intensive surveys (e.g., Yorio et al. 1998), introgression appears unlikely to account for the 7% of individuals with dark bill markings there. A similarly small percentage of Elegant Terns (*S. elegans*), for instance, possess dark markings in the bill, which could represent natural variation (e.g., Gantlett 2003).

Taxonomy

Sandwich and Cayenne Terns were formerly considered specifically distinct. Based on observations in the southern Caribbean, Junge and Voous (1955) and Ansingh et al. (1960) inferred extensive interbreeding and suggested the two were conspecific. Although this conclusion was not followed

by some authors, for example Meyer de Schauensee (1966), it was accepted by the American Ornithologists' Union (1983) and subsequently adopted by most authorities (e.g., Buckley and Buckley 1984, Malling Olsen and Larsson 1995, Gochfeld and Burger 1996, Shealer 1999). In support of this treatment, interbreeding and non-assortative mating have now been documented in the northern Caribbean, and seemingly indiscriminate matings between dark-billed and yellow-billed phenotypes have been observed and photographed in the southern Caribbean (R. van Halewijn, pers. comm.; Figure 5).

Given the emphasis on the criterion of reproductive isolation in the classic Biological Species Concept (Mayr 1970), extensive interbreeding between taxa often has been interpreted as evidence for lack of reproductive isolation, in which case the interbreeding taxa were considered conspecific (Johnson et al. 1999). However, the taxonomic significance of interbreeding is contingent upon the distribution of different phenotypes (or, preferably, genotypes when determined) within a zone of interbreeding (e.g., Short 1969, Helbig et al. 2002). When random mating (free interbreeding) occurs between individuals of two different taxa, the probability of "pure" phenotypes remaining within the zone of interbreeding approaches nil within a few dozen generations. Thus, when essentially all individuals within such a zone are intermediate, free interbreeding is implied and the interbreeding taxa are considered conspecific. Alternatively, the presence of "pure" phenotypes within the zone of interbreeding could result from immigration from areas beyond the zone (in which case the immigrants should be a distinct minority), from an inheritance pattern in which hybrid genes (genotype) are masked by phenotype, from recent secondary contact and formation of a "hybrid zone," or from a tendency toward assortative mating. When assortative mating occurs, the two taxa demonstrate *essential* reproductive isolation and should be considered specifically distinct (Johnson et al. 1999).

In the case of the Sandwich x Cayenne Tern "hybrid" zone in the southern Caribbean, fair numbers of extreme, presumably "pure" phenotypes of both taxa

(resembling individuals beyond the Caribbean) coexist and nest within the breeding colonies (Table 1), suggesting that most are breeding residents rather than immigrants from beyond the hybrid zone. The substantial proportion of individuals

with intermediate bill coloration—which may represent variants of Cayenne Tern or intergrade Sandwich x Cayenne Terns—suggests polygenic control of bill coloration in which hybrid genes are not being masked. Although breeding by both taxa in the southern Caribbean was not detected until half a century ago (Junge and Voous 1955), it was probably overlooked before then. Thus, the current and probable future persistence of extreme phenotypes of both taxa in the southern Caribbean provides possible evidence for a tendency toward assortative mating, despite frequent interbreeding.

Nevertheless, in the absence of biochemical studies and of direct evidence for assortative mating, the two taxa are for now best maintained as conspecific. Additional research on mate choice and molecular genetics in the southern Caribbean and elsewhere are needed to resolve the taxonomic relationship between the two taxa.

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Figure 5. Courtship feeding by a male Cayenne Tern (with two fish) to a female Sandwich-type Tern at Aruba, 1 June 1989. Photograph by Ruud van Halewijn.

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