INTERBREEDING OF ROSEATE AND ARCTIC TERNS

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ABSTRACT.—This study provides evidence for hybridization between Roseate (*Sterna dougallii*) and Arctic (*S. paradisaea*) Terns. I observed a male Arctic and female Roseate Tern engaging in courtship, copulation, incubation and chick-feeding behavior on Country Island, Nova Scotia, Canada in 1996. The Roseate laid a single egg which hatched after 21 days. The chick, which I banded after hatch and weighed every other day, survived for 16 days before it was presumed depredated. The chick most resembled an Arctic Tern because its down lacked the spiny texture of Roseate chicks and it did not develop the dark, U-shaped dorsal markings characteristic of juvenile Roseates. The feeding rate for the mixed-species pair was below the mean, but within the range, of feeding rates for Roseate pairs at Country Island in 1996. The hybrid chick initially grew at the same rate as other Roseate chicks at this colony, but its growth slowed after 9 days such that it weighed less than all Roseate chicks under study. A skewed sex ratio, misimprinting on heterospecific vocalizations or parental inexperience may have led to this mating. *Received 15 March 1997, accepted 27 Oct. 1997.*

Hybridization is known to occur in roughly 10% of all bird species (Grant and Grant 1992). In some groups hybridization is rare, while in others it is quite common. For example, 9 of 23 tern species (family: Laridae) that breed in Europe and North America are known or believed to hybridize with one or more sympatric species (Table 1).

Matings between Roseate Terns (Sterna dougallii) and Common Terns (S. hirundo) have been well documented in both Europe and North America (Robbins 1974, Hays 1975, Zingo et al. 1994). In contrast, hybridization between Roseate and Arctic Terns (S. paradisaea) has apparently not been described, perhaps because these species are sympatric only over a narrow range (Cramp 1985). Roseate and Arctic Terns have been observed sharing incubation on two previous occasions (in Shetland, Scotland and Maine, U.S.A.; Ewins 1987; S. Kress, pers. comm.), but in both cases copulation was not observed and chicks were not found.

I studied the nesting behavior of Roseate Terns on Country Island, Nova Scotia, Canada in 1996, and witnessed hybridization between a Roseate and Arctic Tern. Here, I document the courtship, copulation, incubation and chick-feeding behavior of the mixed species pair, as well as the appearance, behavior and growth of the hybrid chick. I discuss some proximate mechanisms that may have led to this mating, as well as conservation implications of hybridization for Roseate Terns.

METHODS

Country Island is a 19 ha island located in Guysborough County, Nova Scotia (45° 06' N, 61° 32' W). Arctic (330 pairs), Roseate (45-50 pairs) and Common (130 pairs) terns nest on the south end of the island on rocky beach and in tall vegetation dominated by seaside angelica (Coelopleurum lucidum), swamp buttercup (Ranunculus septentrionalis), beach pea (Lathyrus japonicus), raspberry (Rubus spp.), and various sedges (Carex spp.) and grasses (Family: Gramineae). Great Black-backed Gulls (Larus marinus), Herring Gulls (Larus argentatus), American Crows (Corvus brachyrhynchos), Common Ravens (Corvus corax), Common Eiders (Somateria mollissima), Leach's Storm Petrels (Oceanodroma leucorhoa) and various songbirds and shorebirds also nest on the island. Gull predation on tern chicks is high (more than 50% of all tern chicks were depredated by gulls in 1996; Whittam, unpubl. data), but there are no resident mammalian predators.

A co-worker and I observed the male Arctic and female Roseate Tern with 8×36 binoculars and a spotting scope from two blinds located approximately 40 m from the nest and from a tower blind located on the edge of the colony (60 m from the nest). We observed courtship behavior of the pair for a total of 99 hours between 31 May and 11 June. During incubation (11 June-2 July) no formal observations were made but we checked the nest daily from the blinds to ensure the parents were incubating. From 3–18 July we observed the parents feeding the chick for a total of 42.5 hours. Observation periods were two to four hours long and occurred between 05:00 and 19:30 AST throughout courtship and chick-feeding.

Although neither the Roseate nor the Arctic Tern was color banded, I am confident that repeated observations were of the same two individuals because we saw them consistently in a single location. Both terns

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Species believed to hybridize	Evidence	Reference(s)	
Black Tern (Chlidonias niger) & White-Winged Black Tern (C. leucopterus)	Juveniles with mixed plumage charac- teristics	Vinicombe 1980 Davis 1982	
Common Tern (<i>Sterna hirundo</i>) & Arctic Tern (<i>S. paradisea</i>)	None given	Degland and Gerbe 1867 (in Hays 1975)	
Common Tern & Roseate Tern (S. dougallii)	Mixed-species copulation, incubation and chick-feeding behavior; chicks with mixed plumage characteristics	Robbins 1974 Zingo et al. 1994 (and references therein)	
	Adults with intermediate plumage characteristics	Hays 1975	
Roseate Tern & Arctic Tern	Mixed-species incubation	Ewins 1987 S. Kress, pers. comm.	
	Mixed-species copulation, incubation and chick-feeding behavior; chick with mixed plumage characteristics	This paper	
Gull-billed Tern (<i>Gelochelidon</i> nilotica) & Forster's Tern (S. forsteri)	None given	Hill 1965	
Lesser Crested Tern (S. benga- lensis) & Sandwich Tern (S. sandvicensis)	Mixed-species pairs	Brichetti and Foschi 1987	
	Juveniles with intermediate plumage characteristics	Steele and McGuihan 1989 Verroken 1990	

TABLE 1. Evidence for hybridization between some tern species (Family: Laridae).

appeared typical of their respective species. I photographed the egg and chick using a 35 mm SLR camera equipped with a 50 mm focal length lens, and I measured the length and width of the egg with calipers. I used a spring scale to weigh the hybrid as well as 30 Roseate chicks beginning at hatch and continuing every other day until the chicks died or disappeared. I calculated the rates at which both parents fed the hybrid. Mean values are expressed ± 1 SE.

RESULTS AND OBSERVATIONS

I first saw the Roseate and Arctic Tern posturing (in both the "bent" and "erect" positions; Cramp 1985) on 31 May in an area dominated by other courting Roseate Terns. The male Arctic mounted the female Roseate on the mornings of 31 May, 1 June and 2 June but cloacal contact did not occur. On 1 June the Roseate landed beside the Arctic, postured and gave begging calls. The pair was engaged in nest-shaping behavior (Cramp 1985) on 2 June. I observed two mate-feedings on 3 June, and on 5 June the Arctic mounted the Roseate and achieved cloacal contact. I observed four additional mountings on 6 June, two of which resulted in cloacal contact. The fourth mounting was preceded by the Arctic giving the Roseate a small fish, which they passed back and forth five times before it was swallowed by the Roseate. I observed two further instances of both mate-feeding and copulation on 8-9June. The Roseate was seen arranging nest material from 9-11 June.

A single egg was found at the nest on 11 June, one day after the modal date of clutch initiation for other Roseates nesting at this colony (Whittam, unpubl. data). Thirty-five percent (n = 46) of Roseate nests on Country Island in 1996 contained one egg (Whittam, unpubl. data). The egg, which was highly elongate and pyriform (49×28 mm; Fig. 1), differed from both Roseate and Arctic Tern eggs (Table 2). The nest was in dense raspberry and seaside angelica. The nearest nest (1.1 m away) belonged to a pair of Roseate Terns, although three pairs of Common Terns also nested within 2 m. The nearest Arctic Tern nest was approximately 18 m away.

Both the Arctic and Roseate terns incubated the egg. I trapped the Arctic Tern on the nest using a drop-style treadle trap on 30 June, photographed it, and banded it (U.S. Fish and



FIG. 1. Egg of interbreeding Roseate and Arctic Tern.

Wildlife Service #811-26033). The Roseate began incubating four minutes after the Arctic Tern was removed from the trap. The egg hatched on 2 July, after a 21 day incubation period (Table 2), which was two days shorter than the mean incubation period for 27 Roseate Tern eggs on Country Island in 1996 (mean = 23.4 ± 0.9 days, range = 22-25; Whittam, unpubl. data).

I banded the chick (#802-68-342) two days after hatching, and photographed it 2, 6, and 15 days after hatching. The plumage of the

TABLE 2. Egg, chick and fledgling characteristics of Roseate^a and Arctic^a Terns and of the hybrid Roseate \times Arctic Tern.

Characteristic	Arctic	Roseate	Hybrid
Mean egg length × width (mm)	41×30 range 36-46 × 26-33 (n = 300)	43×30 range $38-48 \times 27-32$ (n = 180)	49 × 28
Incubation period (days)	20-24	21–26	21
Texture of chick down	soft	spiny	soft
Color of chick down	pearl grey or buff	cinnamon buff to pale buff, or pale grey to off-white	cinnamon buff
Plumage markings of chick	usually dense black specks or streaks	usually diffuse black- brown specks	large black spots and streaks
Fledgling plumage	mantle, scapulars and tertials light grey with off-white tips and dark grey subterminal spots	black U-shaped markings on mantle/back feath- ers and tertials	no distinctive marks at 15 days
Fledgling bill color	orange tipped with black	black	flesh-colored, tipped with black at 15 days
Fledgling leg color	orange-red	black	purplish brown at 15 days

^a From Cramp (1985) and Malling Olsen and Larsson (1995).



FIG. 2. Hybrid Roseate \times Arctic chick (on right) and Roseate Chick (on left) at two days of age.

chick lacked the characteristic spiny texture of Roseate chicks (Cramp 1985; Fig. 2), and it never developed the dark, U-shaped markings on the mantle, back and tertials which are characteristic of juvenile Roseate, but not Arctic, Terns (Malling Olsen and Larsson 1995). The color and markings of the chick's down resembled those of both Arctic and Roseate chicks, and at 15 days the chick's purplish brown legs and flesh-colored bill were intermediate in appearance between those of Arctic and Roseate fledglings (Table 2).

The Arctic brought 60% (n = 53) of all fish to the chick. Male Arctic Terns generally bring more food to the nest than do females, especially during the first week after hatching (Uttley 1992). The size of prey brought to the nest by the Roseate and Arctic Tern did not differ (mean fish size = 1.15 ± 0.12 and 1.18 \pm 0.10 bill lengths, respectively). The seasonal feeding rate (total number of feedings observed divided by total hours watched during the chick-rearing period) for the mixed species pair (1.24 feeds/hour) was lower than the mean seasonal feeding rate of six conspecific Roseate pairs that were feeding only one chick $(1.63 \pm 0.15 \text{ feeds/hour})$, but was still within the range of seasonal feeding rates for these six pairs (1.24-2.30 feeds/hour). Furthermore, the chick initially grew as quickly as Roseate chicks in the same subcolony, but after nine days its growth rate slowed such that it weighed less than all Roseate chicks under study, and after 15 days its weight actually dropped by 18% (Fig. 3).

On the morning of 19 July (17 days after hatch) both the Roseate and Arctic terns landed with fish near the nest site three to four times, walked around the nest and then flew off, carrying the fish. The chick was not in its regular hiding place that afternoon and I assume it had been taken by a gull. I searched the nest area for the chick's body to ensure it had not starved. The Arctic and Roseate were seen posturing to each other the next day but they brought no fish to the nest.

DISCUSSION

This is the first well-documented case of hybridization between Roseate and Arctic terns. My observations of mate-feeding and copulation as well as the intermediate appearance of the chick (Table 2, Fig. 2) make me confident that hybridization took place between the individuals I observed. There are several possible explanations for this mating; such as the effects of a skewed sex ratio, misimprinting on heterospecific vocalizations by a chick that later affected its mate choice, or parental inexperience.

There is some evidence that the population of Roseate Terns in northeastern North Amer-



FIG. 3. Growth rate of hybrid Roseate \times Arctic chick (\Box) compared with the growth rates of 30 Roseate chicks (\bullet) on Country Island, Nova Scotia, Canada in 1996.

ica supports an excess of females (e.g., 44.5% males, 55.5% females on Bird Island, Massachusetts; Nisbet 1997). This, combined with an excess of male Common or Arctic terns, could provide favorable conditions for hybridization. When all individuals of the limiting sex are mated, the remainder can hybridize, provided the courtship signals of the two species are similar (Grant and Grant 1997). In fact, in almost every recorded case of hybridization between Roseate and Common terns the Roseate Tern has been female (Ewins 1987, Zingo et al. 1994), providing some support for this hypothesis. Cullen (1956, in Ewins 1987) noted an excess of unmated male Arctic Terns in a colony in Scotland, but nothing is known about the sex ratio of either Arctic or Roseate terns on Country Island.

The mechanics of pair formation may also help explain why interbreeding Roseates are always female (I. C. T. Nisbet, pers. comm.). Terns perform a "high-flight" (Cramp 1985) involving two or more birds that functions as a courtship signal for Roseate, Arctic and Common terns and also as a flying contest for Roseate Terns. Roseates fly much faster than Common or Arctic terns (I. C. T. Nisbet, pers. comm.), such that a female Roseate could keep up with a male Common or Arctic tern, but a female Common or Arctic could not keep up with a male Roseate Tern.

Hays (1975) suggested that Common-Ro-

seate hybrids may arise when young Common Terns are raised by adult Roseate Terns or vice versa. This sometimes occurs when eggs of both species are laid together because of competition for nest sites. Chicks of either species may then learn to recognize and respond to the calls of the species feeding them and later prefer that species when they choose a mate (Hays 1975). Cross-fostered Herring Gull and Lesser Black-backed Gull (L. fuscus) chicks later tended to mate with individuals of their foster species (Harris 1970). Grant and Grant (1997) found that song plays a role in the choice of heterospecific mates in Darwin's finches (Geospiza spp.), because within hybrid pairs, the song of a female's father was similar to that of her heterospecific mate. Thus, misimprinting on heterospecific calls by chicks of either Roseate or Arctic terns could lead to incorrect mate choice as adults, and could explain why these two birds mated. Unfortunately, I did not record the calls of either the female Roseate or male Arctic tern, which, according to this hypothesis, might have contained similar elements.

Some Common-Roseate hybrid young fledge (Zingo et al. 1994) and may mate with other hybrids to produce F_2 young (Hays 1975). The Arctic-Roseate hybrid survived to 16 days before it was probably taken by a predator. It is impossible to know whether this chick, in the absence of predation, would have survived to fledge and, eventually, to breed. Its growth rate dropped after both 9 and 15 days (Fig. 3). This decline might be related to either the low rate at which it was fed (i.e., parental inexperience) or to reduced hybrid fitness, but I am unable to separate these possibilities.

Hybridization could be of considerable importance in the conservation of Roseate Terns, which are listed as "Endangered" in the United States and "Threatened" in Canada (U.S. Fish and Wildlife Service 1989, Kirkham and Nettleship 1987). Hybridization with Common or Arctic terns may provide novel gene combinations that could ultimately help individual Roseates adapt to new or changing environments (Grant and Grant 1992). This could be particularly important in populations that suffer from inbreeding depression (Cade 1983). In extreme cases, hybridization can lead to the genetic assimilation of a rare species. For example, the Sevchelles Turtle Dove Streptopelia picturata rostrata was assimilated by interbreeding with the introduced S. picturata picturata from Madagascar (reviewed in Cade 1983). This is unlikely to be a problem for Roseate Terns, however, both because of the apparent infrequency of hybridization and because the Roseate population is still relatively large and widespread.

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