Common Tern *Sterna hirundo* and Arctic Tern *S. paradisaea* hybridization produces fertile offspring

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Abstract

This study provides the first molecular evidence for hybridization between Arctic Terns *Sterna paradisaea* and Common Terns *S. hirundo*. We studied a mixed pair (P1; male Arctic Tern and female Common Tern) and its offspring on Penikese Island, Massachusetts, USA in 2007–2015. The pair maintained a long-term pair bond (8 years); its reproductive performance was comparable to that of Common Terns and higher than that of Arctic Terns at the site. Molecular analyses confirmed that all young raised by the pair (at least 5 males and 4 females) were biological offspring. We describe hybrid young and the adult hybrid in detail to facilitate field identification. Although F1 hybrid young were intermediate between the parent species in certain characteristics, dark feathers extending below the eye, in particular, gave them a distinctly Arctic Tern-like appearance; however, all had secondary feathers that were darker than the wing-coverts, like Common Terns. We detected one male F1 hybrid that returned to breed; it retained some features intermediate between the parent species, but we qualitatively judged it to be more Common Tern-like. It mated with a Common Tern and produced three confirmed backcross hybrid young that closely resembled Common Terns. We speculate that rarity of Arctic Terns, especially females, at and near the study site and age/inexperience of the Common Tern parent were proximate mechanisms for the formation of the P1 pair. Further, because mixed pairs are occasionally observed and hybrids are cryptic, we suggest that Arctic/Common Tern hybridization may occur more commonly than is currently realized.

Introduction

Common Terns *Sterna hirundo* and Arctic Terns *S. paradisaea* have broad breeding distributions in North America and Eurasia, but their area of overlap is not extensive, as the Common Tern breeding range is largely south of that of the Arctic Tern (Cramp 1985; Hatch 2002; Nisbet 2002a). On the northwest Atlantic coast of the USA, where our study occurred, the species' breeding ranges overlap between 41°N and 52°N (Hatch 2002). Because morphological and molecular evidence suggests that Arctic and Common Terns are very closely related (Bridge *et al*. 2005), it follows that hybridization could occur. Mixed Arctic/Common Tern pairs, including multi-year pairings, have indeed been reported in the wild (Kullenberg 1946; Panov 1989; Debout & Debout 1989 in McCarthy 2006) as have presumed hybrid young (Degland & Gerbe 1867; Suchetet 1896). Molecular confirmation is, however, absent.

In June 2007, CSM first observed a Common Tern and an Arctic Tern attending two chicks on Penikese Island (41°27'N 70°55'W) in Buzzards Bay, Massachusetts, USA. Observations over the next three weeks provided further support that these birds were a mated pair. We located this pair in most years from 2007 to 2014 and here we present behavioural and molecular evidence for a long-term pair bond and hybridization of these birds that resulted in production of fertile offspring. We report on: analysis of mitochondrial and nuclear DNA; characteristics of nests, eggs, and young (F1 hybrids); and reproductive performance of the mixed pair in comparison to the parent species. We describe an adult F1 hybrid and its offspring (B1 hybrids) that resulted from backcrossing to a Common Tern and discuss factors that may have contributed to the interspecific pairing at this site.

Methods

Penikese Island, a 30 ha island located in Buzzards Bay, Massachusetts (USA), supports a colony of Common, Roseate *S. dougallii*, and Arctic Terns. Abundance of breeders during the study from 2007 to 2015 was 636–1,216 pairs of Common Terns, 0–102 pairs of Roseate Terns, and 0–2 pairs of Arctic Terns (Massachusetts Division of Fisheries & Wildlife [MassWildlife] unpubl. data). Terns nested mainly on a cobble and boulder beach, sparsely vegetated with Beach Pea *Lathyrus japonicus*, Seaside Goldenrod *Solidago sempervirens*, American Beachgrass *Ammophila breviligulata*, and other coastal plants. Studies of reproductive performance of Common Terns and Roseate Terns were conducted in 2007–2009 and 2012–2015, while Arctic Terns were monitored incidentally.

In 2007, when the mixed pair was first observed, both individuals were already banded; we trapped the Common Tern and read the band of the Arctic Tern through a spotting scope and binoculars. Between 2008 and 2015, we made specific efforts to locate the Arctic/Common pair by listening for Arctic Terns throughout the colony and especially near the 2007 nest site. After locating an Arctic Tern with a nest, we conducted observations of its mate and ascertained the band status of the pair. In most years we attempted to trap both mates with treadle traps, but in some years they could not be captured. In most years (except 2010 and 2011) we also trapped additional Arctic Terns and a sample of Common Terns (3–10% of nesting birds). We did not make a particular effort to detect F1 hybrid adults, but in 2015, we serendipitously located one (Figure 1) while trapping Common Terns.

Eggs and Nest Success: Observers and data collection varied among years. We noted lay date, clutch size, hatch date, hatching success, and fledging success for Common X Arctic Tern, Hybrid X Common Tern, Arctic Tern, and a sample of Common Tern nests and chicks in most years. We weighed one or more F1 hybrid, B1 hybrid, and Arctic Tern eggs in most years. We also weighed the A-egg (first egg

Figure 1. Arctic X Common Tern F1 hybrid adult, Penikese Island, 16 June 2015. © *J. Gahagan.*

laid) in most Arctic Tern nests and a sample of Common Tern nests in all study years except 2010. If eggs were not found the day they were laid, we assumed a 23 d incubation period for Common Tern and Arctic X Common Tern eggs and 22 d for Arctic Tern eggs, estimated lay dates based on hatch dates, and adjusted observed weights to fresh weights (Rahn *et al*. 1976), for nests in which one or more eggs hatched. We measured length and width of F1 hybrid eggs in 2010, 2012, and 2014, B1 hybrid eggs in 2015, Arctic Tern eggs in 2014 and 2015, and a sample of Common Tern eggs in 2010, 2014, and 2015.

Chicks: When possible we followed Common, Arctic, F1 hybrid, and B1 hybrid eggs until hatching and then banded the chicks. Each year, we placed small wooden shelters in the territories of the F1 and B1 hybrid chicks. As part of long-term studies, we fenced in groups of Common Tern nests, provided shelters to most, and in all years except 2010 and 2011, to gauge reproductive performance and growth, we weighed chicks on alternate days through the hatchling period, determined linear growth rates (LGR) between days 3 and 15 and asymptotic weights (AW) after day 17 of chicks predicted to fledge (Nisbet & Drury 1972; Tims *et al*. 2004; MassWildlife unpubl. data). We made periodic observations of Arctic, F1 hybrid, and B1 hybrid chicks to assess survival to fledging; in 2013–2015, we weighed Arctic Terns and fenced and weighed F1 and B1 hybrid terns through the hatchling period and determined LGR and AW for chicks predicted to fledge.

Plumage Characteristics: We photographed most of the F1 and B1 hybrid chicks for evaluation of plumage and bare parts. We attempted to photograph chicks when they were downy and again close to fledging age. Quality of photos was variable and not all characteristics could be evaluated for each chick, making some among-chick comparisons difficult; features that could not be observed well were disregarded. We evaluated plumage and bare parts compared to published descriptions and photographs of Arctic and Common Terns including Richardson (1953), Grant & Scott (1969), Cramp (1985), Hume (1993), Olsen & Larsson (1995), Higgins & Davies (1996), Hatch (2002), Nisbet (2002a), and U.S. Fish and Wildlife Service (2015).

Morphometrics: In 2009, 2014, and 2015, we measured head (tip of bill to back of head), exposed culmen, tarsus, unflattened wing-chord length and weight for F1 or B1 hybrid chicks at 19 or 20 days of age and compared them to a sample of Common Tern chicks of the same ages. Head, culmen, and tarsus were measured to the nearest 0.1 mm (except in 2014, when culmen and tarsus were measured to the nearest 0.5 mm), wing chord to the nearest 0.5 mm (2014) or 1 mm (2009, 2015), and weight to the nearest 1 g. In each year, only one observer took measurements of chicks; however, because observers and chick growth rates varied among years, we did not combine data from different years. We did not have sufficient data from Arctic Terns for comparison.

When adults from the Common/Arctic or hybrid/Common pairs were trapped, we took weights and head length measurements in all years; exposed culmen length was measured in 2007 only. We photographed each adult at least once during the study period. For comparison, we trapped and measured a sample of Common Tern and Arctic Tern adults in all years in which they nested. Means ± 1 standard deviation are shown unless otherwise specified.

Molecular Confirmation: We obtained tissue samples (blood, feathers, or carcass) for molecular analysis for the putative Common Tern and Arctic Tern parents, nine chicks during the period 2007–2009 and 2013–2014, a putative Common Tern mated to the F1 hybrid, and the three backcross chicks they produced in 2015. DNA was isolated from blood or tissue following manufacturer recommendations with Qiagen DNeasy Blood and Tissue Kit. The sex of each individual was determined by amplifying W and/or Z regions of the CHD1 gene using primers 2550F and 2718R (1 μM each; Fridolfsson & Ellegren 1999), 5 μl DNA from extraction, and Promega 2X PCR Master Mix for a 40 μl volume reaction. The polymerase chain reaction (PCR) parameters were 40 cycles of 1 min at 94°C, 1 min at 48°C, and 1 min at 72°C, preceded by 2 min at 94°C and followed by 2 min at 72°C.

Each individual (n=14) was genotyped at ten microsatellite loci to confirm paternity and maternity for all offspring (*RBG 13, 18, 27, 28, 29,* Given *et al*. 2002; *Sdaat20, 27, Sdaac20,* Szczys *et al*. 2005; *K6, 16,* Tirard *et al*. 2002). PCRs included 0.5–1.5 μl DNA, 1 μM each primer, and Promega 2X PCR Master Mix in 10 μl total volume reactions. PCR parameters were 30 cycles of 30 s at 94°C, 30 s at 60°C, and 30 s at 72°C, preceded by 2 min at 94°C and followed by 2 min at 72°C. Additionally, a 320 bp portion of a nuclear intron in the α-Enolase gene was sequenced as described by Friesen *et al*. (1997) to investigate pedigree.

To determine species identity, sequence data was obtained for each individual (n = 14) by amplifying a 690 bp fragment of the Barcode region of the COI gene as described by Aliabadian *et al*. (2013).

Results

Adults and Pair Bond: After the initial observation of the Common/Arctic pair in 2007, we relocated the pair and its nest in 2008–2010 and 2012–2014. The pair may have been missed in 2011, when the site was visited infrequently. The Common Tern was trapped in 2007–2009, 2013, and 2014 and the Arctic Tern in 2008, 2009, and 2013. Band numbers were not confirmed for either mate in 2010 or 2012, or for the Arctic Tern in 2014; however, in these years, position of the bands, locations of nesting territories, and behaviours were consistent with the known individuals, so we were confident that the same individuals were paired. In 2015, we did not observe the mixed pair; however, in mid May we observed a territorial Arctic Tern in the former nesting area of the mixed pair and, based on its location, behaviour, and band position, speculate that this was the same individual that had nested previously. It was courting an already-mated Common Tern, the identity of which we did not determine.

The female Common Tern adult (1172-84716) was banded in 2004 as a chick on Ram Island, Buzzards Bay, Massachusetts (41°37'N 70°48'W, 10 km from the study

Table 1. Microsatellite genotypes for P1 Common Tern and Arctic Tern, F1 hybrid offspring, the F1 hybrid x Common Tern and three B1 offspring. Chicks are labelled by their order in the clutch (A, B, or C) and year. Adults are in bold font. The F1 hybrid chick that returned to breed is noted with an asterisk (*). Genotypes that are underlined indicate null alleles passed from the female Common Tern to three of her offspring.

	Sex	Sdaac20	Sdaat20	Sdaat27	K16	K6	RBG13	RBG18	RBG27	RBG28	RBG29
Common	**F**	**140140**	**159186**	**245245**	**124124**	**130130**	**216218**	**176176**	**189189**	**149151**	**135143**
Arctic	**M**	**130145**	**180183**	**245245**	**120120**	**130134**	**218218**	**176190**	**189191**	**151151**	**149157**
A 2007*	M	130140	159180	245245	120124	130130	216218	176190	189191	149151	135149
A 2008	M	130130	159183	245245	120124	130134	216218	176190	189191	149151	135149
B 2008	M	140145	159183	245245	120124	130130	216218	176176	189189	151151	135149
C 2008	F	140145	183186	245245	120124	130130	218218	176190	189189	151151	143149
A 2009	F	130130	180186	245245	120124	130134	218218	176190	189189	149151	143157
B 2009	M	130130	159183	245245	120124	130130	218218	176176	189189	149151	135149
B 2013	M	130140	159180	245245	120124	130134	216218	176190	189189	151151	143157
B 2014	F	130140	159180	245245	120124	130134	218218	176190	189191	151151	135149
***Hybrid**	**M**	**130140**	**159180**	**245245**	**120124**	**130130**	**216218**	**176190**	**189191**	**149151**	**135149**
Common	**F**	**140140**	**180186**	**245245**	**124124**	**128130**	**216218**	**178178**	**193193**	**151153**	**135135**
A 2015	F	130140	180186	245245	120124	130130	216216	176178	189193	149151	135149
B 2015	F	140140	159186	245245	120124	128130	216216	178190	189193	151151	135149
C 2015	F	140140	159186	245245	120124	130130	216218	178190	189193	151151	135149

site). Compared to other Common Terns captured on Penikese Island from 2007 to 2015, she was of average size, as indicated by head and bill lengths in each year; weight was above average in the last three of five years in which she was captured (data not shown). Plumage, leg and bill colour, and voice were typical of the species.

The male Arctic Tern adult (1162-65488) was presumed to be a Common Tern when banded as a chick on Penikese Island in 1998. He was first recorded breeding on Penikese Island in 2007, although not all banded Arctic Terns were identified in each year. Head length and weight were average compared to those of other Arctic Terns captured on Penikese Island from 2007 to 2015 (data not shown). Plumage, leg and bill colour, and voice were typical of the species.

We did not observe courtship or copulations of the mixed pair. Both adults incubated eggs and brooded and fed chicks. We did not calculate time budgets, but observed that the Common Tern spent more time incubating eggs and attending chicks than did the Arctic Tern.

Molecular Confirmation: *Hybrid Family* - DNA banding patterns confirmed that the adult Common Tern was female and the adult Arctic Tern was male. In 2007–2009 and 2013–2014, the chicks sampled were five male and four female offspring. There were no mismatched microsatellite genotypes between any chick and both parents at all ten loci (Table 1). Two nuclear intron sequence polymorphisms (Genbank Accession Number KX946492-KX946493) corroborated F1 hybrid offspring where heterozygous genotypes in the offspring were noted (Figure 2). COI sequence data (Genbank Accession Number KX946478-KX946491) confirmed the P1 Arctic Tern and Common Tern species identity (41 variable nucleotides between species) and all offspring shared the Common Tern sequence with their mother (Table 2).

Backcross Hybrid Family - Molecular data confirmed the backcross of a male hybrid offspring to a Common Tern female. They produced three backcross hybrid offspring in 2015. All offspring matched both adults at all ten microsatellite loci. This family group followed Mendelian expectations for segregation of alleles at two nuclear introns (Figure 2). The Common Tern female in this pair had a different Common Tern COI haplotype than the P1 hybrid family above (Table 2).

Nests: The nesting territory of the Arctic/Common pair was within the same 30–40 m stretch of beach in all years and the locations of the 2007 and 2008 nests were nearly identical (within 3 m). The 2015 nest of the hybrid/Common pair was located within 5 m of the hybrid male's hatching territory in 2007. In 2007–2009 and 2014, the nesting territory of the Arctic/Common pair was loosely clustered among (20–40 m from) nests of the 1–2 Arctic Tern pairs on the island. Eggs of the Arctic/Common and hybrid/Common pairs were laid on accumulations of dried eelgrass *Zostera marina* and marine algae, typical of both Common Tern and Arctic Tern nests on the island.

Eggs and Lay Dates: Hybrid eggs did not differ in appearance from eggs of either parent species, which are highly

Table 2. Variable sites within a 690 bp fragment of the Barcode region of the COI mitochondrial gene. Forty-one sites are different between Arctic and Common Terns. Only one site (626, bold and underlined) distinguishes the Common Tern 1 haplotype from the Common Tern 2 haplotype. All offspring in this study match their mother's sequence exactly.

Position:	41	113	161	164	179	236	263	269	287	296	299	308	311	326	338	341
ARTE	C	T	A	A	G	G	G	T	C	C	T	G	T	A	T	C
COTE 1	T	C	G	G	A	A	A	C	T	T	C	A	C	G	C	T
COTE 2	T	C	G	G	A	A	A	C	T	T	C	A	C	G	C	T

Position:	344	371	380	386	404	407	416	428	431	449	452	497	503	512	527	554
ARTE	T	G	A	G	C	A	G	G	T	C	G	T	T	A	C	A
COTE 1	C	A	G	A	T	G	C	A	G	T	A	C	C	G	T	G
COTE 2	C	A	G	A	T	G	C	A	G	T	A	C	C	G	T	G

Position:	575	605	614	623	**626**	647	662	665	668
ARTE	A	G	C	G	T	A	T	T	T
COTE 1	G	A	T	A	**T**	G	C	C	C
COTE 2	G	A	T	A	**C**	G	C	C	C

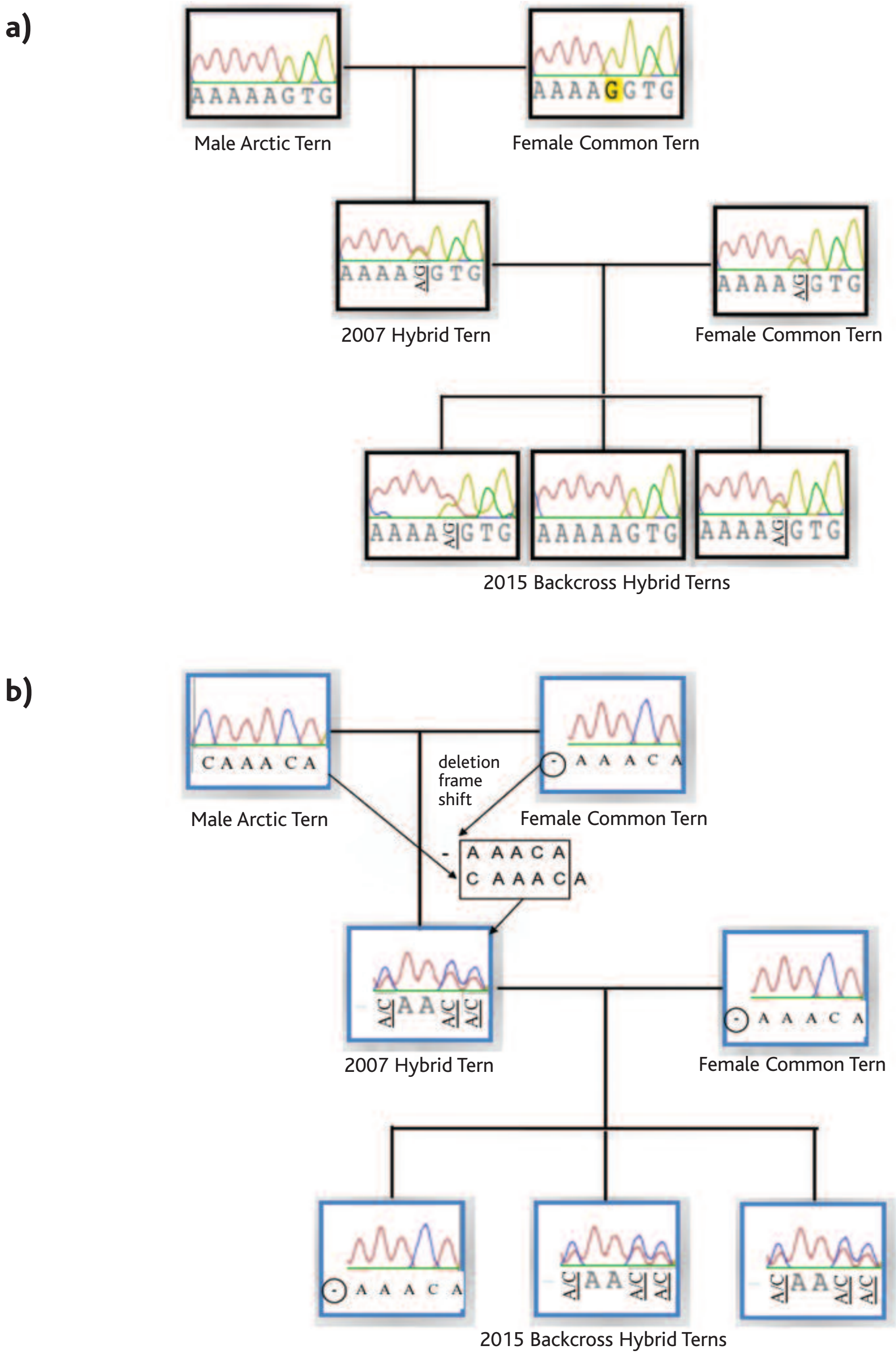


Figure 2. Pedigree highlighting nuclear sequence data and inheritance patterns for two regions of the -Enolase gene. Region 1 (a.) shows the polymorphism at position five where ‘A’ occurs in the Arctic Tern and ‘G’ occurs in the Common Tern resulting in a heterozygote A/G in the Hybrid Tern. Region 2 (b.) shows a deletion mutation of the first position ‘C’ in the Common Tern resulting in a frame shift and three heterozygous positions in the Hybrid Tern.

variable and not reliably distinguishable from each other (Hatch 2002). In six years in which hybrid eggs were photographed, all were light brown with dark brown spots (n = 10). The B1 hybrid eggs (n = 3) were similar. Length and width of F1 and B1 hybrid eggs fell within the range for Common Tern eggs at the site (Table 3). Fresh weights of F1 hybrid A-eggs were similar to, and the B1 hybrid A-egg was greater than, mean Common Tern A-egg weights; both were generally greater than Arctic Tern A-egg weights in those years (Table 3). Clutch sizes of the F1 hybrid nests (2.5 ± 0.5 eggs/nest, range 2–3, n = 6) and the B1 hybrid nest (3 eggs) were comparable to the mean clutch size for Common Terns in the same years (range of annual means, 2.2–2.8 eggs/nest), but greater than mean clutch size for Arctic Terns (2.0 ± 0.00 eggs/nest, n = 8). Known A-egg lay dates for the Arctic/Common pair occurred within 1–5 d (n = 5), and for the hybrid/Common pair within 2 d, of median lay dates for the Common Tern colony.

Reproductive performance: Measures of reproductive performance of the Arctic/Common pair and hybrid/Common pair were comparable to Common Terns and exceeded those of Arctic Terns. Excluding years when clutch size (2007) or hatch outcome (2010) were unknown, and one year (2012) when all 3 eggs were over-washed, hatching success of 10 F1 hybrid eggs was 100%, paralleling generally high Common Tern hatching success (Table 4). All three B1 hybrid eggs hatched. Arctic Tern hatching success was more variable (0–100%) over the years of the study.

At least 13 F1 hybrid chicks were produced from 2007 to 2014. In four years in which total number of hatchlings was known, six of nine hybrid hatchlings (67%) fledged (annual fledging success, 50–100%; Table 4); of the three that died, one was entangled in vegetation and two apparently starved, one of those at 25 days old. Total number of hatchlings was unknown in 2007, but one chick fledged and one died after becoming entangled in vegetation. In 2010, at least two chicks hatched and both fledged. In 2015, three backcross young hatched and all fledged. Common Tern fledging success ranged from 52.5% to 88.1% in the years of the study (Table 4), except 2012, a year of heavy predation. We estimate that only four of ten Arctic chicks fledged in the years of the study (Table 4). Of the six thought to have died, four were found dead (and probably starved) and two went missing. LGR and AW for F1 hybrids, B1 hybrids, Common Terns, and Arctic Terns predicted to fledge were comparable (Table 5).

Characteristics of Hybrid Adult: The voice of the F1 hybrid adult was not specifically detected. Had it sounded strongly like that of an Arctic Tern, it may have been more conspicuous among the much more numerous Common Terns. Photographs of the adult appear in Figures 1 and 3. In the hand, the colouration of the bill and legs of the hybrid adult was a deeper red-orange than that of most Common Terns: indeed, it was this characteristic that prompted the initial observers to check the band number (1182-81508) against those of hybrids hatched at the site. However, this feature was not conspicuous at a distance. Both upper and lower halves of the bill had black tips. The cap was black with

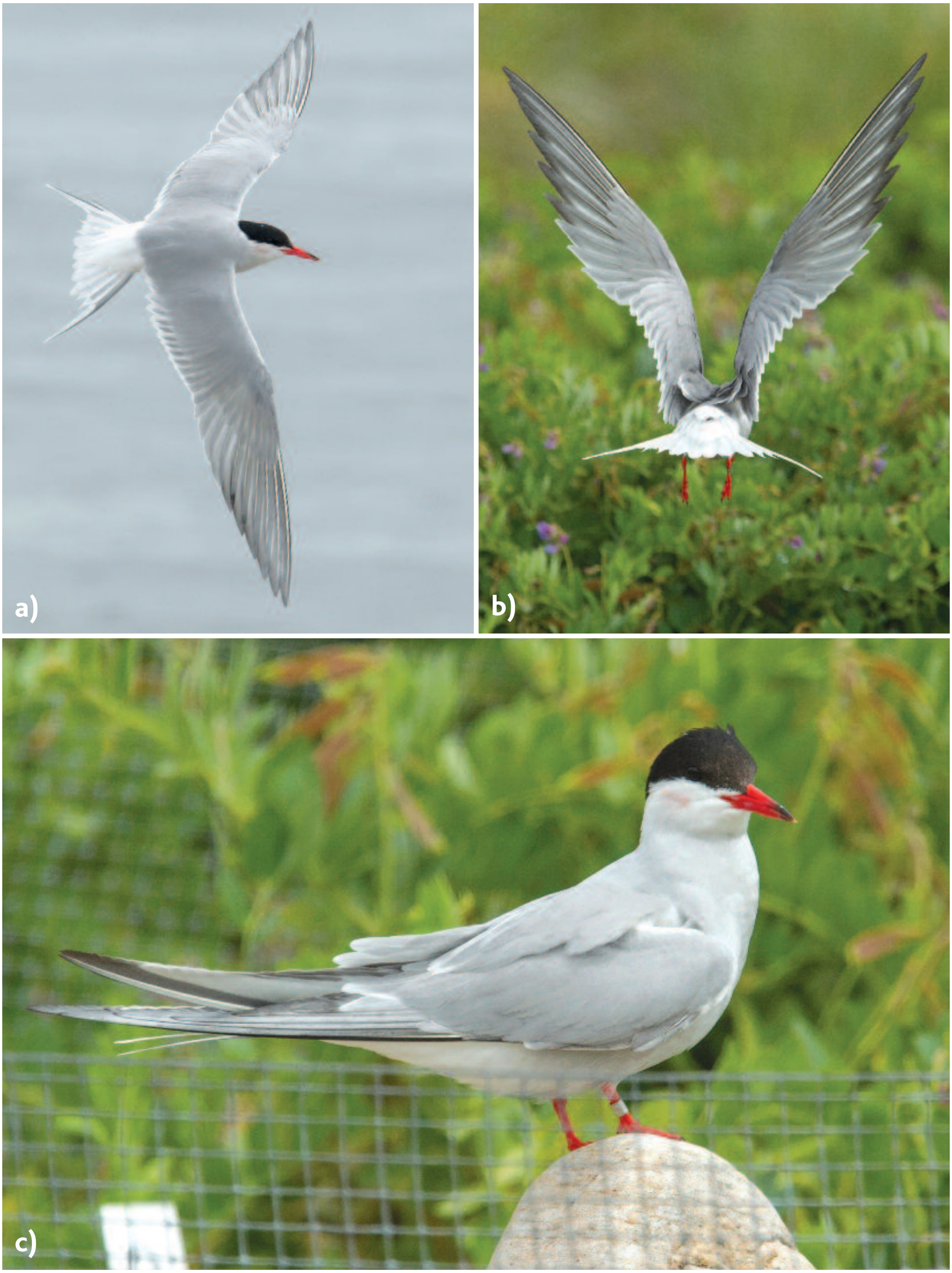


Figure 3 (a–c). Arctic X Common Tern F1 hybrid adult (1182-81508), 16 June 2015. Flight feathers were more Common Tern-like than Arctic Tern-like. Outer tail-streamers were shorter than those of either parent species. Tarsus length and colouration of the bill, legs, and feet appeared to be intermediate between the parent species. Faint pink spot on the cheek is faded dye. © *J. Gahagan*.

Table 3. Egg weights, lengths, and widths for Arctic Terns, Common Terns, and hybrid terns on Penikese Island. ARTE=Arctic Tern, COTE=Common Tern, HYTE=Arctic X Common Tern. Egg weights are for the first-laid egg in the clutch (A-egg) only and are corrected to fresh egg weights based on Rahn *et al*. (1976). Weights that could not be corrected due to uncertain lay dates are noted as approximate (~value). Measurements are given as mean ± standard deviation, range, and (sample size) for all samples of three or more eggs. If samples consisted of two eggs, individual measurements are presented as (value 1, value 2).

Year	A-egg weight (g)				Mean egg length (mm)				Mean egg width (mm)			
	ARTE X COTE	COTE	ARTE	HYTE X COTE	ARTE X COTE	COTE	ARTE	HYTE X COTE	ARTE X COTE	COTE	ARTE	HYTE X COTE
2007	-	20.6 ± 1.5 15.1–25.9 (442)	18.0 (1)	-	-	-	-	-	-	-	-	-
2008	20.4 (1)	20.6 ± 1.5 15.6–24.9 (368)	16.7 ± 1.9 (15.3, 18.0) (2)	-	-	-	-	-	-	-	-	-
2009	20.4 (1)	20.6 ± 1.5 16.1–25.8 (329)	~18.5, ~17.4 (2)	-	-	-	-	-	-	-	-	-
2010	-	-	-	-	43.9 ± 0.9 42.8–44.4 (3)	42.3 ± 1.9 37.7–48.1 (65)	-	-	30.1 ± 0.3 29.9–30.4 (3)	30.5 ± 1.9 27.4–39.8 (65)	-	-
2012	~19.3 (1)	20.5 ± 1.6 13.2–24.1 (229)	-	-	43.4 ± 1.3 42.6–44.9 (3)	-	-	-	29.7 ± 0.6 29.1–30.2 (3)	-	-	-
2013	20.2 (1)	20.1 ± 1.5 15.4–23.5 (174)	-	-	-	-	-	-	-	-	-	-
2014	18.2 (1)	19.9 ± 1.8 14.6–24.0 (194)	19.4 (1)	-	42.0 ± 1.6 (40.9, 43.1) (2)	41.9 ± 1.8 38.3–45.9 (50)	-	-	29.7 ± 0.2 (29.5, 29.8) (2)	29.9 ± 0.8 27.6–31.8 (50)	-	-
2015	-	20.3 ± 1.8 4.2–26.3 (230)	16.9 (1)	22.1 (1)	-	42.1 ± 2.0 35.5–46.3 (100)	37.4 ± 0.4 (37.1, 37.6) (2)	40.8 ± 1.9 38.6–41.9 (3)	-	30.0 ± 0.9 27.9–31.9 (100)	29.8 ± 0.2 (29.6, 29.9) (2)	30.3 ± 0.7 29.7–31.1 (3)

some white speckling on the forehead. The head appeared relatively rounded. White cheeks contrasted with the very pale grey throat, breast, and belly; there was no sharply demarcated cheek stripe. The vent and undertail-coverts appeared whitish. The mantle was light grey. The rump and uppertail-coverts were white. The uppersides of the outer six primaries (P5–10) were dark to medium grey with a white wedge in the centre of the inner web, separated from the rachis by a relatively broad, grey area; the outer web of the outermost primary (P10) was blackish. The remaining four primaries (P1–4) were distinctly paler (appearing similar to, or slightly paler than, the mantle) and edged with

Table 4. Hatching success (% of eggs that hatched) and fledging success (% of hatchlings that fledged) for Arctic Terns, Common Terns, and hybrid terns on Penikese Island. Sample sizes are shown in parentheses.

	Hatching success (%)				Fledging success (%)			
Year	ARTE X COTE	COTE	ARTE	HYTE X COTE	ARTE X COTE	COTE	ARTE	HYTE X COTE
2007	66.7–100 (2–3)[a]	87.3 (370)	50 (4)	-	33.3–50 (2–3)[a]	63.4 (112)	50 (2)	-
2008	100 (3)	88.1 (379)	100 (4)	-	66.7 (3)	92.1 (177)	0 (4)	-
2009	100 (2)	74.2 (368)	0 (4)	-	100 (2)	67.8 (152)	-	-
2010	100 (3)[b]	excellent[c]	-	-	66.7–100 (3)[d]	excellent[c]	-	-
2012	0	84.4 (205)	-	-	-	25 (92)	-	-
2013	100 (2)	72.1 (326)	-	-	50 (2)	86.5 (104)	-	-
2014	100 (2)	81.5 (329)	100 (2)	-	50 (2)	52.5 (101)	50 (2)	-
2015	-	83.9 (242)	100 (2)	100 (3)	-	81.4 (102)	100? (2)[e]	100 (3)

[a] Clutch size was unknown, but at least two eggs were laid and at least two chicks hatched; only one fledged.

[b] Two eggs hatched and the third was starring when last observed. It was not found failed later and is presumed to have hatched.

[c] Reproductive performance of Common Terns was not studied, but hatching and fledging success were judged to be excellent based on periodic observations of the colony.

[d] At least two chicks fledged, but the third egg in the clutch was last seen while starring. The nest was next visited around the time of fledging and we could not identify the presumed third chick.

[e] The two Arctic Tern chicks were last seen at eight and 12 days of age, after which the parents may moved them away from the nest site. Their linear growth rates were comparable to those of Common Terns predicted to fledge and predation rates were low, so we consider it likely that they fledged.

Table 5. Linear growth rates (rate of growth from day three to day 15) and asymptotic weights (weights from day 17 onward) for Arctic Terns, Common Terns, and hybrid terns on Penikese Island. Measurements are given as mean ± standard deviation, range, and (sample size) for all samples of three or more individuals. If samples consisted of two individuals, individual measurements are presented as (value 1, value 2).

	Linear growth rate (g/d)				Asymptotic weight (g)			
Year	ARTE X COTE	COTE	ARTE	HYTE X COTE	ARTE X COTE	COTE	ARTE	HYTE X COTE
2013	6.91 (1)	7.2 ± 1.1 2.6–10.3 (89)	-	-	112.5 (1)	117.5 ± 6.9 96.0–134.5 (70)	-	-
2014	5.9 (1)	6.6 ± 1.1 3.5–8.6 (51)	5.2 (1)	-	101.6 (1)	104.7 ± 11.2 82.3–131.8 (51)	106 (1)	-
2015	-	7.1 ± 1.1 2.6–8.8 (83)	7.0 ± 1.3 (6.1, 7.9) (2)	7.6 ± 0.4 7.2–8.0 (3)	-	115.7 ± 7.7 91.0–133.3 (72)	-	110.2 ± 3.0 107.2–113.3 (3)

white. The secondaries, broadly edged in white, were darker than both the adjacent inner primaries and the mantle. Visually, the secondaries and outer primaries combined to form a darker (although not starkly so) trailing edge to the wing, interrupted by a pale panel of inner primaries (P1–4). Overall, the upperwing, while not uniformly grey, lacked strong contrast between the primaries and the rest of the wing; however, stronger contrast as a result of feather wear may have developed later. Underwing-coverts appeared whitish. The tail was mostly whitish. The outer retrix (T6) was elongated into a short streamer, the outer web of which was blackish and the inner web whitish. The rest of the retrices (except the central one [T1], which appeared to be uniformly whitish) had very pale grey outer webs and whitish inner webs.

The head measurement (76.6 mm) was well within the range of values for Common Terns in 2015 (77.2 ± 2.4 mm, range 71.1–83.9, n = 110) and greater than that of all Arctic Terns measured during the study period (70.6–75.7 mm, n = 11), although measurements are not strictly comparable as they were taken by multiple observers. Its weight (120 g and 125 g on different dates) was average compared to Common Terns in 2015 (125.2 ± 8.9 g, range 110–144, n = 109) and greater than weights of all Arctic Terns measured during the study period (107–119 g, n = 10). In the field, the legs appeared markedly shorter than those of typical Common Terns and longer than those of typical Arctic Terns, but we did not have enough data from either parent species for a quantitative comparison. The tail-streamers (not measured) seemed conspicuously shorter than those of typical Common, and especially Arctic, terns. Based on our photographic time series, the streamers may still have been growing during the breeding season: they appeared barely longer than adjacent retrices in mid May, but substantially longer in mid June, when they still fell far short of extending to the wing-tips when the bird was standing with wings folded.

Comparison of Hybrids to Parent Species: Photographs of F1 and B1 hybrids at the downy chick and feathered young stages appear in Figures 4–6. Detailed descriptions are included in Appendix I. Common and Arctic Tern juveniles exhibit considerable intraspecific variability in appearance. In young and adults, many features of the various plumages are shared by both species (e.g. the black caps, grey mantles, and pale underparts of adults) or differ only in degree (e.g. the shade of grey on the breast). Additionally, feather wear can substantially change the shade and/or hue of feathers. For these reasons, it is difficult to attribute certain features to one or the other parent species. Downy and feathered F1 and B1 hybrid young and the adult F1 hybrid showed a combination of features of the parent species and some features that were intermediate between the parent species. The B1 hybrids showed a much stronger resemblance to Common Terns than did the F1 hybrids, as would be expected given the parentage.

Some downy F1 hybrids were grey: Common Tern chicks are always buff-toned, whereas Arctic Tern chicks are buff, grey, or intermediate. B1 hybrids were all buff. The bold, blackish forehead of many downy Arctic Terns was not seen in F1 or B1 hybrids. We did not quantitatively assess the size and distribution of black dorsal spots, which can differ between the parent species, but we qualitatively judged that spotting resembled that found in Common Terns, with which we were more familiar. The down of one of the B1 hybrids was an unusual yellowish hue; this may be an example of heterosis (Shull 1914), in which a trait of a hybrid individual falls outside the normal range of the parent species; this is typically associated with polygenic traits (McCarthy 2006).

Figure 4. Arctic X Common Tern F1 hybrid chick, 6 July 2008. Dark feathers that extended below the eye on all F1 hybrids gave them a distinctly Arctic Tern-like appearance. Green on the forehead is dye. © *J. Cunningham/MassWildlife*.

Figure 5 (a–c). Arctic X Common Tern F1 hybrid chicks (**a, b**) and B1 backcross hybrid (F1 hybrid X Common Tern; **c**). On the F1s, the grey of the mantle feathers was generally colder (more Arctic Tern-like) than that of the B1 hybrids or Common Terns, which was more heavily washed with brown. Rumps were white for F1 hybrids and grey for B1 hybrids. Secondaries were darker than upperwing-coverts on both F1s and B1s, a Common Tern (but not Arctic Tern) characteristic. © *D. LaFlamme/MassWildlife, 2014* (**a,b**) and *A. Smith, E. Berge, C. Bates/MassWildlife, 2015* (**c**).

Table 6 summarizes the salient features of feathered hybrid young compared to the parent species. In all feathered F1 hybrid young, the mask formed by blackish feathers that extended under the eye (typical of Arctic Terns, but not Common Terns) was perhaps the most obvious feature that made the hybrids stand out from

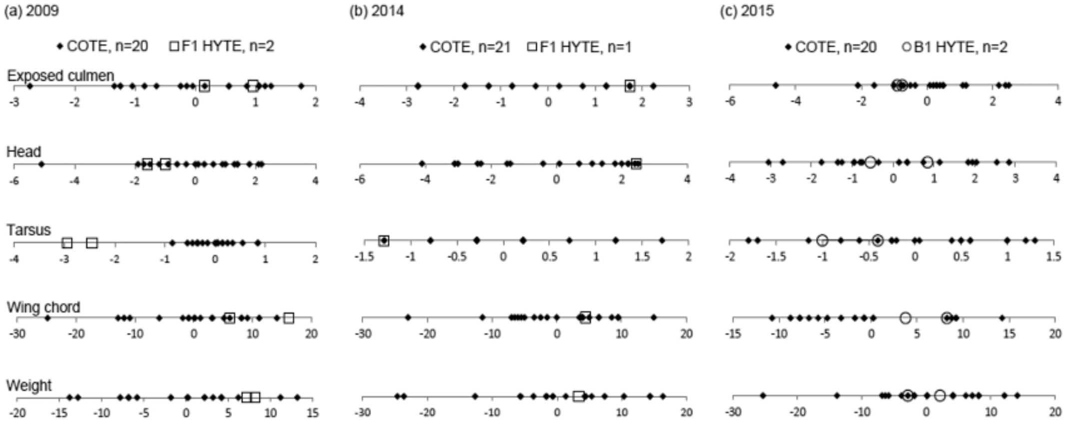
Figure 6. B1 backcross hybrid chicks (F1 hybrid X Common Tern), 16 June 2015. As downy young, the B1 hybrids were Common Tern-like, but the down of one chick (on the right) had an unusual yellowish hue. © *J. Gahagan*.

Table 6. Characteristics of feathered F1 and B1 hybrid young in comparison to Common Terns and Arctic Terns, the juveniles of which exhibit considerable intraspecific variability in appearance. Conclusions were limited by small sample size and lack of Arctic Tern young for comparison.

ARTE	F1 HYTE			B1 HYTE			COTE
	ARTE -like	Inter- mediate	COTE -like	ARTE -like	Inter- mediate	COTE -like	
Dark under-eye feathers	x	-	-	x	-	x	White under-eye feathers
Cold grey mantle feathers	x	x	-	-	-	x	Warm grey mantle feathers
Secondaries paler than upperwing-coverts	-	-	x	-	-	x	Secondaries darker than upperwing-coverts
White rump	x	-	-	-	-	x	Grey rump
Short tarsus (relative to COTE)	x?	x?	-	-	-	x	Long tarsus (relative to ARTE)

Common Terns when not in the hand; this feature appeared in only one of three B1 hybrids. F1 hybrids were generally a colder grey than Common Terns, which are typically brownish, and the B1 hybrids. In all feathered F1 and B1 hybrids, the secondaries were darker than the wing-coverts. This is a diagnostic criterion that separates Common Tern and Arctic Tern juveniles: in Common Terns the secondaries are never paler than the median and greater coverts, whereas in Arctic Terns the secondaries are the palest part of the wing. Rumps of the F1 hybrids were white (like Arctic Terns), but rumps of the B1 hybrids were grey (like Common Terns). Although it was difficult to completely gauge colour of head feathers on most young due to retention of down, it appeared that there was more contrast between cap colour and carpal bar colour on F1 hybrids compared to B1 hybrids, due to darker caps and lighter carpal bars on the F1s (more similar to Arctic Terns). None of the F1 hybrids or B1 hybrids exhibited red on the feet, legs, or base of the bill, sometimes noted in juvenile Arctic Terns at the time of fledging; it is possible that red would have developed in juveniles older than those we photographed.

Although our analysis of measurements suffered from small sample size and a lack of Arctic Tern chicks for comparison, it appeared that F1 hybrid young were shorter legged and perhaps longer winged than Common Tern young (Figure 7), paralleling differences in the adults (Craik 1998; Hatch 2002; Nisbet 2002a). Craik & Harvey (1984) maintained that Common Tern and Arctic Tern young of bill lengths >21 mm (as all hybrid and most Common Tern young in our study were) can be reliably distinguished from each other by tarsus measurements. The substantial difference between F1 hybrid tarsus lengths and mean Common Tern tarsus lengths largely disappeared in the B1 hybrids. We expected F1 hybrid bills to be intermediate between the shorter bill of the Arctic Tern and the longer bill of the Common Tern (Olsen & Larsson 1995), but we saw no evidence of this.



(a) 2009 (b) 2014 (c) 2015

Figure 7. Difference of measurements (exposed culmen, head, tarsus, unflattened wing chord, and weight) from mean Common Tern measurements for Common Tern (COTE) and F1 and B1 hybrid tern chicks on day 19 or 20 of age in 2009 (a), 2014 (b), and 2015 (c). Chicks found dead prior to fledging or not predicted to fledge by age-weight criteria (see text) were excluded; therefore, in 2014 one F1 hybrid B-chick that died prior to fledging was excluded. In 2015, a B1 hybrid C-chick measured only on day 18 was excluded. Both of these chicks were smaller in all measurements than the other hybrid chicks in those years.

Table 7. Characteristics of an individual F1 Common Tern X Arctic Tern hybrid adult in comparison to the parent species.

ARTE	F1 HYTE				COTE
	ARTE -like	Inter- mediate	COTE -like	Outside normal range	
Outer primaries: narrow grey band separates rachis and white wedge	-	-	x	-	Outer primaries: wide grey band separates rachis and white wedge
Primaries: weaker contrast between P1–4 and P5–10 (relative to COTE)	-	-	x	-	Primaries: stronger contrast between P1–4 and P5–10 (relative to ARTE)
Secondaries: paler than upperwing-coverts	-	-	x	-	Secondaries: darker than upperwing-coverts
Tail: outer webs darker than inner webs on T5–6	-	-	x	-	Tail: outer webs darker than inner webs on T2–6
Tail streamers: extend past wingtips	-	-	-	shorter than ARTE or COTE	Tail streamers: approximately even with wingtips
Colour of bill, legs, feet: blood red	-	x	-	-	Colour of bill, legs, feet: red-orange
Shorter head (relative to COTE)	-	-	x	-	Longer head (relative to ARTE)
Shorter tarsus (relative to COTE)	-	x	-	-	Longer tarsus (relative to ARTE)
Lower weight (relative to COTE)	-	-	x	-	Higher weight (relative to ARTE)

The F1 hybrid adult showed characteristics of both parent species, but our qualitative impression was that it was more Common Tern-like overall (Table 7). Indeed, the adult hybrid would not stand out in a Common Tern colony unless it were closely scrutinized. The upperwing pattern more closely recalled that of Common Terns. The dark grey of outer primaries P5–10, that obviously, though not starkly, contrasted with paler inner P1–4; the relatively wide grey area that separated the white wedge on the inner web of the outer primaries from the rachis; and secondaries that were darker than the upperwing-coverts are features that distinguish Common Terns from Arctic Terns. The latter show little contrast between outer and inner primaries and have secondaries that are paler than upperwing-coverts. The relative translucency of the outstretched primaries when viewed from underneath is often cited as a useful field mark to distinguish Arctic Terns from Common Terns (e.g. Grant & Scott 1969; Hume 1993); however, we found this difficult to judge, as it is influenced by lighting and position of the primaries. The tail was more Common Tern-like, with outer webs of T2–6 darker than inner webs, whereas for Arctic Terns, typically only T5–6 show darker outer webs. The very short tail, substantially shorter than typical for either parent species, may have been a result of an unusually delayed moult or feather regrowth following symmetrical loss earlier in the season; however, it also could be an example of negative heterosis. The deep red-orange of the bill, legs, and feet of the hybrid adult was intermediate between the blood red of Arctic Terns and the red-orange of Common Terns. We qualitatively judged that the head was rather rounded (Arctic-like), less angular than typical Common Terns. The black bill-tip was Common Tern-like, although Arctic Terns occasionally show diffuse black on the bill-tip during the breeding season. Leg (tarsus) length also appeared to be intermediate between the parent species. Based on how similar in appearance the adult F1 hybrid was to a Common Tern, we speculate that B1 hybrid adults might be essentially indistinguishable from Common Terns, at least when not in the hand.

Discussion

To the best of our knowledge, the combination of several years of field observations and molecular data in this study provide the first conclusive evidence for a long-term pair bond between Common Terns and Arctic Terns, hybridization of these species, and production of fertile offspring capable of backcrossing with Common Terns. Natal site fidelity of the F1 hybrid adult was very high: it nested within 5 m of its natal territory. Although data for Arctic Terns are lacking (Hatch 2002), long-term pair bonds between Common Terns (14 years; Nisbet 2002a) have been documented. The 8-year pair bond between the Arctic and Common Tern in this study may have been maintained (see below) by the rarity of Arctic Terns at Penikese Island throughout the study period, the costliness of seeking a new mate, and/or the high nesting success of the pair, although unsuccessful nesting does not appear to be linked to divorce in Common Terns (Gonzáles-Solís *et*. *al*. 1999).

Viability and Fitness of Hybrids: Interspecific mating may result in reduced fitness of hybrid offspring of the F1 or subsequent generations (Ficken & Ficken 1968; Harris *et al*. 1978, Lanyon 1979; Arnold 1992; Rhymer & Simberloff 1996; Veen *et al*. 2001; Johansen-Morris & Latta 2006; Casas *et al*. 2012). While survival to fledging was very good, overall survival of the Arctic X Common F1 and B1 hybrids from fledging to first breeding is unknown. At least one F1 hybrid returned and we easily could have missed others; only a small fraction of the colony was studied annually, hybrids are cryptic, and no specific efforts were directed towards detecting them. While at least one F1 hybrid was fertile, overall fertility of the F1 and B1 hybrids is unknown. At least some Common X Roseate hybrids are fertile and can backcross to either parent species (Nisbet 2002a) and each other (Hays 1975; Nisbet *et al*. 2014). In hybrid animals, the heterogametic sex (in birds, the female) is more likely to be sterile (Haldane 1922). The fertile F1 hybrid in our study was male and another fertile, probable Arctic X Common hybrid we studied on nearby Bird Island, Massachusetts, was male (see below). In some bird species, females may pair and mate with heterospecifics, but also produce pure offspring from extrapair copulations with conspecifics to offset the loss of fitness from less fit hybrid offspring (Veen *et al*. 2001). We saw no evidence of extrapair copulations: all F1 and B1 young sampled had the same biological parents.

Frequency of Hybridization: Although previous observations of Arctic/Common pairings and possible hybrid young suggest that Arctic X Common hybridization has probably occurred in the past, its frequency is uncertain. Observations in Massachusetts and Maine, USA (see below), suggest that low levels of hybridization between Arctic and Common Terns may be occurring in the western Atlantic. Given the breeding range overlap (Hatch 2002), high degree of relatedness (Bridge *et al*. 2005), and similar plumage, vocalizations, and courtship behaviours of the parent species (Cullen 1956), it is perhaps surprising that Arctic X Common Tern hybridization has not been confirmed previously. Potential explanations for this include:

1) Low frequency of occurrence. The production of hybrid eggs and offspring may truly be rare. There may be strong behavioural, physical, or biochemical isolating mechanisms that discourage the formation of Arctic/Common pairs and/or prevent copulation or production of fertile eggs. For instance, Pierotti (1987) suggested that in seabirds, species pairs with similar foot and bill colours were more likely to hybridize than those pairs in which bill and foot colours differed. Cullen (1956) speculated that the distinctive advertising calls of Arctic and Common Terns used during courtship evolved as an isolating mechanism to prevent hybridization. Heterospecifics courted by experimentally cross-fostered Common and Arctic Terns failed to react to, avoided, or threatened the cross-fostered individuals, some of which eventually paired successfully with conspecifics, demonstrating that innate species-recognition abilities had a strong effect on mate choice (Busse & Franck 1988);

2) Failure to publish. Hybridization may be underreported due to failure to publish (McCarthy 2006). Arctic/Common Tern pairs with eggs and chicks are occasionally observed in large, mixed-species colonies in Maine (S. Williams and L. Welch, pers. comm.; DL pers. obs.), but these observations have not been published and confirmation of hybridization is lacking;

3) Failure to detect. Hybridization also may be underreported due to the difficulty of detecting hybrids amongst birds with very similar plumages (Randler 2004; McCarthy 2006). Hybrid terns can be quite cryptic within a colony (Nisbet 2002b). In June 2011, we observed a downy grey chick and a buff sibling on Bird Island, Buzzards Bay, Massachusetts (41°40'N, 70°43'W; 29 km from Penikese Island) in a Common and Roseate Tern colony with no known history of nesting Arctic Terns. Both parents were considered to be Common Terns when initially banded as chicks. One (9822-58513, a male banded in 1998 on Bird Island) appeared Common Tern-like but for exceptionally deep red-orange legs. It is virtually certain that this bird was a hybrid: Common Terns chicks are not grey and the adult's leg colouration was outside the range typical of Common Terns. In Massachusetts, the most plausible explanation for a red-legged Common Tern-like individual that produces a grey chick is that it has Arctic Tern ancestry, as the atypical features it exhibited are consistent with those of Arctic Terns, but not with those of any of the other sympatric, congeneric breeding terns (Forster's Tern, *S. forsteri*, a rare breeder; Roseate Tern) or Roseate X Common hybrids (Hays 1975; Veit & Petersen 1993; McNicholl *et al*. 2001, Nisbet 2002b; Cabot & Nisbet 2013). The other parent (802-80819, a female banded in 1994 in Maine) appeared to be a typical Common Tern. DNA from both birds was sequenced for species identity (COI) and both carried mitochondrial haplotypes indicating their mothers were Common Terns (data not shown). This analysis could not rule out a paternal Arctic Tern lineage giving 9822-58513 hybrid status.

Proximate Mechanisms for Hybridization: Behavioural isolating mechanisms in mixed tern colonies generally appear to prevent pairing of Arctic and Common Terns. Three proximate mechanisms may, however, have been responsible for the initial pairing of the Arctic/Common Tern pair at Penikese Island.

1) Availability of mates (overall rarity and sex ratio). Rarity of conspecifics is implicated in many animal hybridizations (Hubbs 1955; Short 1969; Rhymer & Simberloff 1996; Grant & Grant 1997; Randler 2002). To our knowledge, Penikese Island is the southernmost nesting location for Arctic Terns in the world and Arctic Terns comprise only ca. 0.1% of the Penikese colony. Fewer than 10 additional pairs nest south of the closest sizeable colony 300 km north of Penikese Island (Eastern Egg Rock, Maine; 43° 51′ 36′′N, 69° 22′ 55′′W; 68 pairs; Gulf of Maine Seabird Working Group 2013). In California, USA, an extralimital Arctic Tern summered in a Forster's Tern colony for five consecutive years before securing a Forster's Tern mate in years six and seven (Yee *et al*. 1994; Yee *et al*. 1995; Bailey *et al*. 1996; Roberson *et al*. 1997; Roberson *et al*. 1998; Roberson *et al*. 1999; Terrill *et al*. 2000). Rarity of Roseate Terns in a predominantly Arctic Tern colony in Scotland was implicated in a suspected Arctic X Roseate Tern hybridization (Ewins 1987). Frequency of Common X Roseate Tern hybridizations is higher in small colonies where Roseate Terns are marginal (Nisbet 2002a). At the level of the individual, the proximate mechanism is likely the rarity of conspecifics of the opposite sex, which would be exacerbated when one species is rare. In most or all years that the Penikese Island colony was studied (1998–2015), male Arctic Terns appeared to outnumber females and unpaired presumed males spent entire nesting seasons advertising and courting already-mated, presumed female Arctic Terns (CSM, pers. obs.; MassWildlife unpubl.), behaviours also observed in a colony in England with an apparent excess of Arctic Tern males (Cullen 1956, 1957). Common Terns also may have had an unbalanced sex ratio as evidenced by the presence of female-female pairs in the Buzzards Bay population (Nisbet *et al*. 2007) and unusually high numbers of supernormal Common Tern clutches (>3 eggs) in Buzzards Bay colonies for several years starting in 2009 (MassWildlife unpubl. data). As Common Terns are not known to employ brood parasitism as a reproductive strategy (Nisbet 2002a), we consider it most plausible that the supernormal clutches resulted from multi-female pairings due to an excess of females in the population, as occurs in some other seabirds (Hunt & Hunt 1977; Nisbet & Hatch 1999). An excess of female Roseate Terns in the northwest Atlantic may have been a factor in an Arctic X Roseate Tern hybridization (Whittham 1998). Related to mate availability, costs to waiting to secure a mate (Real 1990) may also precipitate heterospecific pairings and hybridizations (Grant & Grant 1997). In Common and Roseate Terns in Buzzards Bay, late-nesting can result in reduced productivity (Burger *et al*. 1996; Arnold *et al*. 2004; Arnold *et al*. 2006). Delayed mate acquisition does not appear to be a factor in the pairing of the Arctic and Common Tern in this study, as in the first year of nesting and most subsequent years, the pair nested earlier than the median nesting dates for Common Terns and Arctic Terns in the colony.

2) Misimprinting. It is possible that either the Common Tern or the Arctic Tern was naturally cross-fostered in a nest of the other species. In Buzzards Bay and at other sites, nests containing eggs of both Common and Roseate Terns occur (Hays 1975; CSM pers. obs.) and newly hatched Common and Roseate Tern chicks are not uncommonly adopted into neighbouring terns' nests (Nisbet 2002a; CSM pers. obs.). Young raised in the nest of a heterospecific may later seek mates exhibiting visual or auditory cues of this parent instead of those of a conspecific (Grant & Grant 1997). When experimentally cross-fostered Common and Arctic Tern young returned to the colony as adults, they courted individuals of their heterospecific foster parents' species, demonstrating a strong effect of imprinting (Busse & Franck 1988).

3) Age and breeding experience. Inexperienced birds may lack fully developed mate recognition systems, which can lead to heterospecific pairings (Grant & Grant 1997). The Common Tern was 3 years old and therefore likely a first-time breeder (Austin & Austin 1956; Nisbet *et al*. 1984) when first observed breeding with the Arctic Tern. This inexperience may have enabled a pairing unlikely to occur if prior mating experience with conspecifics had reinforced behavioural isolating mechanisms. The Arctic Tern's highly vigorous courtship displays and longer tail may have acted as supernormal stimuli, facilitating the pairing. In contrast, observations that the Arctic Tern interacted regularly with the few conspecifics on the island in 2007 suggests a strong innate species recognition system, with heterospecific mate choice occurring due to a lack of conspecific mates. Courtship of and pairing with heterospecifics is not inconsistent with the ability to differentiate them from conspecifics (Baker 1996; Kozak *et al*. 2009).

Conclusions: Our study reported indisputable evidence of a long-term pair bond and reproductive success of an Arctic/Common Tern mixed pair. We also provide some insight to the relative dominance of Arctic and Common Tern alleles affecting plumage and morphology in F1 hybrid and backcross offspring; details reported here may serve as a 'field guide' to hybrid detection for those monitoring tern colonies. However, our study provides little information on hybrid ecology. While these species' nesting ecology at the breeding sites is similar, their ecology outside of the breeding area is drastically different. Common Terns from Buzzards Bay fly south over the northwest Atlantic to the Caribbean and winter on the north and east coasts of South America (Nisbet *et al*. 2011; Nisbet & Mostello 2015). After heading southwest from nesting areas in Greenland and Iceland, Arctic Terns take routes along the coasts of South America and Africa before wintering in the Southern Ocean (Egevang *et al*. 2010; Hensz 2015). We suggest that tracking and/or stable isotope analysis of feathers should be the next step to provide information on at-sea movements and ecology of hybrid terns in the breeding region, along migration routes, and in wintering areas.

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References

Aliabadian, M., Beentjes, K. K., Roselaar, H. V. B., Nijman, V. & Vonk, R. 2013. DNA barcoding of Dutch birds. *ZooKeys* 365: 25–48.

Arnold, J. M., Hatch, J. J. & Nisbet, I. C. T. 2004. Seasonal declines in reproductive success of the common tern *Sterna hirundo*: timing or parental quality? *Journal of Avian Biology* 35: 33–45.

Arnold, J. M., Hatch, J. J. & Nisbet, I. C. T. 2006. Effects of egg size, parental quality and hatch-date on growth and survival of common tern *Sterna hirundo* chicks. *Ibis* 148: 98–105.

Arnold, M. L. 1992. Natural hybridization as an evolutionary process. *Annual Review of Ecology and Systematics* 23: 237–261.

Austin, O. L. & Austin, O. L., Jr. 1956. Some demographic aspects of the Cape Cod population of common terns (*Sterna hirundo*). *Bird-Banding* 27: 55–66.

Baker, M. C. 1996. Female buntings from hybridizing populations prefer conspecific males. *Wilson Bulletin* 108: 771–775.

Bailey, S. F., Singer, D. S. & Yee, D. 1996. The Nesting Season: Middle Pacific Coast Region. *National Audubon Society Field Notes* 50: 992–995.

Bridge, E. S., Jones, A. W. & Baker, A. J. 2005. A phylogenetic framework for the terns (Sternini) inferred from mtDNA sequences: implications for taxonomy and plumage evolution. *Molecular Phylogenetics and Evolution* 35: 459–469.

Burger, J., Nisbet, I. C. T., Safina, C. & Gochfeld, M. 1996. Temporal patterns in reproductive success in the endangered roseate tern (*Sterna dougallii*) nesting on Long Island, New York, and Bird Island, Massachusetts. *Auk* 113: 131–142.

Busse, K. & Franck, D. 1988. Cross-fostering experiments between common and arctic terns (*Sterna hirundo* and *Sterna paradisaea*) and the problem of species isolating mechanisms. *Zoologische Jahrbucher* 92: 213–220.

Cabot, D. & Nisbet, I. C. T. 2013. *Terns*. Collins, London.

Casas, F., Mougeot, F., Sánchez-Barbudo, I., Dávila, J. A. & Viñuela, J. 2012. Fitness consequences of anthropogenic hybridization in wild red-legged partridge (*Alectoris rufa*, Phasianidae) populations. *Biological Invasions* 14: 295–305.

Craik, J. C. A. 1998. Biometric differences between Common Terns *Sterna hirundo* and Arctic Terns *S. paradisaea*. *Ringing and Migration* 19: 75–78.

Craik, J. C. A. & Harvey, S. M. 1984. Biometrics and colour forms of chicks of common terns and arctic terns. *Ringing and Migration* 5: 40–48.

Cramp, S. 1985. *Handbook of the Birds of Europe, the Middle East, and North Africa: The Birds of the Western Palearctic*. *Vol. 4: Terns to Woodpeckers*. Oxford University Press, Oxford.

Cullen, J. M. 1956. A study of the behavior of the arctic tern (*Sterna macrura*). Ph.D. dissertation. University of Oxford, U.K.

Cullen, J. M. 1957. Plumage, age and mortality in the arctic tern. *Bird Study* 4: 197–207.

Debout, C. & Debout, G. 1989. Nidification d'un couple mixte *Sterne pierregarin* x *Sterne arctique*. *Cormorán* 6: 217.

Degland, C. D. & Gerbe, Z. 1867. *Ornithologie europeenne, ou, Catalogue descriptif, analytique et raisonne des oiseaux observes en Europe*. *2nd edn. Vol. 2.* J.B. Bailliere et Fils, Paris.

Egevang, C., Stenhouse, I. J., Phillips, R. A., Petersen, A., Fox, J. W. & Silk, J. R. D. 2010. Tracking of Arctic terns *Sterna paradisaea* reveals longest animal migration. *Proceedings of the National Academy of Sciences USA* 107: 2078–2081.

Ewins, P. J. 1987. Probable breeding of roseate and arctic terns. *Scottish Birds* 14: 215–216.

Ficken, M. S. & Ficken, R.W. 1968. Reproductive isolating mechanisms in the blue-winged warbler-golden-winged warbler complex. *Evolution* 22: 166–179.

Fridolfsson, A. K. & Ellegren, H. 1999. A simple and universal method for molecular sexing of non-ratite birds. *Journal of Avian Biology* 30: 116–121.

Friesen, V. L., Congdon, B. C., Walsh, H. E. & Birt, T. P. 1997. Intron variation in marbled murrelets detected using analyses of single-stranded conformational polymorphisms. *Molecular Ecology* 6: 1047–1058.

Given, A. D., Mills, A. & Baker, A. J. 2002. Isolation of polymorphic microsatellite loci from the red-billed gull (*Larus novaehollandiae scopulinus*) and amplification in related species. *Molecular Ecology Notes* 2: 416–418.

González-Solís, J., Becker, P. H. & Wendeln, H. 1999. Divorce and asynchronous arrival in common terns, *Sterna hirundo*. *Animal Behaviour* 58: 1123–1129.

Grant, P. J. & Scott, R. E. 1969. Field identification of juvenile common, arctic and roseate terns. *British Birds* 62: 297–299.

Grant, P. R. & Grant, B. R. 1997. Hybridization, sexual imprinting, and mate choice. *American Naturalist* 149: 1–28.

Gulf of Maine Seabird Working Group. 2013. 2013 Gulf of Maine Seabird Working Group Census Results (http://gomswg.org/pdf_files/GOMSWG%20Census%20Data%202013.pdf). Accessed 19 February 2016.

Haldane, J. B. S. 1922. Sex ratio and unisexual sterility in hybrid animals. *Journal of Genetics* 12: 100–109.

Harris, M. P., Morley, C. & Green, G. H. 1978. Hybridization of Herring and Lesser Black-backed Gulls in Britain. *Bird Study* 25: 161–166.

Hatch, J. J. 2002. Arctic Tern (*Sterna paradisaea*). In: Poole, A. & Gill, F. (eds.), *The Birds of North America, No. 707*. The Birds of North America, Inc., Philadelphia, PA.

Hays, H. 1975. Probable common x roseate tern hybrids. *Auk* 92: 219–234.

Hensz, C. M. 2015. Environmental factors in migratory route decisions: a case study on Greenlandic Arctic Terns (*Sterna paradisaea*). *Animal Migration* 2: 76–85.

Higgins, P. J. & Davies, S. J. J. F. (eds.) 1996. *Handbook of Australian, New Zealand and Antarctic Birds*. *Volume 3: Snipe to Pigeons*. Oxford University Press, Melbourne.

Hubbs, C. L. 1955. Hybridization between fish species in nature. *Systematic Zoology* 4: 1–20.

Hume, R. A. 1993. Common, arctic and roseate terns: an identification review. *British Birds* 86: 210–217.

Hunt, G. L. & Hunt, M. W. 1977. Female-female pairing in western gulls (*Larus occidentalis*) in southern California. *Science* 196: 1466–1467.

Johansen-Morris, A. D. & Latta, R. G. 2006. Fitness consequences of hybridization between ecotypes of *Avena barba*: hybrid breakdown, hybrid vigor, and transgressive segregation. *Evolution* 60: 1585–1595.

Kozak, G. M., Reisland, M. & Boughmann, J. W. 2009. Sex differences in mate recognition and conspecific preference in species with mutual mate choice. *Evolution* 63: 353–365.

Kullenberg, B. 1946. Über verbreitung und wanderungen von vier Sterna-Arten. *Arkiv för Zoologi* 38: 1–80.

Lanyon, W. E. 1979. Hybrid sterility in meadowlarks. *Nature* 279: 557–558.

McCarthy, E. M. 2006. *Handbook of avian hybrids of the world*. Oxford University Press, New York.

McNicholl, M. K., Lowther P. E. & Hall, J. A. 2001. Forster's Tern (*Sterna forsteri*). In: Rodewald, P. G. (ed.), *The Birds of North America*. Cornell Lab of Ornithology, Ithaca.

Nisbet, I. C. T. 2002a. Common Tern (*Sterna hirundo*). In: Poole, A. & Gill, F. (eds.), *The Birds of North America, No. 618*. The Birds of North America, Inc., Philadelphia, PA.

Nisbet, I. C. T. 2002b. Hybrid terns cryptically similar to Forster's terns nesting in Massachusetts. *Bird Observer* 30: 161–171.

Nisbet, I. C. T., Bridge, E. S., Szczys, P. & Heidinger, B. J. 2007. Sexual dimorphism, female-female pairs, and test for assortative mating in common terns. *Waterbirds* 30: 169–179.

Nisbet, I. C.T. & Drury, W. H. 1972. Measuring breeding success in Common and Roseate Terns. *Bird-Banding* 43: 97–106.

Nisbet, I. C. T. & Hatch, J. J. 1999. Consequences of a female-biased sex-ratio in a socially monogamous bird: female-female pairs in the roseate tern *Sterna dougallii*. *Ibis* 141: 307–320.

Nisbet, I. C. T., Gochfeld, M. & Burger, J. 2014. Roseate Tern (*Sterna dougallii*). In: Poole, A. (ed.), *The Birds of North America Online*. Cornell Lab of Ornithology, Ithaca. http://bna.birds.cornell.edu/bna/species/370.

Nisbet, I. C. T. & Mostello, C. S. 2015. Winter quarters and migration routes of common and roseate terns revealed by tracking with geolocators. *Bird Observer* 43: 222–231.

Nisbet, I. C. T., Mostello, C. S., Veit, R. R., Fox, J. & Afanasyev, V. 2011. Migrations and winter quarters of five common terns tracked using geolocators. *Waterbirds* 34: 32–39.

Nisbet, I. C. T., Winchell, J. M. & Heise, A. E. 1984. Influence of age on the breeding biology of Common Terns. *Colonial Waterbirds* 7: 117–126.

Olsen, K. M. & Larsson, H. 1995. *Terns of Europe and North America*. Princeton University Press, New Jersey.

Panov, E. N. 1989. *Natural hybridisation and ethological isolation in birds*. Nauka, Moscow.

Pierotti, R. 1987. Isolating mechanisms in seabirds. *Evolution* 41: 559–570.

Rahn, H., Paganelli, C. V., Nisbet, I. C. T. & Whittow, G. C. 1976. Regulation of incubation water loss in eggs of seven species of terns. *Physiological Zoology* 49: 245–259.

Randler, C. 2002. Avian hybridization, mixed pairing and female choice. *Animal Behaviour* 63: 103–119.

Randler, C. 2004. Frequency of bird hybrids: does detectability make all the difference? *Journal of Ornithology* 145: 123–128.

Real, L. 1990. Search theory and mate choice. I. Models of single-sex discrimination. *American Naturalist* 136: 376–405.

Rhymer, J. M. & Simberloff, D. 1996. Extinction by hybridization and introgression. *Annual Review of Ecology and Systematics* 27: 83–109.

Richardson, R. A. 1953. A distinction in flight between arctic and common terns. *British Birds* 46: 411–412.

Roberson, D., Bailey, S. F. & Singer, D. S. 1997. The nesting season: middle Pacific coast region. *National Audubon Society Field Notes* 51: 1048–1051.

Roberson, D., Bailey, S. F. & Singer, D. S. 1998. The nesting season: middle Pacific coast region. *National Audubon Society Field Notes* 52: 498–502.

Roberson, D., Rottenborn, S. C., Terrill, S. B. & Singer, D. S. 1999. Middle Pacific coast region. *North American Birds* 53: 428–431.

Short, L. L. 1969. Taxonomic aspects of avian hybridization. *Auk* 86: 84–105.

Shull, G. H. 1914. Duplicate genes for capsule-form in *Bursa bursa-pastoris*. *Molecular and General Genetics* 12: 97–149.

Suchetet, A. 1896. *Des hybridies a l'etat sauvage*. *Regne Animal*, *vol. 1, Classe des oiseaux*. Lille, Paris.

Szczys, P., Hughes, C. R. & Kesseli, R. V. 2005. Novel microsatellite markers used to determine the population genetic structure of the endangered Roseate Tern, *Sterna dougallii*, in Northwest Atlantic and Western Australia. *Conservation Genetics* 6: 461–466.

Terrill, S. B., Singer, D. S., Glover, S. A. & Roberson, D. 2000. Middle Pacific coast region. *North American Birds* 54: 322–325.

Tims, J., Nisbet, I. C. T., Friar, M. S., Mostello, C. & Hatch, J. J. 2004. Characteristics and performance of common terns in old and newly-established colonies. *Waterbirds* 27: 321–332.

Tirard, C., Helfenstein, F. & Danchin, E. 2002. Polymorphic microsatellites in the black-legged kittiwake *Rissa tridactyla*. *Molecular Ecology Notes* 2: 431–433.

U.S. Fish & Wildlife Service. 2015. The Feather Atlas. (**https://www.fws.gov/lab/featheratlas/**). Updated 28 October 2015. Accessed 31 July 2016.

Veen, T., Borge, T., Griffith, S. C., Saetre, G., Bures, S., Gustafsson, L. & Sheldon, B. C. 2001. Hybridization and adaptive mate choice in flycatchers. *Nature* 411: 45–50.

Veit, R. R. & Petersen, W. R. 1993. *Birds of Massachusetts*. Massachusetts Audubon Society, Lincoln, MA.

Whittham, R. M. 1998. Interbreeding of roseate and arctic terns. *Wilson Bulletin* 110: 65–70.

Yee, D. G., Fix, D. & Bailey, S. F. 1994. Middle Pacific coast region. *National Audubon Society Field Notes* 48: 984–987.

Yee, D. G., Bailey, S. F. & Singer, D. S. 1995. Middle Pacific coast region. *National Audubon Society Field Notes* 49: 975–979.

APPENDIX 1. Appearance of F1 and B1 hybrid young

Photographs of young appear in Figures 4–6.

Downy young: Downy F1 hybrid chicks were buff (9/12 chicks), grey (2/12), or intermediate (1/12), with blackish spots. B1 hybrid chicks were buff with blackish spots (3/3); one of them had a striking yellowish hue, atypical of either Arctic or Common Terns. Most F1 hybrids (10/11) had a brownish or blackish wash (slightly darker than the background colour of the down on the dorsal surface) in a narrow band on the forehead at the base of the upper mandible, extending through the lores; 1/11 hybrids lacked this forehead band, and 3/3 backcross young had this band. Throat was brownish-black on hybrids (12/12) and backcross young (3/3). Bills of F1 hybrids were pink (8/11) or orangey-pink (3/11) with a black tip, and B1 hybrids, pink with a black tip (3/3). Legs and feet of F1 hybrids were pink (5/8) or orangey (3/8), and B1 hybrids, pink (3/3).

Feathered young: Upper halves of the bills of F1 hybrids (9/9) and B1 hybrids (3/3) were greyish or blackish with pink or orange undertones and had pink or orangey margins along the cutting edge and greyish or blackish tips. Lower halves of the bills of F1 hybrids (9/9) and B1 hybrids (3/3) were pink or orangey with greyish or blackish tips. Feet and legs were pink (3/8), greyish-pink (2/8), or orangey (3/8) for F1 hybrids and pink for B1 hybrids (3/3).

The head remained substantially downy on most near-fledglings, but enough feathers were usually visible for assessment of colour. On F1 hybrids, the forehead near the base of the bill was pale to light buff (7/7). Cap (crown, nape, ear-coverts, and around eye) was grey-black (5/8) or brownish-black (3/8) and forecrown was streaked with white or pale buff on a few individuals for which it was visible. Dark feathers extended below the eye for 9/9 individuals, giving the appearance of a mask. On 3/3 B1 hybrids, forehead was pale buff, cap was brownish-black, and forecrown was streaked with pale-buff. One (1/3) had dark feathers extending below the eye.

The carpal bar of F1 hybrids was medium to dark grey (6/8) or grey-brown (2/8) and lighter than the cap (8/8), but to varying degrees. The carpal bar of B1 hybrids was medium to dark grey-brown (3/3), approximately as dark as the cap. Although we lack detailed data for each primary, outer primaries were dark grey, becoming lighter proximally; all but the outermost 1–3 primaries had white edges, successively widening proximally. In all individuals for which the information could be determined (6/6), the secondaries, broadly edged in white, were a darker grey than the median and greater wing-coverts.

Mantle feathers of the F1 hybrids had grey centres, dark subterminal crescents, and light tips. Centres were cold, neutral grey (2/9) or grey with a faintly brownish wash (7/9). Subterminal crescents were dark grey-brown (7/9) or brown (2/9). Tips were pale (4/9), light (2/9), or medium (3/9) buff. B1 hybrids had a distinctly warmer, browner look than did the F1 hybrids due to a stronger brown wash to greyish feather centres (3/3). Subterminal crescents were dark grey-brown (3/3) and tips were light (1/3) to medium (2/3) buff. Dark subterminal markings and light tips extended from the upper back, scapulars, and tertials onto the proximal upperwing-coverts on F1 hybrids (8/8) and B1 hybrids (3/3), with subterminal markings disappearing, but light tips remaining, on the distal portion of the inner wing.

F1 hybrids had white rumps and uppertail-coverts (8/8); 2/8 had faint dusky tips on the coverts. Rumps of B1 hybrids were pale grey in the centre and uppertail-coverts were white (3/3); 2/3 had faint dusky tips on the coverts. Although we lack detailed data on each retrix, for both F1 hybrids and B1 hybrids, outer retrices were darker than inner retrices and outer webs darker than inner webs: the outer web of the outermost retrix was dark grey/blackish and inner webs of inner retrices were palest grey, slightly darker than the white uppertail-coverts. All visible retrices of F1 hybrids and B1 hybrids had buff tips. Pale retrices had dark subterminal markings on 2/9 F1 hybrids and 2/3 B1 hybrids.

Measurements of hybrids and Common Tern chicks appear in Figure 7. Head length, exposed culmen length and weights of F1 hybrid chicks on days 19–20 fell within the ranges of values for Common Terns of the same ages. Data suggested a tendency towards longer wings for F1 hybrids compared to Common Terns, with 3/3 hybrid wing chord measurements greater than the mean for Common Terns (one of these was above the range for Commons in that year). F1 hybrids had shorter tarsi than Common Terns. Tarsus lengths of 2/3 F1 hybrid chicks were shorter than those for all Common Terns in that year (2009) by 1.6–2.1 mm (and were 4–5 standard deviations below the mean); the length of the third F1 hybrid's tarsus was equal to that of the shortest Common Tern tarsus measured in that year (2014). For the two B1 hybrids measured, head, exposed culmen, weight, wing chord, and tarsus measurements all fell within the ranges of values for Common Terns, with tarsus lengths shorter, and wing chord lengths greater, than the mean values for Common Terns.