HYBRIDIZATION IN TERNS: A REVIEW

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ABSTRACT

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Hybridization—the interbreeding of different species—is a relatively common phenomenon in birds, but its study is biased towards certain taxa. In this review, we focus on a bird group that has received less attention: terns (Laridae, Sterninae). Based on an extensive literature search, we found records for 16 hybrids between tern species, with varying levels of supporting evidence: ten cases had strong support, one had medium support, one had low support, and four cases were deemed unreliable (two were refuted and two could not be evaluated). The strongly supported hybrid records involved 14 different tern species (out of 41 species, 34%). The underlying mechanisms of tern hybridization remain to be studied in more detail. The most likely processes that can result in the breakdown of reproductive isolation are (1) a scarcity of conspecifics, (2) interspecific extra-pair copulations, and (3) mis-imprinting after brood parasitism. Based on the available evidence, a scarcity of conspecifics appears to be the mechanism that most frequently results in the formation of mixed pairs and the production of hybrid offspring in terns. Our literature search revealed that population-level genetic analyses of tern hybridization are currently lacking. Given the occurrence of multispecies hybridization, it is possible that some tern species act as "genetic bridges" within a network of tern hybrids. All in all, the interbreeding of tern species provides exciting opportunities for further research that may generate novel insights into avian hybridization and speciation.

Key words: Hubbs' principle, hybrid network, introgression, mixed pairs, population genetics, reproductive isolation, Sterninae

INTRODUCTION

Hybridization—the interbreeding of different species—is a relatively common phenomenon in birds, with an estimated 15%–20% of hybridizing species (Ottenburghs, 2023). However, the study of avian hybridization is biased towards certain bird groups. Within the family Laridae (gulls, terns and skimmers), for example, most research efforts have focused on hybridization between several gull species in the subfamily Larinae (Bell, 1996; Gay et al., 2007; Given et al., 2023; Neubauer et al., 2014; Sonsthagen et al., 2016; Sternkopf et al., 2010). Other subfamilies within the Laridae remain to be studied in more detail. In this paper, we focus on the subfamily Sterninae because no hybrids have been reported in the White Terns (subfamily Gyginae) or Skimmers (subfamily Rynchopinae), and suggestions of hybridization among Noddies (subfamily Anouninae) are unreliable (Bourne, 1997; McCarthy, 2006; Stokes & Hinchey, 1990). We provide an overview of tern hybrids, followed by an exploration of potential mechanisms for hybridization and the genetic consequences of hybridizing terns. This review acts as a primer for further research into tern hybridization, possibly providing more general insights into avian hybridization and speciation.

AN OVERVIEW OF TERN HYBRIDS

We used three main sources as a starting point to collect records of hybrid terns: the *Handbook of Avian Hybrids of the World* (McCarthy, 2006), the online *Serge Dumont Bird Hybrids Database* (Dumont, 2003), and species descriptions on the *Birds of the World* website (Billerman et al., 2022). For each hybrid record, we tracked down the original reference to assess its reliability. Each reference was subsequently checked for additional hybrid records using a snowballing method. We distinguished between primary hybridization (i.e., pairing between two parental species, PP) and secondary hybridization (i.e., pairings between two hybrids, HH; or backcrossing between a hybrid and a parental species, HP). Moreover, we discriminated between direct observations of interbreeding and sightings of putative hybrid individuals. Based on the strength of the available evidence, the hybrid records were classified as "Strong," "Medium," "Low," "Not Evaluated," or "Refuted" (see Table 1). We follow the taxonomic classification of the International Ornithological Congress (IOC) World Bird List (Gill et al., 2024), which recognizes 41 tern species (excluding the genera *Anous*, *Gygis*, and *Rynchops*).

Overall, we found 16 pairs of tern species that have been reported to have hybridized: ten cases with strong evidence, one with medium evidence, one with low evidence, and four that were unreliable (two refuted and two not evaluated; Table 1). The hybrid combinations with strong evidence involved 14 different tern species (out of 41 species, 34%). No hybrids have been documented in the genera *Hydroprogne*, *Onychoprion*, *Phaetusa*, and *Larosterna*. In the following sections, we discuss the supporting evidence for the reported hybrids per genus.

Genus *Chlidonias*

Two hybrid combinations have been reported in this genus. Mixed pairs (PP) between White-winged Tern *Chlidonias leucopterus* and Black Tern *C. niger* have been reported in Sweden (Alexandersson, 1979), the Netherlands (Van IJzendoorn, 1980), and the USA (Heath et al., 2020). There have been several sightings of putative

TABLE 1
List of tern species pairs reported to have hybridized, with the major supporting references for each species pair[a]

Species 1	Species 2	Strength of evidence[b]	Divergence time (million years ago)	References
Chlidonias leucopterus	*Chlidonias niger*	Strong	2	Alexandersson, 1979; Heath et al., 2020; Van IJzendoorn, 1980
Chlidonias hybrida	*Chlidonias leucopterus*	NE	4	Mel'nikov, 1985
Sterna dougallii	*Sterna hirundo*	Strong	4	Cabot & Nisbet, 2013; Robbins, 1974; Zingo et al., 1994
Sterna dougallii	*Sterna paradisaea*	Strong	3.5	Whittam, 1998
Sterna forsteri	*Sterna paradisaea*	Strong	-	Roberson et al., 1999
Sterna forsteri	*Sterna hirundo*	Low	-	Berry, 2000
Sterna dougallii	*Sterna sumatrana*	Medium	2	Lashko, 2004
Sterna hirundo	*Sterna paradisaea*	Strong	4	Mostello et al., 2016
Sternula albifrons	*Sternula nereis*	Strong	1.5	Cox & Close, 1977; Ross et al., 1999
Sternula albifrons	*Sternula antillarum*	Refuted	2.5	Pyle et al., 2001
Thalasseus bergii	*Thalasseus bernsteini*	Strong	0.75	Yang et al., 2018
Thalasseus bengalensis	*Thalasseus sandvicensis*	Strong	2.5	Cabot & Nisbet, 2023; Dies & Dies, 1998
Thalasseus elegans	*Thalasseus sandvicensis*	Strong	3.6	Dufour et al., 2021
Thalasseus elegans	*Thalasseus acuflavidus*	Strong	3.6	Collins, 1997; Paul et al., 2003; Velarde & Rojo, 2012
Gelochelidon nilotica	*Sterna forsteri*	Refuted	-	Veit & Petersen, 1993
Sternula albifrons	*Sterna hirundo*	NE	-	Mel'nikov, 1985; Mlíkovský, 2009; Ochagov, 1982

[a] Detailed explanation of the supporting evidence can be found in the text. Most divergence times are based on the phylogenetic analysis of Bridge et al., (2005), except for *Thalasseus bergii* × *T. bernsteini* (Yang et al., 2018) and the two hybrids involving *T. elegans* (Efe et al., 2009).
[b] NE = not evaluated

hybrids, describing individuals with characteristics of both species (Campbell, 2011; Corbeau et al., 2021; Davis, 1982; Vinicombe, 1980). Taken together, there is thus strong evidence for hybridization between White-winged Tern and Black Tern.

Mel'nikov (1985) mentioned a hybrid between Whiskered Tern *C. hybrida* and White-winged Tern in a Russian paper, but we could not evaluate its reliability.

Genus *Sterna*

Most tern hybrids occur in this genus. Mixed pairings (PP) between Roseate Tern *Sterna dougallii* × Common Tern *S. hirundo* have been extensively described by Zingo et al. (1994). Between 1984 and 1993, they recorded several instances of interbreeding in a mixed colony at Falkner Island, Connecticut, USA, and in 1993, they followed one mixed pair from courtship to fledging of chicks. Similar observations of mixed pairings (PP) in the USA and UK have been published by Robbins (1974) and Cabot & Nisbet (2013). The resulting hybrids are viable and often survive to breed, mating with either of the parental species (HP – Cabot & Nisbet, 2013; Courtens et al., 2008; Nisbet, 2002) and usually raising young that return to mate with one of the parental species (Arnold et al., 2020). Interestingly, there are also three observations of pairing between Common x Roseate tern hybrids (HH – Cabot & Nisbet, 2013; Hays, 1975); these three pairs were found breeding at four different sites (Arnold et al., 2020). It is remarkable that these hybrids paired with each other despite the presence of numerous potential mates from both parental species. Apart from these observations of mixed pairings (PP, HP, and HH), there are numerous reports of putative hybrids and backcrosses (Arnold et al., 2020; Gochfeld & Burger, 2020; Mullarney, 1988; Nisbet, 2002). Hence, there is strong evidence for hybridization between Common Tern and Roseate Tern.

With regard to hybridization between Roseate Tern and Arctic Tern *S. paradisaea*, two studies documented mixed pairings (PP). Whittam (1998) followed courtship, copulation, incubation, and chick-feeding behavior of a mixed pair in Canada, providing strong evidence for hybridization. Ewins (1987) reported individuals of both species incubating the same egg.

Roberson et al. (1999) provided photographic evidence of interbreeding between Arctic Tern and Forster's Tern *S. forsteri* in California, USA. The Arctic Tern frequented the Forster's Tern colony for seven years, pairing with a Forster's Tern in the sixth and seventh years (1999–2000) and raising one chick in 1999, which was banded and returned in the following year (Terrill et al., 2000). This provides strong support for hybridization between these two species.

Berry (2000) described observations of a courtship flight between a Forster's Tern and a Common Tern in the USA, as well as a Forster's Tern defending a nest of three eggs. However, there is no definitive proof of hybridization (i.e., low support).

Two tern hybrids in this genus have been investigated with genetic analyses. Lashko (2004) found mitochondrial haplotypes of the *ND2* gene from both Roseate Tern and Black-naped Tern *S. sumatrana* in one individual. However, this finding requires paternal leakage of mitochondrial DNA, and morphological hybrids between these species have not been documented (Gochfeld & Burger, 2020). Hence, we considered this hybrid to have medium support; more research is needed to confirm hybridization between Roseate Tern and Black-naped Tern.[1] Finally, Mostello et al. (2016) provided convincing molecular evidence for hybridization between Common Tern and Arctic Tern, as well as detailed observations of the breeding pair over multiple years (see also Arnold et al., 2020).

Genus *Sternula*

One of the first documented reports of hybridization between Little Tern *Sternula albifrons* and Fairy Tern *St. nereis* occurred at the Price Saltfields, on the northwestern shore of Gulf St. Vincent, Australia. Cox & Close (1977) made careful observations of the behavior and morphology of birds at two nests: one housed a mixed pair (PP), whereas the other pair consisted of a Little Tern and an apparent hybrid (HP). During the summer of 1996/97, a mixed pair (PP) of a female Little Tern and a male Fairy Tern nested on Towra Spit Island, Botany Bay, Australia (Ross et al., 1999). Several other putative hybrids have been reported by Gochfeld et al. (2020). Hence, there is strong evidence for hybridization between Little Tern and Fairy Tern.

We also came across a report of hybridization between Little Tern and Least Tern *St. antillarum*. The *Handbook of Avian Hybrids of the World* and the *Serge Dumont Bird Hybrids* database refer to Pyle et al. (2001), but that paper reported only assortative mating of both species at the same location (Midway Atoll). The Least Tern is a vagrant at that location, while the Little Tern appears to be colonizing from Asia. In addition, the *Handbook of Avian Hybrids of the World* cites Boyd & Thompson (1985), but that study described hybridization between two subspecies of the Least Tern (*St. a. antillarum* and *St. a. athalassos*). Hence, there is no convincing evidence for hybridization between these two species. This case highlights the importance of assessing the original sources.

Genus *Thalasseus*

Observations at mixed colonies suggested hybridization between Greater Crested Tern *Thalasseus bergii* and Chinese Crested Tern *T. bernsteini* (Chen & He, 2011). Hybridization was confirmed with genetic analyses (Yang et al., 2018).

Sandwich Tern *T. sandvicensis* has been reported to interbreed with Lesser Crested Tern *T. bengalensis* in Spain (Dies & Dies, 1998). In the UK, Cabot & Nisbet (2013) provided detailed descriptions of a mixed pair (PP) and a pair consisting of the hybrid offspring of the PP pair and a Sandwich Tern (HP). Several putative hybrids have also been reported on migration (Dies & Dies, 1998; Steele & McGuigan, 1989; Verroken, 1990). Hence, there is strong evidence for hybridization between Sandwich Tern and Lesser Crested Tern. In Europe, several mixed pairs (PP and HP) of Sandwich Tern and Elegant Tern *T. elegans* have been reported (summarized in Dufour et al., 2021; see also Shealer et al., 2020), providing strong evidence for hybridization.

Mixed pairs (PP) between Elegant Tern and Cabot's Tern *T. acuflavidus* have been documented in several breeding colonies in North America (Collins, 1997; Paul et al., 2003; Velarde & Rojo, 2012; see also Pranty et al., 2022, for observations of putative hybrids), providing strong evidence for hybridization. Here, it is important to note that the taxonomic treatment of Cabot's Tern differs between authorities: the American Ornithological Society classifies Cabot's Tern as a subspecies of Sandwich Tern whereas version 14.2 of the IOC World Bird List treats these terns as separate species (following Efe et al., 2009). We have followed the latter classification in this paper.

Intergeneric tern hybrids

Our literature search uncovered two reports of alleged intergeneric tern hybrids. In *The Birds of Cape Cod, Massachusetts*, Hill (1965) mentioned a hybrid between Gull-billed Tern *Gelochelidon nilotica* and Forster's Tern. However, this unlikely combination was refuted by Veit & Petersen (1993):

> "A re-examination of a specimen alleged to be a Gull-billed × Forster's tern hybrid (MCZ # 271643) collected at Nauset, Eastham, 6 September 1941 (Griscom, see Hill 1965) proved to be a juvenile Forster's Tern, based on both plumage characteristics and measurements (Veit)."

We have examined photographs of the specimen and concur with its re-identification as a juvenile Forster's Tern.

In an overview of waterbirds at Lake Baikal, Russia, Mlíkovský (2009) reported a possible hybrid and a mixed pair between Little Tern and Common Tern. The accompanying references guided us to a Russian paper by Mel'nikov (1985), which also included another report of this hybrid combination (Ochagov, 1982). However, neither case could be verified.

BREAKDOWN OF ISOLATION MECHANISMS

Several behavioral mechanisms have been proposed to explain the occurrence of avian hybridization (Leighton et al., 2021; Randler, 2006). With regard to tern hybrids, we focus on three potential processes that can lead to the breakdown of reproductive isolation: (1) a scarcity of conspecifics or of conspecifics of the opposite sex, (2) interspecific extra-pair copulations, and (3) mis-imprinting after brood parasitism.

First, a scarcity of conspecifics can lead to hybridization (Baker, 1996; McCracken et al., 2013), a phenomenon also known as Hubbs' Principle or the Desperation Hypothesis (Hubbs, 1955). Individual birds might be faced with this situation during a range

[1] Note added in proof: Fordham et al. (2024) reported hybridization between Roseate Tern and Black-naped Tern at St. François Atoll, Seychelles. One or more interbreeding pairs were seen in several years; one or more birds identified as hybrids were seen interbreeding with Roseate Terns in multiple years and raised several backcrossed young. This upgrades the evidence for hybridization between these two species from medium to strong and increases the number of hybrid combinations with strong evidence to 11, involving 15 different tern species.

expansion or contraction, when blown off course, or after making navigational errors during migration. A scarcity of conspecifics explains most of the hybridization events cited in the previous section. For example, the northward expansion of Fairy Terns into New South Wales, Australia, probably brought this species into contact with the previously allopatric Little Tern (Ross et al., 1999). Mostello et al. *(*2016) reported that the Arctic Tern that interbred with a Common Tern in Massachusetts, USA, was the only remaining individual of its species at that site after a long-term decline at the southern limit of the species' range. Hybridization events between Black Tern and White-winged Tern in Europe have been attributed to the westward expansion of the latter species (Corbeau et al., 2021). In several other PP combinations referred to above, one of the species was a single individual far outside the normal range of its species (e.g., White-winged Terns in the USA; Roseate Tern in Shetland, Scotland; Arctic Tern in California; Lesser Crested Tern in the UK and Spain; Elegant Tern in Florida, USA, and at several locations in Europe).

Scarcity of potential conspecific partners could also be related to a lack of potential male partners. Individual females often form same-sex couples (e.g., Roseate Terns; Nisbet & Hatch, 1999) or they might settle for a heterospecific mate (Grant & Grant, 1997). A biased sex ratio has been proposed to explain hybridization between Common Tern and Roseate Tern (Whittam, 1998) at a site on the edge of the Roseate Tern's range where few Roseate Terns were present. In the USA, where there is a female-biased sex ratio in Roseate Tern populations (Nisbet & Hatch, 1999), all fully documented cases of hybridization (PP) with Common Terns have involved male Common Terns and female Roseate Terns (Cabot & Nisbet, 2013; Zingo et al., 1994; I.C.T. Nisbet, unpublished data). At sites where there are only small numbers of one species, stochastic variations in the sex ratio are likely to leave some individuals without conspecific mates of the opposite sex in some years; this might explain why individuals of the critically endangered Chinese Crested Tern sometimes interbreed with the much more numerous Greater Crested Tern (Chen & He, 2011). However, it is very difficult to measure sex ratios in large seabird colonies without extensive sampling and careful sampling designs to eliminate biases: the Roseate Tern × Common Tern combination is the only case for which lack of conspecific mates has been shown to be a likely cause of hybridization.

Although the evidence cited above shows a strong relationship between hybridization and the lack of conspecifics of the opposite sex for one of the hybridizing species, this addresses only one half of the problem. Why should the other member of the pair accept a heterospecific mate when there are abundant birds of its own species available as mates, presumably including plenty of individuals of the opposite sex? In a few cases where interbreeding pairs have been studied in detail (e.g., Mostello et al., 2016; Whittam, 1998; Zingo et al., 1994), the behavior of the second bird appears to have been normal for its species and different from that "expected" by its mate. We suggest that this issue (i.e., behavior of the mate and reasons for its unusual mate choice) is important to address in future studies of hybridization between tern species.

Second, hybridization can be the outcome of extra-pair copulations between different species. Copulations outside the social bond have been documented in numerous bird groups (Valcu et al., 2021). Extra-pair copulations have been reported in a few tern species, such as Common Tern (González-Solís et al., 2001), Little Tern (Toba, 1989), Fairy Tern (Greenwell et al., 2020), and Whiskered Tern (Ledwoń & Szczys, 2022). However, extra-pair mounting can occur without cloacal contact and can be misinterpreted as a copulation (Cabot & Nisbet, 2013). Genetic analyses are thus required to confidently identify extra-pair offspring (e.g., Shealer et al., 2014). Given that intraspecific extra-pair copulations are already quite rare among terns, it is very unlikely that interspecific extra-pair copulations lead to the production of hybrid offspring in terns.

Third, brood parasitism can lead to hybridization. Brood parasitism can occur at the egg stage (i.e., birds laying eggs in other nests; Yom-Tov, 1980) or at the chick stage (i.e., "adoption"; Saino et al., 1994). Intraspecific brood parasitism at the egg stage occurs in several bird species (Payne, 1998; Petrie & Møller, 1991; Yom-Tov, 1980). In terns, this behavior has been observed in the Whiskered Tern (Minias et al., 2014; Paillisson et al., 2008). Intraspecific brood parasitism at the chick stage is fairly frequent in Common Terns, but interspecific brood parasitism has not been reported (Arnold et al., 2020). In waterfowl, it has been shown that interspecific brood parasitism can result in hybridization, as being raised by a foster parent from a different species could result in sexual imprinting on that species, leading to subsequent interspecific mate selection (Ottenburghs et al., 2016). Whether this mechanism also explains cases of hybridization in terns remains to be investigated. However, the low occurrence of intra- and interspecific brood parasitism suggests that this mechanism is less relevant in this group of birds.

The available evidence indicates that a rarity of conspecifics, especially those of the opposite sex, plays the most important role in tern hybridization. Extra-pair copulations and interspecific brood parasitism seem to be unlikely mechanisms to explain the occurrence of hybrid terns. However, detailed observations should be collected to quantify the frequency of these behaviors, potentially in combination with genetic methods to determine the exact parentage of broods.

TERN HYBRIDS AS GENETIC BRIDGES

Our literature review of tern hybridization uncovered few genetic studies. Although some studies applied genetic techniques to identify putative hybrid individuals (Lashko, 2004; Mostello et al., 2016; Yang et al., 2018), no studies performed extensive population-level genetic analyses. Given the widespread occurrence of introgression (i.e., interspecific gene flow) in birds, and given the observations that many hybrid terns form backcross pairs (HP) with parental species and that these backcross pairs themselves produce fertile offspring (see above), we would expect some genetic exchange between several hybridizing tern species (Ottenburghs et al., 2017). Indeed, most hybridizing tern species diverged recently—between 0.75 and 4.00 million years ago (Table 1)—and are thus within the time window of introgression (Pulido-Santacruz et al., 2020). Nonetheless, this knowledge gap remains to be addressed, potentially using genomic analyses (Hibbins & Hahn, 2022; Taylor & Larson, 2019).

A closer look at hybridization patterns among terns reveals an interesting possibility of some species acting as "genetic bridges." A hybrid network of tern species shows several species that interbreed with multiple other species, such as Common Tern, Arctic Tern, Elegant Tern, and Sandwich Tern (Fig. 1). These so-called "hub species" can act as bridges between other tern species in the hybrid network, funneling genetic variation from one species to

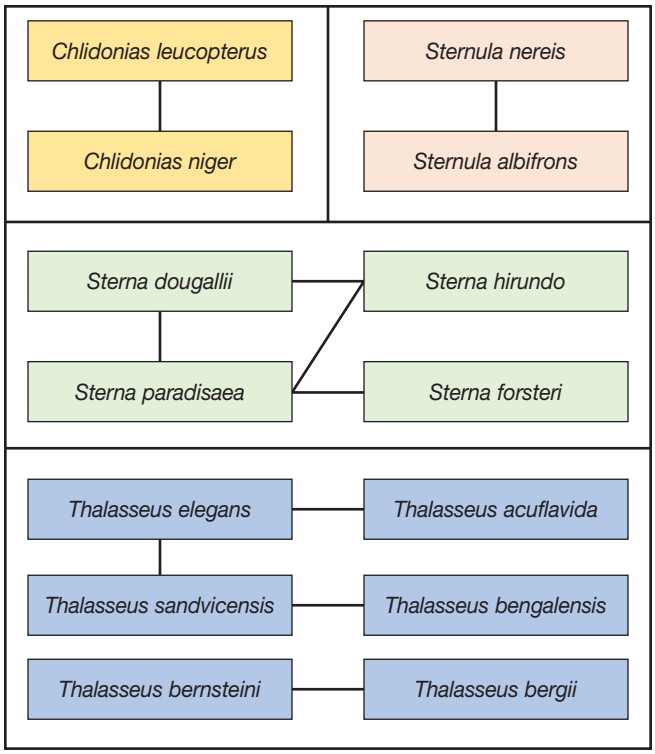

Fig. 1. Hybrid network of tern species, including only hybrid records with strong supporting evidence. The colors represent different genera, and the lines between the boxes indicate hybridization (see Table 1 for details).

another through introgressive hybridization (Ottenburghs, 2019). This mechanism has been described in Darwin's finches where "*Geospiza fortis* acted as a conduit for the passage of genes between two others that have never been observed to interbreed on Daphne: *Geospiza fuliginosa*, a rare immigrant, and *Geospiza scandens*, a resident" (Grant & Grant, 2020). Whether similar dynamics occur in terns remains to be investigated.

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AUTHOR CONTRIBUTIONS

JO conceived the idea and wrote the first draft. JO and ICTN revised subsequent versions of the manuscript.

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