The role of behavior in tern conservation

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Abstract   Behavioral research has long had an important role in the conservation of terns (Aves: Sternidae). Habitat management and restoration of breeding colony sites depends on knowledge of the cues used to select colony and nest sites. For example, conspecific attraction with playback and decoys is commonly used to bring terns to suitable colony sites and habitat modification is often used to increase the availability of suitable nest sites. Tern colonies are interconnected by dispersal, and a metapopulation approach is needed for effective management. Population dynamics are therefore affected by behaviors that influence the frequency of movement among colony sites: site fidelity, natal and breeding dispersal, and group adherence. The monogamous breeding system of terns should keep effective population size similar to census population size, but variation in sex ratios (likely resulting from sex differences in behavior) and in parental quality can result in a smaller than expected effective population size. In addition to the behavior of terns, knowledge of the behavior of predators on terns contributes to management plans, because predator behavior can sometimes be manipulated and predation is often performed by only a few specialized individuals. Other examples of links between tern behavior and conservation are also briefly reviewed, such as behavioral toxicology research and studies of behavioral responses to human disturbance and manmade structures. More work is needed on the behavior of migratory terns at staging sites, stopover sites and wintering grounds, and on the behavior of less well-studied species and species in less well-studied geographic regions [*Current Zoology* 60 (4): 500–514, 2014].

Keywords   Effective population size, Habitat modification, Metapopulations, Predator control, Restoration, Sternidae

Since the mid-1990's there has been growing awareness of the importance of the link between behavior and conservation (reviewed in Caro and Eadie, 2005), but behavioral ecologists have been slow to link with conservation biologists and managers (and vice versa). Fortunately the barriers to exchange are largely imaginary and can be overcome (Caro and Sherman, 2013). Conservation and management of terns (Aves: Sternidae) has long incorporated behavior, both implicitly and explicitly. Additionally, field biologists studying terns have often been on the "front-line" of conservation efforts (Nisbet and Spendelow, 1999).

Terns are colonial waterbirds found in marine and freshwater environments around the world, and are closely related to gulls and skimmers (Gochfeld and Burger, 1996; Paton and Baker, 2006). As in most seabirds, terns have "slow" life histories: they are long-lived, lay relatively small clutches, and most individuals do not breed until three years of age or later (Gochfeld and Burger, 1996; Schreiber and Burger, 2002; Cabot and Nisbet, 2013). Clutch sizes tend to be smaller and the periods of incubation and chick rearing longer in tropical species than at higher latitudes (Morris and Chardine, 1995; Schreiber and Burger, 2002). The majority of these relatively small seabirds feed mainly on small schooling fish captured close to the surface, but the diet may also consist of crustaceans, insects, and other prey with variation among tern species and habitats. Although much research on terns has occurred in North America and Europe at the breeding colonies of long-distance migrants, terns are actually more abundant and widespread in the tropics and subtropics (Gochfeld and Burger, 1996; Cabot and Nisbet, 2013).

Threats to tern populations include habitat loss especially via coastal and wetland development, introduced predators, displacement from colony sites by gulls (although previously expanding gull populations have recently declined), variation in food availability, and perhaps predation by humans (Parnell et al., 1988; Burger and Gochfeld, 1994; Gochfeld and Burger, 1996; Becker and Sudmann, 1998; Szostek and Becker, 2012; Cabot and Nisbet, 2013; Nisbet et al., 2013). Historically, terns suffered greatly from collection of eggs for food, which does still occur in some locations (e.g. Feare and Lesperance, 2002; Chen et al., 2009), and hunting of adults for feathers. Rising sea levels and other effects of climate change are likely to be the largest future threats (Becker and Anlauf, 1988; Burger and Gochfeld, 1994;

Rounds et al., 2004; Nisbet et al., 2013). Although aggregation in colonies may cause tern populations to be particularly susceptible to the effects of localized predation and disturbance events, colonial breeding also makes it possible for management action to benefit a large number of individuals simultaneously (Parnell et al., 1988).

Globally endangered and threatened terns include the critically endangered Chinese crested tern (*Thalasseus bernsteini*, Chen et al., 2009; BirdLife International, 2010), three endangered species (black-bellied tern *Sterna acuticauda*, black-fronted tern *Chlidonias albostriatus*, Peruvian tern *Sternula lorata*), one species listed as vulnerable (fairy tern *Sternula nereis*), and five listed as near threatened (*Larosterna inca*, *Sterna aurantia*, *Sterna virgata*, *Sternula balaenarum*, *T. elegans*; BirdLife International, 2010; scientific names follow Bridge et al., 2005). Even among species with large total numbers and a wide geographic distribution, particular populations or subspecies may be endangered, such as the Bermuda population of the common tern (*Sterna hirundo*, Nisbet et al., 2010; Szczys et al., 2012), North Atlantic populations of the roseate tern (*Sterna dougallii*, Nisbet and Spendelow, 1999; Szczys et al., 2005; Ratcliffe et al., 2008), and the California and interior North American populations of the least tern *Sternula antillarum* (Draheim et al., 2010). Most species of terns are on the conservation lists of particular nations, states or provinces.

I review here four major areas in which behavioral research has contributed to tern conservation and has the potential to contribute further, and in which conservation work has similarly increased our understanding of behavior. 1) Knowledge of habitat selection cues (including conspecific attraction) applied to habitat manipulation and colony site restoration. 2) Studies of movement behavior with applications to metapopulation dynamics. 3) Effects of sex differences in behavior and individual differences in reproductive success on effective population size. 4) Knowledge of predator behavior in the development of effective and ethical management strategies. This review is not exhaustive. I have focused on conservation issues related to concepts that tend to interest behavioral ecologists: habitat selection (including social influences on habitat selection), group living, dispersal decisions, mating systems and sex roles, antipredator behavior, and individual differences in foraging strategies. I also briefly touch on other connections between tern behavior and conservation and discuss areas where information is lacking but potential benefits

to conservation are large.

1 Habitat Selection and Conspecific Attraction

Habitat management and restoration of breeding colonies depends on knowledge of the cues used to select colony and nest sites, including social cues (Reed and Dobson, 1993; Reed, 1999, 2004). It is important that restoration sites are selected carefully (Nisbet and Spendelow, 1999; Ward et al., 2011) and that the determinants of habitat quality are well understood, so terns do not fall into an ecological trap by being attracted to suboptimal habitat that causes further population declines (Battin, 2004; Reed, 2004; Sih, 2013). Selection of colony and nest sites reflect trade-offs (which vary among species) between predation risk, flooding risk, and proximity to preferred foraging sites (Burger and Lesser, 1978; Becker and Anlauf, 1988; Burger and Gochfeld, 1990, 1991; O'Connell and Beck, 2003; Rounds et al., 2004; Cruz et al., 2013). For example, low-lying islands without trees or shrubs are less likely to harbor predators but are more susceptible to flooding. Such sites are often maintained by processes that inhibit succession, such as wash over by winter storms (Nisbet, 2002). Although there are species that nest on off-shore islands far from mainland predators, most species of terns tend to nest in unpredictable, impermanent locations such as barrier beaches, sandbars, and marshes (Gochfeld and Burger, 1996; Cabot and Nisbet, 2013). Management is made more difficult by the dynamic nature of these habitats.

Conspecific attraction with decoys and playback is commonly used to bring terns and other colonial seabirds to unoccupied or recently restored colony sites (Kress, 1983, 1997, 2000; Becker, 1996; Arnold et al., 2011; Ward et al., 2011), and can be used experimentally to determine preferred social conditions (Burger, 1988). Terns may interact with decoys as during courtship and nest among the decoys (Burger, 1988; Kress, 1997). Although in some cases decoys have been used successfully without playback, auditory cues provided by playback may be more effective at encouraging terns to nest (Arnold et al., 2011). Conspecific attraction is necessary because, even after predators have been removed and formerly occupied sites made otherwise suitable again, terns usually nest colonially and are unlikely to nest at locations lacking conspecifics. Sites are also more likely to be used if they are near existing colonies (Fasola and Canova, 1992; Kress, 1997; Zarza et al., 2013) and are probably colonized more quickly if

they were occupied recently (Kress, 1997).

Many species of terns nest in association with other terns or other ground-nesting colonial waterbirds, which can result in nest site competition. Some species, like the roseate tern, nest within colonies of other more aggressive terns, and common or Arctic terns *Sterna paradiseae* must be established before roseate terns will colonize a restored island (Kress, 1983; Nisbet and Spendelow, 1999). Sandwich terns *Sterna sandvicensis* in Europe similarly benefit from the aggressive antipredator behavior of black-headed gulls *Larus ridibundus*, but at the cost of kleptoparasitism (Stienen et al., 2001).

Depending on the habitat preferences of a species, which may vary geographically, the best overall conservation strategy will differ in a manner analogous to the old SLOSS debate (single large or several small, reviewed in Primack, 1998). There is variation in whether terns and other colonial waterbirds prefer to nest in relatively small colonies on small islands (or small mainland patches), necessitating protection of a large network of small sites, or to nest in a few large colonies on large islands or mainland habitats (Burger and Gochfeld, 1991; Erwin et al., 1995; Heinänen et al., 2008; Zarza et al., 2013). Aggregation in a small number of colonies can put a species at risk if suitable breeding habitat is lost. Regardless of typical colony size, which varies enormously among species (Gochfeld and Burger, 1996; Cabot and Nisbet, 2013), it is best to have multiple protected sites so that loss of one or a few sites does not lead to loss of the population (Erwin et al., 1995; Matthiopoulos et al., 2005). If site fidelity is low (see Philopatry and Dispersal, below) it may also be important to protect currently unoccupied but suitable sites (Erwin et al., 1998). If site fidelity is high, then protecting existing sites takes on added urgency because the terns may be unlikely to colonize new locations (Burger and Lesser, 1978; Heinänen et al., 2008).

Although there is also much variation in colony size within tern species and some species are likely only facultatively colonial (Burger and Gochfeld, 1991), it is possible that a minimum group size or nest density is necessary for persistence for many species, because terns often gain antipredator benefits and perhaps reproductive benefits from group living (Gochfeld, 1980; Becker,1984; Burger and Gochfeld, 1991, 1994; Becker, 1995). It is therefore likely that most species of terns will suffer from Allee effects (negative effects of low density), and thus an increased probability of local extinction if colonies become too small and scattered (Reed and Dobson, 1993; Courchamp et al., 1999; Reed,

1999; Stephens and Sutherland, 1999). Site fidelity and conspecific attraction should help decrease the prevalence of very small colonies by maintaining local density via aggregation at a small number of sites (Reed and Dobson, 1993; Stephens and Sutherland, 1999). However, if overall metapopulation size has decreased below a minimum level, then Allee effects may be impossible to avoid and population declines will accelerate. At the other extreme, colonies that are too large may suffer density-dependent declines in productivity due to intraspecific competition for food within the foraging range of the colony (Furness and Birkhead, 1984; Tims et al., 2004; Szostek et al., 2014a).

Habitat modification is often used to improve the availability or quality of suitable nest sites, both in restored and existing colonies. There have been many observational and experimental studies of nest site selection in terns (e.g. Burger and Lesser, 1978; Becker and Anlauf, 1988; Burger and Gochfeld, 1988, 1990, 1991; Fasola and Canova, 1992; Neubauer, 1998; Guicking et al., 2001; Cook-Haley and Millenbah, 2002; Rounds et al., 2004; Colchero et al., 2010; Hu et al., 2013) that have led to improvements in management techniques, such as vegetation control, manipulation of water regimes, and the construction of nest boxes for particular species (reviewed in Kress, 2000; Cabot and Nisbet, 2013). Wide variation in preferred nesting substrate occurs across species, from mats of floating vegetation in marshes to low terrestrial vegetation to cobble beaches to bare sand. Some of these differences reflect species-specific differences in antipredator strategies (Gochfeld and Burger, 1996). Common terns aggressively mob nest predators (see Predator Behavior and Management, below) and nests are usually placed on relatively exposed substrate, while roseate terns instead protect their young by choosing nest sites with cover (under boulders, logs, dense vegetation) and also benefit from antipredator aggression by neighboring common terns (Burger and Gochfeld, 1988). Because of this preference for placing nests in protected locations, construction of nest boxes and/or placement of old tires has been a successful conservation strategy for roseate terns (Spendelow, 1982; Nisbet and Spendelow, 1999; Kress, 2000; Morrison and Gurney, 2007; Cabot and Nisbet, 2013).

It is important to note, however, that as with colony site selection, the substrate or location within a colony attracting the largest number of nests is not always in the habitat associated with the highest reproductive success (Cook-Haley and Millenbah, 2002; Rounds et

al., 2004; Palestis, 2009b) and can instead represent an ecological trap. For example, the preferred nesting substrate may be present at a lower elevation than neighboring sites and subject to increased risk of flooding (Rounds et al., 2004). Or for marsh-nesting terns, flooded fields may attract terns to nest, but result in breeding failure when the fields dry up (Paillisson et al., 2006). Such a mismatch between habitat selection cues and fitness is most likely in locations where traditional colony sites have been lost or the nesting habitat has recently undergone rapid change (Cook-Haley and Millenbah, 2002; Battin, 2004; Rounds et al., 2004; Sih, 2013). Managers must therefore ensure that habitat manipulation does not simply attract terns to nest, but also improves nest success (Cook-Haley and Millenbah, 2002; Paillisson et al., 2006).

Habitat use differs not just between species but also within species at different locations (Burger and Gochfeld, 1991; Gochfeld and Burger, 1996; Neubauer, 1998; Nisbet and Spendelow, 1999; Nisbet, 2002; Becker and Ludwigs, 2004; Shealer et al., 2005; Colchero et al., 2010; Cabot and Nisbet, 2013; Hu et al., 2013). In many locations habitat is successfully managed for common terns by removing vegetation or inhibiting succession (Burgess and Hirons, 1992; Morris et al., 1992; Becker, 1996; Kress, 2000; Nisbet, 2002; Cabot and Nisbet, 2013; but see Cook-Haley and Millenbah, 2002), but in saltmarsh colonies instead by adding dead eelgrass (*Zostera*) and other wrack, the preferred nesting substrate at these sites (Burger and Lesser, 1978; Burger and Gochfeld, 1991; Rounds et al., 2004; Palestis, 2009b). Adding wrack or moving it farther from the water's edge provides nesting substrate that is less susceptible to flooding (Palestis, 2009b). Increasing the elevation of substrate under the wrack could further increase this benefit (Rounds et al., 2004). A similar strategy should work in freshwater marshes for Trudeau's terns *Sterna trudeaui*, which prefer wrack on semi-dry land to floating mats when available (Guicking et al., 2001).

At many sites terns now nest in man-made bodies of water (Neubauer, 1998; Ledwón et al., 2013) or on dredge spoil islands and other man-made structures, such as gravel rooftops and floating docks or rafts (Dunlop et al., 1991; Burgess and Hirons, 1992; Morris et al., 1992; Becker, 1996; Quinn et al., 1996; Becker and Sudmann, 1998; Neubauer, 1998; Krogh and Schweitzer, 1999; Kress, 2000; Van der Winden et al., 2004; Shealer et al., 2006; Ward et al., 2011; Szostek and Becker, 2012; Cabot and Nisbet, 2013). Structures such as rafts have been constructed specifically for tern nesting, but in other cases terns have opportunistically used available man-made habitat. The increased usage of artificial sites (and perhaps the use of saltmarsh habitat by common terns described above) has probably occurred in response to human development of and disturbance at traditional breeding sites, such as barrier beaches (Erwin et al., 1995; Krogh and Schweitzer, 1999). Knowledge of modes of competition is important when designing artificial habitat. Intraspecific competition for nest sites may be alleviated by providing additional nearby rafts or other nesting habitat, but intraspecific competition for food necessitates creation of habitat outside the foraging range of the main colony (Szostek et al., 2014a).

Knowledge of optimal nesting substrates is also needed to attract terns to suitable sites, construct sites intended for usage by terns, and enhance the productivity of existing sites. For example, Krogh and Schweitzer (1999) make specific recommendations for attracting and improving the success of roof-nesting least terns. Availability of suitable dredge spoil islands and rooftops is declining, because fewer new islands and gravel rooftops are being constructed than in the past and artificial islands require continued maintenance (Becker and Sudmann, 1998; Kress, 2000). Construction of anchored rafts has been particularly useful in the conservation of black terns *C. niger* in habitats with low human disturbance but limited availability of stable emergent or floating vegetation (Van der Winden et al., 2004; Shealer et al., 2006). Black terns can also benefit from vegetation removal in areas where vegetation is too dense to provide open water and suitable nest sites (Linz and Blixt, 1997).

2 Philopatry and Dispersal

Population dynamics and population genetics are influenced by immigration and emigration. Because of the flight ability of terns, it is likely that any limits to immigration and emigration are behavioral rather than physical (Matthiopoulos et al., 2005; Faria et al., 2010). Behaviors that affect the frequency of movement among colony sites include site fidelity (philopatry), natal and breeding dispersal, and group adherence. The degree of specialization in habitat selection also contributes to differences among species, as species with more flexible habitat requirements can disperse to a wider pool of locations (Ledwón et al., 2014). Tern colonies are interconnected by dispersal, and a metapopulation approach is therefore needed for effective management

(Burger and Gochfeld, 1991; Erwin et al., 1995; Spendelow et al., 1995; Devlin et al., 2008; Ratcliffe et al., 2008). Additionally, range expansion and local population increases often result from immigration, thus via dispersal from natal or breeding colonies (Ledwón et al., 2014). In tern colonies, immigration can be the key driver of temporal variation in colony growth rate (Szostek et al., 2014b) and helps prevent inbreeding (Szczys et al., 2005; Ludwig and Becker, 2012), while philopatry may have the opposite effect (Sruoga et al., 2006).

Dispersal results in gene flow between colonies and between geographic regions (Szczys et al., 2005; Draheim et al., 2010; Faria et al., 2010), and may also allow terns to respond quickly to changes in climate or other ecological factors (Møller et al., 2006). Lack of dispersal, on the other hand, contributes to genetic differentiation (Sruoga et al., 2006; Szczys et al., 2012; Boutilier et al., 2014) and can prevent recovery of genetic variation in small populations (Szczys et al., 2012). Population genetic research can provide evidence for or against subspecific status (Szczys et al., 2005; Draheim et al., 2010) and helps to define management units for conservation (Boutilier et al., 2014).

Information on philopatry and dispersal is critical not just because of the importance of tracking movements between breeding sites and quantifying colony site connectivity, but also because the accuracy of estimates of mortality rates are affected by the rates of dispersal. Although genetic studies can help indicate the occurrence of mixing between populations, studying philopatry and dispersal in detail is difficult, because it requires recapturing and/or resighting marked individuals at multiple sites (e.g. Spendelow et al., 1995; Lebreton et al., 2003; Shealer et al., 2005; Møller et al., 2006; Devlin et al., 2008; Ratcliffe et al., 2008; Ledwón et al., 2013) and dispersal out of the study area is likely to go undetected (Møller et al., 2006; Coulson and Coulson, 2008). Individuals who disappear between breeding seasons may have died, but they may also have moved to another location. Research on tern metapopulations has led to important advances in the development of multistate capture-recapture modeling (Spendelow et al., 1995; Lebreton et al., 2003; Szostek and Becker, 2012). Studies of prospecting behavior may further improve the accuracy of survivorship estimates (Cabot and Nisbet, 2013), because pre-breeding terns often return to the natal site even if they eventually breed elsewhere (Dittmann et al., 2007).

Although terns and other seabirds are often assumed to be highly philopatric, the degree of site fidelity varies substantially both between species (McNicholl, 1975; Møller, 1982; Burger, 1984; Erwin et al., 1998; Renken and Smith, 1995; Ward et al., 2011; Ledwón et al., 2013; Zarza et al., 2013) and between colony sites within species (Austin, 1949; Haymes and Blokpoel, 1978; Tims et al., 2004; Spendelow et al., 1995; Feare and Lesperance, 2002; Lebreton et al., 2003; Sánchez et al., 2004; Shealer et al., 2005; Devlin et al., 2008; Ratcliffe et al., 2008; Draheim et al., 2010). Most measures of philopatry are probably biased toward high values because it is difficult to detect individuals who disperse (Coulson and Coulson, 2008). As in most birds, dispersal is generally female-biased (Dittmann et al., 2007; Becker et al., 2008; Draheim et al., 2010; but see Devlin et al., 2008), and male recruits therefore frequently pair with female immigrants (Becker et al., 2008; Szostek et al., 2014b). Terns are more faithful to colonies where they previously nested (breeding philopatry) than to colonies where they hatched (natal philopatry) (Austin, 1949; Haymes and Blopoel, 1978; Lebreton et al., 2003; Møller et al., 2006; Draheim et al., 2010). Philopatry also tends to be higher in large, stable colonies than small colonies and/or colonies in less stable habitat (Austin, 1949; McNicholl, 1975; Renken and Smith, 1995; Nisbet, 2002; Sánchez et al., 2004; Dittmann et al., 2007; Ratcliffe et al., 2008; Braby et al., 2012). Because most research has focused on large, stable colony sites, an additional upward bias in estimates of philopatry exists. Sites with frequent and/or heavy losses to flooding, predation, or human disturbance may be abandoned or experience higher rates of dispersal (Møller, 1982; Burger and Gochfeld, 1991; Holt, 1994; Erwin et al., 1998; Feare and Lesperance, 2002; Nisbet, 2002; Sánchez et al., 2004; Shealer et al., 2005; Ward et al., 2011), and in locations where terns nest mainly at managed sites dispersal rates may be lower than among unmanaged sites (Devlin et al., 2008). Site fidelity is probably lower for the marsh terns (*Chlidonias*) than for most other terns because of the unpredictability of the habitat (Ledwón et al., 2013).

Group adherence, a preference for nesting with many of the same neighbors in a colony (Austin, 1951; McNicholl, 1975), can have opposing effects on the degree of philopatry. Among typically philopatric species, group adherence may enhance site fidelity, as terns are attracted not just to familiar colony and territory sites but also to familiar neighbors and are thus less likely to disperse. However, when dispersal does occur many breeding pairs may all move together to a new

site, resulting in large fluctuations in colony size (Russel and Rosales, 2010). Species that nest in more ephemeral habitat tend to have low site fidelity but high group adherence, allowing colonies to reestablish quickly at new locations (McNicholl, 1975; Møller, 1982; Renken and Smith, 1995; Ward et al., 2011).

Variation in philopatry and dispersal has important consequences for population dynamics at both local (colony-level) and regional (metapopulation) scales. Philopatry can cause local density to increase, possibly resulting in density-dependent decreases in productivity (Tims et al., 2004; Matthiopoulos et al., 2005). Although terns often move from sites affected by predation and flooding to safer sites, in more stable locations they may continue to return to locations where they have been successful in the past, rather than colonizing nearby sites (including newly restored sites), even if current reproductive success is low (Burger and Gochfeld, 1991; Sánchez et al., 2004; Tims et al., 2004; Sruoga et al., 2006; Braby et al., 2012; Szostek et al., 2014b). Philopatry and conspecific attraction (see Habitat Selection and Conspecific Attraction, above) can therefore result in suitable colony sites remaining unoccupied and a smaller number of breeding colonies (Matthiopoulos et al., 2005; Heinänen et al., 2008; Zarza et al., 2013), which causes the metapopulation to be more vulnerable to extinction (Reed, 1999; Matthiopoulos et al., 2005). In philopatric species, vacancies created by mortality of breeders or availability of new sites are more likely to be filled by young, inexperienced recruits rather than experienced breeders moving from other sites (Morris and Chardine, 1995; Tims et al., 2004). When movements occur, they tend to be directed toward larger colonies (Spendelow et al., 1995; Dittmann et al., 2007; Ratcliffe et al., 2008; but see Devlin et al., 2008) that are either more productive (Ratcliffe et al., 2008) or contain more prospectors and recruits (Szostek et al., 2014b). Exchange among colonies is also more likely among colonies that are closer together (Spendelow et al., 1995; Devlin et al., 2008). In some cases local populations can be maintained or grow despite low productivity or low apparent survival by immigration from other colonies that are declining or have disappeared (Szostek and Becker, 2012; Ledwón et al., 2014; Szostek et al., 2014b), but such population dynamics are unlikely to be sustainable. In other cases movement away from less successful colonies contributes to further local declines (Lebreton et al., 2003), but probably results in greater recruitment in the metapopulation as a whole.

3 Mating Systems, Sex Roles, and Sex Ratios

Because it accounts for the number of breeding individuals, which affects genetic variation and maximal production of young, effective population size (N_e) is more important to population persistence than the total number of individuals present (population size, N). For a given population size, the monogamous breeding system of terns should keep effective population size larger than in polygamous species (Parker and Waite, 1997; Anthony and Blumstein, 2000). However, variation in sex ratios can result in a smaller than expected effective population size, particularly for typically monogamous species dependent on biparental care, because individuals of the over-represented sex will be excluded from mating or have reduced reproductive success (Komdeur and Deerenberg, 1997). An unbalanced sex ratio in a monogamous species can also result in the formation of same-sex pairs.

Northwest Atlantic roseate terns have a female-biased sex ratio (at the best-studied site ~1.27: 1 females: males) and female-female pairs and other multi-female associations occur (Nisbet and Hatch, 1999). By decreasing effective population size, the unbalanced sex ratio has likely contributed to reduced genetic diversity in this population (Szczys et al., 2005). Although some young are produced by extra-pair copulation or by females joining already-paired males to form trios or similar groups, reproductive success is greatly reduced for surplus females relative to females paired monogamously with males. Female-female pairs lay many infertile eggs, lack courtship feeding by males, and are likely comprised of low-quality females (Nisbet and Hatch, 1999; Palestis et al., 2012). Surprisingly, males who obtain more than one female mate are probably not high-quality males (Palestis et al., 2012). Instead a trio may result when a low-quality female, who is thus paired with a low-quality male, fails to prevent an additional female from joining them.

It is likely that unbalanced sex ratios result from sex differences in behavior leading to sex-biased mortality. Most terns have long periods of post-fledging parental care (Schreiber and Burger, 2002), allowing young terns time to learn how to capture prey. Female common terns leave breeding colonies to migrate earlier than males, while males are still performing post-fledging care (Nisbet et al., 2011). In addition to higher parental investment costs to males late in the breeding season, this sex difference in the timing of autumn migration may

directly cause sex differences in mortality. In the tiny Bermuda common tern population, all males disappeared when the islands were hit by a hurricane in early September, but females had presumably already left the colony and returned the next year (Nisbet et al., 2010). This severe population bottleneck resulted in an extremely small effective population size and the loss of genetic diversity (Szczys et al., 2012). Sex differences in behavior can also lead to sex-biased mortality at wind farms (Stienen et al., 2008). During egg-laying and incubation females are generally at the nest while males perform most of the foraging for the pair, therefore increasing the risk of collision among males (for information on behavior associated with wind turbines and other man-made structures see Additional Links Between Behavior and Conservation, below).

In addition to pairing with other females or joining existing pairs, female roseate terns occasionally hybridize with males of co-nesting species (Whittam, 1998 and references therein). Hybridization, although infrequent, is probably more common in roseate terns than in other species because of the combination of a female-biased sex ratio and the greater numbers of common or Arctic terns nesting at the same location. Hybridization may be an important conservation problem for Chinese crested terns. This rare species also nests within colonies of other, much more numerous terns and putative hybrids with great crested terns *T. bergii* have been observed (Chen and He, 2011). With the entire global population estimated at fewer than 50 adults (Chen et al., 2009), the presence of even a few hybrids represents a proportionally large impact on the species.

Differences in reproductive success among individuals also lead to a decreased effective population size (Parker and Waite, 1997; Anthony and Blumstein, 2000; Reed, 2004), especially if they result from consistent differences in individual performance rather than simply variation with age (Nunney, 1996; Lee et al., 2011). Within-colony differences among individuals related to parental quality are consistent from year to year in terns (Nisbet et al., 1998; Wendeln and Becker, 1999b; Ezard et al., 2007) and performance continues to improve until very late in life (Limmer and Becker, 2010; Rebke et al., 2010). Differences in parental quality are, in part, likely to result from differences in foraging ability, which in terns requires a great deal of skill (reviewed in Gochfeld and Burger, 1996; Cabot and Nisbet, 2013). Foraging ability affects provisioning to chicks, courtship feeding and self-maintenance. Consistent differences among individuals mean that the number of young produced in a colony will disproportionately be produced by the same individuals, and many others may have low reproductive success throughout their reproductive lifespan. Within a breeding season, these disparities in reproductive success reflect differences in clutch size, egg size, laying date, and ultimately chick survival. In common terns, chick survival controlled for hatching order (Langham, 1972) and developmental stability of first-hatched chicks (Palestis, 2009a) both improve with increasing clutch size. Hatching success in little terns *Sternula albifrons* is also higher in larger clutches (Hong et al., 1998). In whiskered terns *C. hybrida*, preferred central locations in colonies are occupied by parents who nest earlier and produce larger eggs, resulting in enhanced chick survival (Minias et al., 2013).

In addition to within-season reproductive success, individual quality should also affect length of life, and thus the number of breeding opportunities. This prediction is supported by the tendency for longer-tailed roseate terns to not only be preferred as mates, but also to live longer (Palestis et al., 2012). Correlations between longevity and traits associated with breeding success have also been recorded in other seabirds (Moreno, 2003). Although reproductive and parental investment costs lead to shortening of telomeres, which should lead to decreased longevity, the most successful common terns experience less telomere loss than expected (Bauch et al., 2013, 2014) and may live longer (Arnold et al., 2006). Additionally, nonbreeding common terns appear to suffer higher mortality rates than same-aged breeders, and individuals rarely transition from breeder to nonbreeder (Szostek and Becker, 2012). Individuals that recruit into the breeding population earlier have additional opportunities to reproduce, and early recruitment is probably also related to individual quality (Becker and Bradley, 2007; Becker et al., 2008; Limmer and Becker, 2010). Differences in lifetime reproductive success can therefore be very large: high-quality parents can breed more often and can produce larger numbers of surviving young per breeding attempt. Population dynamics and genetic contribution to the next generation are thus controlled by a smaller number of individuals than the number of breeding pairs would suggest (Moreno, 2003).

4 Predator Behavior and Management

In many locations predation is the main current threat to tern populations (Burger and Gochfeld, 1994; Sudmann et al., 1994; Gochfeld and Burger, 1996; Becker and Ludwigs, 2004; Cabot and Nisbet, 2013; Nisbet et

al., 2013). Predation on adult terns typically has a much larger negative effect than predation on eggs or young, but tends to be performed by other protected, charismatic species, such as falcons or owls, exacerbating the ethical, legal and social dilemmas that predator control involves (Holt, 1994; Nisbet and Spendelow, 1999). Nocturnal predators also tend to have a large impact on terns, because when terns are threatened by nocturnal predation they often abandon their nests at night (Nisbet and Welton, 1984; Shealer and Kress, 1991; Holt, 1994; Sudmann et al., 1994; Wendeln and Becker, 1999a; Nisbet, 2002; Nordström et al., 2004). This strategy acts to limit predation on adults, but exposes eggs and young to predation and the elements. Nocturnal predation on adult terns may also make terns more "flighty" during the day, and therefore more exposed to diurnal nest predation (Morris and Wiggins, 1986). Gulls are frequent predators on tern chicks or eggs (see below), but often have a greater impact on terns via nest site competition. They generally nest earlier, are larger than terns, and are potential predators that can cause terns to nest in suboptimal habitat or displace terns from breeding sites (Burger and Gochfeld, 1991; Quinn et al., 1996; Kress, 1997; Neubauer, 1998; O'Connell and Beck, 2003). Predation and nest-site competition can interact. For example, the presence of gulls may force terns to nest in locations more susceptible to flooding, and flooded nests may be more susceptible to predation (O'Connell and Beck, 2003).

In addition to the behavior of terns, knowledge of the behavior of predators on terns contributes to management plans, because predator control methodology and timing must fit the species of predator that is causing harm (Cabot and Nisbet, 2013). Common methods to limit predation on terns include fencing off nesting areas, construction of shelters, lethal predator control, removal and translocation of predators, predator nest and egg destruction or egg oiling, and nonlethal predator harassment (Kress, 1983, 1997, 2000; Morris et al., 1992; Burger and Gochfeld, 1994; Quinn et al., 1996; Nisbet and Spendelow, 1999; Nisbet, 2002; Donehower et al., 2007; Cabot and Nisbet, 2013). Predator control usually cannot stop after initial management action or after new colonies have been established, because predators may be attracted to breeding colonies (Ward et al., 2011).

Predator behavior can be manipulated to reduce pre-

dation (Curio, 1996; Reed, 2004). Harassment depends on fear reactions of predators to stimuli such as loud noises, bright lights, or humans. For example, gulls flee from canids, and dogs have been used to successfully clear islands or sections of islands of nesting gulls (Kress, 2000; Nisbet, 2002). Gulls can also be prevented from nesting in specific locations by covering the substrate with plastic sheeting, which can then be removed to allow the later-arriving terns to nest (Quinn et al., 1996). Conditioned taste aversion has reduced avian predation on tern eggs in some cases but not others, with variation likely due to differences in the behavior of the predators (Avery et al., 1995; Kress 2000; Catry and Granadiero, 2006; Neves et al., 2006). Supplemental feeding of kestrels *Falco tinnunculus* has been shown to reduce predation on little tern chicks, although there was variation among years perhaps due to differing availability of alternate natural prey (Smart et al., 2009[1]). Reed (2004) speculates that applying conspecific scents could cause territorial mammalian predators to keep away if they perceive that another individual occupies that area.

Predation on tern adults, eggs or young is often performed by only a few specialized individuals (Morris et al., 1992; Becker, 1995; Quinn et al., 1996; Yorio and Quintana, 1997; Donehower et al., 2007; Guillemette and Broussard, 2001; Hall and Kress, 2008; Cabot and Nisbet, 2013). Knowledge of intraspecific differences in predatory behavior can therefore help in protecting tern colonies. Predator culling is more costly and labor-intensive, and less likely to receive public support, than removing the small number of individual specialists (Guillemette and Broussard, 2001). Specialization by individual predators also means that species which act as predators in one location or at one time may not be a threat in another location or time, if predatory individuals are absent. It is therefore hard to justify reducing the populations of potentially predatory native species without direct evidence of harm to local terns or other protected species (Holt, 1994). There are exceptions, however. Predator (and/or nest site competitor) removal is a necessary first step in the restoration of former tern colonies (Kress, 1983, 1997, 2000; Nisbet and Spendelow, 1999), and eradicating local populations of introduced predators is a justifiable goal (Burger and Gochfeld, 1994).

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[1] Smart J, Ratcliffe N, Bolton M, Lewis S, Cliffe C, 2009. Diversionary feeding: Is it effective at reducing kestrel predation? Raptor Research Foundation Conference.

In addition to ethical concerns, it is questionable whether large scale culling of predators is effective (Oro and Martínez-Abraín, 2007). Removal of specialists is likely to be more effective than widespread culling, because it is targeted to those individuals who pose a threat (Morris et al., 1992; Guillemette and Broussard, 2001; Hall and Kress, 2008; Cruz et al., 2013). Hall and Kress (2008; see also Kress, 2000) demonstrated that removal of a single specialist black-crowned night-heron *Nycticorax nycticorax* resulted in the absence of night-heron predation in a tern colony for several years, and tern reproductive success improved dramatically during predator-free periods. Although generally improving productivity of tern colonies, lethal or nonlethal removal of specialists, can be difficult to achieve. In some cases the individual specialists may not nest near the tern colony, making them hard to identify or locate (Donehower et al., 2007). At least some species of predatory gulls appear to have a despotic foraging distribution, and other individuals may increase their rates of predation on tern young or eggs after a high-ranking specialist is removed (Guillemette and Broussard, 2001; Donehower et al., 2007). Predator management therefore cannot stop after the first few specialists are removed. On the other hand, Quinn et al. (1996) report an end to egg predation after the removal of 1 to 3 specialist gulls. Donehower et al. (2007) suggest that human presence, which can discourage predatory gulls, and the destruction of nearby gull nests can result in greater benefits to terns than efforts to remove predatory individuals. If one or a few gull nests are present within a tern colony, removing the nests can cause the gulls to leave and predation to cease (J. Burger, personal communication). However, if a gull colony is present it is unlikely that nest destruction alone will cause gulls to abandon the site (Kress, 1997).

Intra- and inter-specific variation in predatory behavior has also lead to variation in the antipredator behavior of terns. During the day most terns actively defend their eggs and young. Antipredator behavior of terns is flexible, and nest defense is biased toward the species that act as nest predators in a particular location (Becker, 1984; Burger and Gochfeld, 1991; Palestis and Burger, 1997; Whittam and Leonard, 2000; Nordström et al., 2004; Palestis, 2005) (There are exceptions, as terns often fail to mob ruddy turnstones *Arenaria interpres*, which can act as egg predators, perhaps because most other shorebirds are completely harmless, e.g., Morris and Wiggins, 1986; Burger and Gochfeld, 1991; Rounds et al., 2004). Interestingly, the antipredator behavior of

terns also appears to reflect the threat posed by specific individuals. Terns can recognize and are more aggressive toward familiar investigators (Burger et al., 1993), who are likely perceived as nest predators, and may also recognize and direct mobbing to natural predatory individuals (Palestis and Burger, 1997). Nest defense also varies with the behavior of potential predators, with mobbing more likely when a predatory species exhibits behavior associated with predation rather than more benign behavior (Whittam and Leonard, 2000). Terns also tend to be more aggressive when defending chicks than when defending eggs (Becker, 1984; Burger and Gochfeld, 1991; Whittam and Leonard, 2000; Palestis, 2005 and references therein). Because of the aggressive antipredator behavior of most terns, it is possible that if predators or nest site competitors are prevented from successfully nesting near terns early in the breeding season, then the terns themselves can discourage late nesting and re-nesting by their enemies (Morris et al., 1992; Kress, 1997).

5   Additional Links between Behavior and Conservation

There are other areas where research on tern behavior and conservation have come together. For example, terns have often been used as bioindicators for environmental contamination, especially heavy metal contamination (reviews in Burger and Gochfeld, 2002; Becker, 2003; Blévin et al., in press). This work has included studies of behavioral toxicology (Burger and Gochfeld, 1985) and of the relation between exposure and foraging niche in wintering versus breeding grounds (Nisbet et al., 2002).

Bird strikes can be a source of mortality at tall, man-made structures, such as buildings, bridges, wind turbines, and power lines. Terns are agile flyers, but risks still may exist if structures are located in areas where terns aggregate in large numbers or if they are placed across regular flight paths. Risk of collision is probably highest near breeding colonies, because central place foraging and tight time budgets during chick rearing mean parents will travel repeatedly along similar paths and attempt to minimize flight times (Henderson et al., 1996; Burger et al., 2011). Studies of potential effects of wind farms rarely include direct observations of avoidance behavior and flight patterns, but some studies have been conducted with terns (reviewed in Burger et al., 2011). As discussed above (see Mating Systems, Sex Roles, and Sex Ratios), wind turbines can

cause male-biased mortality (Stienen et al., 2008). Knowledge of flight lines can aid in decisions on the siting of wind farms to minimize risk. Strikes with power lines, although rare, are probably more likely when adults must feed nestlings and when wind speed is high, and are perhaps more likely among fledglings than adults (Henderson et al., 1996). Risk can be decreased by increasing visibility of wires with brightly colored diverters (Henderson et al., 1996). Plans for a bridge through the Niagara River Corridor Important Bird Area were modified, in part due to direct observations and radar studies on common terns and other birds [the bridge was eventually not built for budgetary reasons] (CM Adams, personal communication). These studies demonstrated that nesting common terns never flew under nearby bridges and flew low over them, raising concerns about increased energy expenditure and potential strikes if a taller bridge with cables was present, particularly under conditions of poor visibility (Yonker and Landon, 2006).

Studies of the behavioral responses of terns to human disturbance are common (reviews in Burger and Gochfeld, 1994; Nisbet, 2000; Nisbet et al., 2013) and include studies of responses to handling by researchers (e.g. Gochfeld, 1981; Nisbet, 1981; Shealer and Haverland, 2000; Palestis and Stanton, 2013). Although negative effects of research activities have occasionally been recorded, terns often habituate to repeated intrusions, and the presence of researchers can have positive effects, such as keeping away predators and vandals (Burger and Gochfeld, 1994; Nisbet and Spendelow, 1999; Kress, 2000; Nisbet, 2000; Donehower et al., 2007; Cabot and Nisbet, 2013). At many sites management must be for multiple uses, such as beach recreation and ecotourism, in addition to nesting terns. If they are enforced, simple measures like fencing, signage, and buffer zones can allow terns and other waterbirds to behave normally (Burger et al., 1995; Becker, 1996; Ikuta and Blumstein, 2003). However, behavioral responses do not necessarily indicate the effect of human disturbance on reproduction and survival, and may be misleading when used to determine which species are more susceptible to disturbance (Gill et al., 2001). Nisbet (2000) proposed that managers and researchers could actively promote habituation by repeatedly entering nesting areas, thus decreasing the damaging effects of intrusions by casual visitors and making it possible to increase public interest in terns and tern conservation by allowing controlled visitors to closely view breeding colonies (e.g. Farne Islands, UK; Cabot and Nisbet, 2013).

6 Discussion

I reviewed four major areas in which behavioral information is critical: Knowledge of habitat selection is needed to increase or improve nesting habitat. Metapopulation dynamics are determined not only by patterns of local extinction and colonization, but also by regularly occurring dispersal, philopatry, and group adherence. Studies of reproductive and parental behavior aid in determining the causes and interpreting the effects of sex differences in mortality and unbalanced sex ratios. Finally, knowledge of the specialized behavior of predators and tern antipredator behavior can make predator control more effective and ethical. In addition to these four topics, behavioral toxicology and studies of behavioral responses to human disturbance and tall manmade structures also link behavior and conservation. However there are several areas where information is lacking.

The area most in need of further research is behavior outside the breeding season (Hays et al., 1999; Van der Winden, 2003). Although most research and management actions occur at breeding colonies, the largest current threat to many migratory tern populations may be mortality on the wintering grounds, rather than low productivity on the breeding grounds (Nisbet and Spendelow, 1999; Wendeln and Becker, 1999c; Nisbet, 2002; Shealer et al., 2005; Cabot and Nisbet, 2013). Conditions at the wintering grounds, such as food availability, may also have effects that carry-over to the breeding season (Møller et al., 2006), and shared wintering areas can provide opportunities for pairing among conspecifics from geographically isolated breeding areas (Faria et al., 2010). Discrete staging areas where entire regional populations may gather after breeding and before migration have been discovered: roseate terns of the northeastern United States and Canada at and near Cape Cod, USA (Trull et al., 1999; Jedrey et al., 2010) and black terns of Europe and western Asia in and around IJsselmeer, the Netherlands and Sivash, Ukraine (Van der Winden, 2003). That a population can become concentrated at a few locations makes studies of these areas a high priority, including research on habitat use, response to disturbance, threats to these locations, and how to mitigate such threats. As in other migratory birds, a complete flyway approach is necessary for effective conservation (Vickery et al., 2014). New technology, such as geolocators, have helped in this regard, as it is now possible to track migration routes and timing and to more readily identify key staging, stopover, and win-

tering sites (Egevang et al., 2010; Nisbet, Mostello et al., 2011; Nisbet, Szczys et al., 2011; Vickery et al., 2014). However, direct observations of the behavior of terns outside the breeding season are relatively rare.

In addition, research is clearly needed on the behavior of less well-studied species and of species in less well-studied geographic regions. Most published work has involved widespread and abundant species, which may be threatened in areas of the United States and Canada or western Europe, rather than species of global conservation concern. Particular species, such as the Chinese crested tern, black-bellied tern, black-fronted tern, Peruvian tern, and fairy tern, desperately need study and conservation action. A major theme that runs through many of the studies reviewed above is that the behavior of terns is highly variable, both between and within species. Therefore conservation plans based on indicator species are unlikely to be successful (Cruz et al., 2013), and short-term studies at single colonies are not sufficient, due to temporal and geographic variation. Nest site selection, for example, often varies geographically. Life history and demography can also differ between temperate and tropical populations of the same species (e.g. roseate tern: Shealer et al., 2005; Nisbet and Ratcliffe, 2008).

Behavioral research has contributed to the conservation of terns and will continue to do so. The reverse is also true, as applied research on terns has increased our knowledge of behavior. For example, restoration work to reestablish colonies of terns and other seabirds has lead to increased awareness of the importance of conspecific attraction in habitat selection and the evolution of coloniality (Danchin and Wagner, 1997). However, there are many species and locations that are poorly studied, and there are species and populations of terns that are threatened and need conservation action. Despite the large body of work on tern conservation and behavior, there is much more to be learned.

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