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RESEARCH ARTICLE

Resource partitioning in three congeneric sympatrically breeding seabirds: Foraging areas and prey utilization

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ABSTRACT

Morphologically similar sympatric species reduce competition by partitioning resources, for example by occupying different dietary niches or foraging in different areas. In this study, we examine the foraging behavior of Arctic (*Sterna paradisaea*), Common (*Sterna hirundo*), and Roseate terns (*Sterna dougallii*) breeding on Coquet Island, northeast England, using colony-based observations and coincident at-sea visual tracking of foraging birds to quantify interspecific overlap in prey selection and foraging areas. Although visual tracking methods have been used in previous studies, our study is the first example of this method being used to quantify multi-species overlap in foraging areas and the first time Roseate Tern foraging locations have been conclusively identified using a visual tracking method. Percentage overlap in foraging areas varied among species with Arctic and Common terns sharing a higher percentage of their foraging range with each other (63%) than either species did with Roseate Terns (Common = 41% and Arctic = 0%). Arctic and Common terns utilized similar foraging areas and partitioned resources by diet while Roseate Terns differed from other species in both diet and foraging area. Arctic and Common terns varied provisioning rate, prey length, and foraging areas with increasing brood age, while Roseate Terns fed similar prey and foraged consistently inshore. Although there were some similarities in areas utilized by these species, there were sufficient differences in behavior to minimize interspecific competition. Our study further demonstrates the successful use of a visual tracking method to show how morphologically similar sympatric seabird species partition resources by diet, foraging area, and response to increasing brood age.

Keywords: resource partitioning, interspecific competition, seabirds, foraging, diet, terns, visual tracking

Partición de recursos en tres aves marinas reproductivas simpátricas del mismo género; áreas de forrajeo y utilización de presas

RESUMEN

Las especies simpátricas morfológicamente similares reducen la competencia mediante la partición de los recursos, por ejemplo ocupando diferentes nichos dietarios o forrajeando en diferentes áreas. En este estudio, examinamos el comportamiento de forrajeo de individuos de *Sterna paradisaea*, *S. hirundo* y *S. dougallii* nidificando en la isla Coquet, al noreste de Inglaterra, mediante observaciones de la colonia y rastreos visuales simultáneos en el mar de aves forrajeando, para cuantificar la superposición entre especies en la selección de presas y áreas de forrajeo. Aunque los métodos de rastreo visual han sido usados en estudios previos, nuestro estudio es el primer ejemplo de uso de este método para cuantificar la superposición de múltiples especies en las áreas de forrajeo, y es la primera vez que las localizaciones de forrajeo de *S. dougallii* han sido identificadas con certeza usando un método visual de rastreo. El porcentaje de superposición en las áreas de forrajeo varió entre especies, con *S. paradisaea* y *S. hirundo* compartiendo entre ellas un porcentaje mayor de sus rangos de forrajeo (62.63%) que lo compartido por cada una de estas especies con *S. dougallii* (*S. hirundo* = 40.50% y *S. paradisaea* = 0%). *S. paradisaea* y *S. hirundo* utilizaron áreas de forrajeo similares y separaron los recursos usados en la dieta, mientras que *S. dougallii* difirió de las otras especies tanto en la dieta como en el área de forrajeo. *S. paradisaea* y *S. hirundo* variaron en la tasa de provisión, el largo de la presa y las áreas de forrajeo a medida que aumentó la edad de la nidada, mientras que *S. dougallii* se alimentó con las mismas presas y forrajeó consistentemente en el área costera. Mientras que hubo algunas similitudes en las áreas utilizadas por estas especies, hubo suficientes diferencias en el comportamiento como para minimizar la competencia interespecífica. Nuestro estudio demuestra además el uso exitoso de un método de rastreo visual para mostrar cómo especies de aves marinas simpátricas morfológicamente similares separan los recursos de la dieta, el área de forrajeo y la respuesta con el aumento de la edad de la nidada.

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Palabras clave: aves marinas, competencia inter-específica, dieta, forrajeo, partición de recursos, rastreo visual, *Sterna*

INTRODUCTION

Interspecific competition occurs in closely related morphologically similar species with similar resource requirements and limited foraging ranges. Various studies examining how seabirds reduce interspecific competition through resource partitioning have been carried out (Duffy 1986, González-Solís et al. 1997, Mori and Boyd 2004, Lance and Thompson 2005), however most of these have compared only 2 species. While studies on 2 species provide useful data on resource partitioning, studies on larger seabird assemblages can determine the extent to which variation in foraging strategies, such as diet and foraging area, reduce interspecific competition in a highly competitive environment. Fewer studies have compared foraging behavior in 3 or more seabird species (Pearson 1968, Surman and Wooller 2003, Linnebjerg et al. 2013), and many of these used only colony-based data. For those that also compared species' foraging areas, locations of feeding birds were recorded indirectly using boat transects, which cannot determine the origin and breeding status of observed birds or the extent of potential competition (Tasker et al. 1984, Daunt et al. 2002, Surman and Wooler 2003). Although the more established bird-borne device tracking method has allowed interspecific comparisons of foraging areas (Phalan et al. 2007, Young et al. 2010), foraging locations have to be inferred from track characteristics (e.g., sinuosity). In this study, a visual tracking method allowed us to use observed, rather than inferred, foraging location data by visually confirming the locations of dive sites (Perrow et al. 2011). There is a need to compare foraging behavior of multiple seabird species using a direct estimation of foraging locations, to link foraging areas to a specific breeding colony and develop a comprehensive understanding of how species partition resources.

Terns (*Sterna* spp.) are small seabirds that feed mainly by snatching food from the sea surface or by plunge-diving up to 1 m in depth (Shealer 2001). Most tern species have relatively short foraging ranges of $<$10 km (Cabot and Nisbet 2013), while larger seabird species such as gannets have been shown to have mean foraging ranges of $\sim$200 km (Hamer et al. 2000, Hamer et al. 2001). This makes terns more vulnerable to local food shortages than species with greater foraging ranges (Furness and Ainley 1984, Furness and Tasker 2000). Terns are useful species for studying resource partitioning as they are morphologically similar with limited foraging ranges and diving ability. Most species carry prey individually in their bills, allowing dietary observations to be made (Burness et al. 1994).

Morphologically similar tern species foraging in a limited area around the breeding colony may be expected to reduce interspecific competition by varying diet or foraging areas. Sympatrically breeding tern species exhibit considerable dietary overlap by feeding chicks high percentages of the same prey types and sizes (Hopkins and Wiley 1972, Safina et al. 1990, Surman and Wooller 2003); for example, 3 tern species breeding at the same colony were found to share 78–87% of prey species (Surman and Wooller 2003). However, studies have also shown that some sympatrically breeding tern species exhibit different prey preferences (Safina 1990a, 1990b, Safina et al. 1990, Rock et al. 2007). Arctic Terns (*Sterna paradisaea*) tend to deliver a higher percentage of small prey items ($<$4 cm) than Common (*Sterna hirundo*) and Roseate terns (*Sterna dougallii*) (Uttley et al. 1989, Safina et al. 1990, Cabot and Nisbet 2013), and when nesting in the same colony as Arctic or Roseate terns, Common Terns deliver a greater diversity of prey to chicks (Safina et al. 1990, Robinson et al. 2001). Tern species can also partition resources by varying the location of foraging areas around the breeding colony. Previous studies in the tropics and North America found that Roseate Terns have more restricted foraging areas than other tern species and tend to forage in shallow inshore waters, associate with predatory fish (Randall and Randall 1980, Safina 1990b, Safina et al. 1990, Shealer 1996), and rely on relatively few prey species during the breeding season (Nisbet 1981, Safina et al. 1990). Due to the small number of Roseate Tern colonies, little is known about foraging interactions between Roseate Terns and other tern species in the North Sea.

The way in which species partition resources has been shown to vary throughout the year, depending on spatial overlap and prey availability (Cherel et al. 2008, Linnebjerg et al. 2013). As chick energy demands change during the breeding season (Drent and Daan 1980), the mechanisms by which species partition resources (provisioning rate, prey size, and foraging area) may vary temporally (Williams and Rothery 1990, Bertram et al. 1996). If species utilize different mechanisms to partition resources, we may predict that responses to increasing brood age will also vary interspecifically.

We combine colony-based data on parental provisioning behavior with coincident at-sea tracking data for Arctic, Common, and Roseate terns breeding on Coquet Island, Northumberland, England, to examine resource partitioning in a multi-species seabird assemblage in the North Sea. We (1) compare the type and size of prey items delivered to chicks by different tern species, (2) compare the location

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FIGURE 1. Arctic Tern watching over its nest on Coquet Island, England. Photo credit: Wesley Davies

of foraging areas used by each species, and (3) examine how resource partitioning changes throughout the breeding season, with the expectation that morphologically similar sympatric species use provisioning rate, diet, or foraging area to partition resources and that response to increasing brood age varies interspecifically. We expect species to use at least one mechanism to partition resources; species exhibiting an overlap in foraging areas should differ in diet, and species with similar diets should forage in different areas. We discuss the implications of our results for understanding interspecific competition in a multi-species seabird assemblage.

METHODS

Study Site

The study took place on Coquet Island, Northumberland, England (55° 37′N, 1° 32′W) during the 2011 breeding season. Coquet Island provides a unique location to study interspecific foraging behavior among 3 tern species of similar size and foraging preference (average body weights of Common Tern = 130 g, Arctic Tern = 110 g, Roseate Tern = 110 g; Snow and Perrins 1998), as Arctic, Common, and Roseate terns breed annually on the island (mean number of breeding pairs 2006–2010: Arctic = 1,140.6, Common = 1,212.4, Roseate = 82.0; www.jncc.defra.gov.uk/page-4460).

Arctic, Common, and Roseate terns were studied during chick-rearing from June 2 to July 9, 2011. Prey delivered to chicks was recorded for a sample of 10 Arctic and Common tern nests and 12 Roseate Tern nests. Each Arctic and Common tern study nest was checked daily to obtain accurate hatching dates. Precise Roseate Tern hatching dates are not known as nests were checked every 7 days to limit disturbance to the colony. As in other studies using tern diet observations (Pearson 1968, Ramos et al. 1998), 1–4 m^2 was enclosed around each Arctic and Common tern study nest using plastic netting ~0.3–0.5 m high. This facilitated feeding observations by preventing the precocial chicks from moving away from the nest site when adults delivered food. Roseate Tern nests were not enclosed to reduce disturbance since this is one of few UK breeding sites for this endangered species.

Colony-Based Data Collection

Provisioning watches took place from a hide positioned <12 m from study nests from June 2 to July 9. Common Tern study nests started hatching ~5 days before Arctic Tern nests (Figure 1) although there was considerable overlap in hatching dates (Table 1). Mean age of chicks on the first day of provisioning observations differed only slightly among species (Table 1). By comparing foraging behavior when chicks were approximately the same age, interspecific variation in diet and foraging areas could be examined while avoiding bias caused by variation in chick age.

Three-hour watches included every time period from 0400 hours to 2100 hours for each tidal state. Species and size categories of prey items delivered to chicks were recorded and grouped into 4 categories: lesser sandeel (*Ammodytes marinus*; hereafter "sandeel"), sprat (*Sprattus sprattus*), juvenile fish (larvae not identifiable at species level), and miscellaneous (including crustaceans, cephalopods, and demersal fish). Prey size was measured in tern bill lengths as in previous studies (Safina et al. 1990, Shealer 1998, Rock et al. 2007). Type and size categories

TABLE 1. Hatching dates, data collection start dates, mean chick ages ± SE when data collection began, and percentage survival for Arctic, Common, and Roseate tern chicks on Coquet Island in 2011.

	Arctic Tern	Common Tern	Roseate Tern
Hatch dates			
Min	June 1	May 26	June 14
Median	June 5	May 30	June 21
Max	June 11	June 6	June 29
Date provisioning watches started	June 9	June 2	June 15
Chick age (days after hatching) on first day of provisioning watches	5.79 ± 0.27	4.15 ± 0.23	~1.08 ± 0.08
Date tracking started	June 7	June 7	June 20
Chick age (days after hatching) on first day of tracking	3.88 ± 0.27	8.71 ± 0.13	6.06 ± 0.03
Chicks survived to fledging	65%	63%	83%

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were agreed on by observers before watches started and were validated by examining discarded fish. Bill lengths of Arctic (3.0–3.4 cm), Common (3.4–4.1 cm), and Roseate terns (3.7–4.0 cm) differ only slightly, and there is considerable overlap between species (Lemmetyinen 1976, Ramos et al. 1998). Prey length (cm) was calculated by multiplying prey size category by median bill length. Roseate Tern watches were carried out by WD while GSR observed Arctic and Common terns. Prey size recording methods were standardized for different observers by agreeing on prey size categories of items carried by the same selected individuals. Separate observations were only carried out by different observers after prey size category estimations made during simultaneous test watches were found to be comparable.

At-Sea Data Collection

While GPS devices have been used to track various seabird species (Weimerskirch et al. 2005, Guilford et al. 2008, Stauss et al. 2012), terns are considered too small to carry such devices (Perrow et al. 2011). We used a visual tracking method that successfully identified foraging areas of tern species in a previous study carried out in Norfolk and North Wales, UK (Perrow et al. 2011), but that has not been used to track Roseate Terns or to quantify overlap in foraging areas utilized by multiple species.

Individual terns were tracked to and from foraging sites by observers on board a rigid inflatable boat (RIB) using tracks obtained from the onboard GPS as proxies for foraging tracks. The starting position around the colony was varied so as to track an adequate representation of the breeding population. We took care to observe any changes in behavior, such as evasive flight, which might indicate an adverse reaction to the presence of the vessel, and, if so, increased the distance of the RIB from the bird. Observers recorded few instances of birds visibly reacting to the RIB, and most appeared to ignore the vessel, consistent with Perrow et al. (2011). Birds were tracked for the duration of foraging trips although trips were aborted if birds were lost or if it was no longer possible to follow them due to deteriorating sea conditions (64 of 122 tracks were aborted). Locations of foraging attempts (where birds dived or surface-dipped) were recorded as was the duration of each track. Incomplete tracks were those where individuals were lost before returning to the colony and comprised 27/49 (55%), 24/42 (57%), and 16/31 (52%) of Arctic, Common, and Roseate tern tracks, respectively. Tracked birds dived throughout the trip allowing dive locations to be recorded even if tracking was later aborted. The cumulative probability of losing visual contact with a bird by chance increases with time, and if birds are likely to travel farther with time, this may have resulted in maximum foraging distance being underestimated. However, we found no significant difference in maximum foraging distances calculated from complete and incomplete tracks (mean ± standard error = 3.17 ± 0.26 and 3.49 ± 0.36, respectively; t-test: $t_{78.79} = -0.72$, $p = 0.47$, $n = 115$). Arctic and Common terns were tracked from June 7 to July 1 and Roseate Terns from June 20 to July 1.

Data Analyses

To avoid temporal bias, tracking and provisioning data from June 20 to July 1 were used for species comparisons, and data collected before June 20 and after July 1 were used to examine changes in foraging behavior with increasing brood age. Provisioning rate was defined as the number of deliveries made to each chick per hour. The proportion of sandeel (most commonly fed prey item) fed to chicks, and variation in the mean length of prey items (cm) in each nest, were compared among species using Kruskal-Wallis tests.

Foraging trip parameters (maximum foraging distance, total distance traveled, trip duration, and mean bearing on departing the colony) were compared among species using a circular ANOVA and Kruskal-Wallis tests. The circular ANOVA (from packages CircStats and circular in R version 2.14.1) compared mean bearings calculated from the first 5 bearings in each track (Patrick et al. 2013), accounting for the bounded nature of data between 0° and 359°. Tracks where the start or end time had not been recorded were excluded from analysis.

Kernel density plots were generated using dive locations from complete and incomplete tracks, to compare species- and stage-specific foraging areas for all 3 species and for those tracked during early and late chick-rearing. Dive locations were not observed during every track; 111 Arctic, 77 Common, and 206 Roseate tern dive locations were used in kernel density estimations. We examined species-specific differences in foraging ranges (95% volume contour) and core foraging areas (25% volume contour) from fixed kernel density estimation in a European Albers equal-area conic projection (ArcGIS 10.1, ESRI, Redlands, CA, USA) using a grid size of 100 m^2 calculated in R with adehabitatHR and maptools packages (Calenge 2006). The ad hoc method was used to calculate the smoothing parameter (h) where $h = \sigma n^{(-1/6)}$, $\sigma = 0.5\,(sd(x) + sd(y))$ and n = number of locations, which resulted in a smoothing parameter that retained sufficient detail in distribution patterns to allow identification of high-density areas without excessive smoothing. Percentage overlap in species' foraging ranges and core foraging areas was calculated by dividing the area of overlap by the combined area utilized by both species and multiplying by 100. This quantifies the degree of similarity between foraging areas used by Arctic, Common, and Roseate terns. The percentage of foraging areas used by one tern species that coincided with that of another tern species was also calculated.

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TABLE 2. Percentage of prey types fed to chicks and lower quartiles, medians, and upper quartiles of prey lengths (cm) and provisioning rates (deliveries per chick per hour) for each species.

	Arctic Tern	Common Tern	Roseate Tern	Number of deliveries
Sandeel (%)	50	69	86	1,675
Sprat (%)	3	26	14	241
Juvenile fish (%)	34	2	0	516
Miscellaneous (%)	13	2	0	210
Number of observations	1,497	338	821	
Prey length (cm)	1.60, 1.60, 3.20	3.75, 5.63, 5.63	3.85, 5.78, 5.78	
Provisioning rate (deliveries per chick per hour)	3.00, 3.58, 4.90	0.88, 1.31, 1.57	1.09, 1.32, 1.72	

Brood age (in days after hatching) was separated into seven 5-day categories from 0 to 35 days. For each category, mean provisioning rate and prey length were calculated for each species and plotted against brood age. Relationships between provisioning rate and brood age, and prey length and brood age, were examined using generalized linear mixed models (GLMMs) fitted using the lme4 package in R. We included species, brood age, brood size, and the interaction between species and brood age as fixed effects, and nest ID as a random factor. We fitted fully parameterized models using maximum likelihood (ML), and removed terms by sequential deletion while testing for significant changes in model variance using Likelihood Ratio Tests (LRTs) and by examining changes in AIC (Crawley 2007). We then refitted the minimum adequate model using restricted maximum likelihood (REML) to estimate effect sizes. Provisioning rate and prey length were log-transformed to reduce heteroscedasticity.

Differences in size and location of core foraging areas during early chick-rearing (before June 20 when chicks were <18 days old) and late chick-rearing (from June 20 when chicks were >18 days old) were compared for Arctic and Common terns. Sample sizes of Roseate Tern tracks were too small to allow foraging areas at different chick-rearing stages to be examined. Kernel density estimations were generated for each species and breeding stage using the ad hoc method to estimate h (value varies depending on number of dive locations) and a grid size of 100 m^2. Overlap in foraging ranges and core foraging areas between stages was quantified for both species, illustrating the degree of similarity in foraging areas as brood age increased. Analyses were carried out in R version 2.14.1 (R Development Core Team 2011) and ArcGIS version10.1. Means are presented ± 1 standard error throughout.

RESULTS

Prey Selection

There were significant differences in the proportion of sandeel (Kruskal-Wallis test: $\chi^2_2 = 25.67$, $p<0.001$, $n = 31$) and mean prey length (Kruskal-Wallis test: $\chi^2_2 = 19.71$, $p<0.001$, $n = 31$) fed to chicks of different tern species. Arctic Tern chicks received the highest percentage of juvenile fish (Table 2) and were fed smaller prey items than chicks of other tern species. Roseate Tern chicks were fed a higher percentage of sandeel than were Arctic or Common tern chicks and were fed significantly larger prey items than Arctic Terns ($\chi^2_1 = 15.66$, $p<0.001$, $n = 22$; Table 2). Provisioning rates were significantly higher for Arctic Terns than for Common or Roseate terns (Table 2).

Foraging Areas

Maximum foraging distance, total distance traveled, and trip duration were calculated from complete tracks; mean bearing on leaving the colony was calculated using complete and incomplete tracks. Figure 2 illustrates foraging tracks and dive locations for Arctic, Common, and Roseate terns from June 20 to July 1. Arctic Terns foraged north of the colony (Figure 2A) and Common Terns farther south (Figure 2B). Core foraging areas of both species were centered close to the colony (Figure 3A, B) while that of Roseate Terns was situated slightly farther away and closer to shore (Figure 3C). There were no significant differences in mean maximum foraging distance, total foraging distance, or trip duration among tern species (Table 3). However, there were significant differences in mean bearing on departing the colony with Roseate Terns leaving to forage almost exclusively to the northwest (Figure 2). There was less variation in departure direction among Roseate Terns than among Arctic and Common terns and Roseate Terns left the colony in a significantly different direction than other species (Table 3).

There were differences in the extent of species' foraging ranges with Arctic Terns covering a larger area than those of Common and Roseate terns (Table 4). Common and Roseate tern core foraging areas were only slightly smaller than those of Arctic Terns and, while species shared less than 41% of core foraging areas, high percentages of Common and Roseate tern foraging ranges and Common Tern core foraging areas were found within those of Arctic Terns (Table 4).

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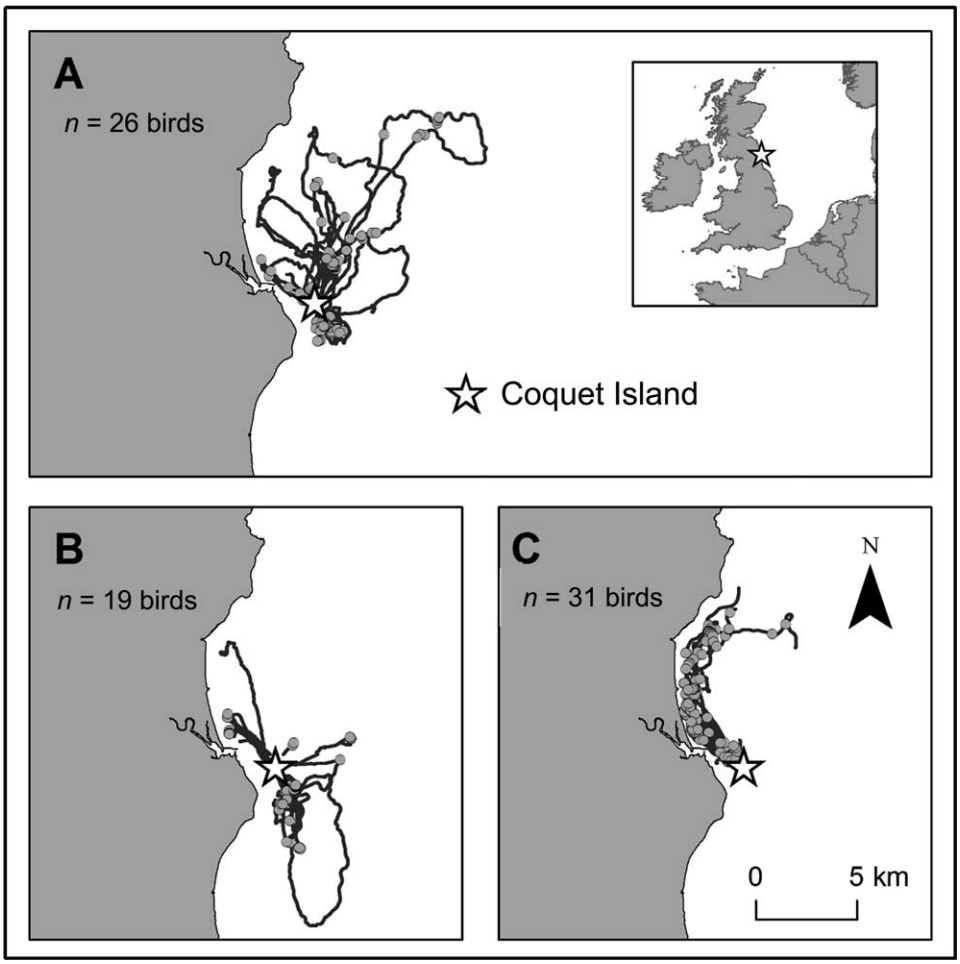


FIGURE 2. Complete and incomplete foraging tracks and dive locations for (**A**) Arctic Terns (number of track locations = 19,467; number of dive locations = 111), (**B**) Common Terns (number of track locations = 11,136; number of dive locations = 77), and (**C**) Roseate Terns (number of track locations = 18,001; number of dive locations = 206) from June 20 to July 1. Tracks represented by solid lines and dive locations by shaded dots. Coquet Island is represented by a star.

Effect of Brood Age and Size on Foraging Behavior

Relationships between provisioning rate, prey length, and brood age were examined for each species using diet observations from June 2 to July 9. While Arctic and Common tern provisioning observations were available for broods 0–35 days old, Roseate Tern observations were only available for broods aged 0–25 days. Arctic Tern mean provisioning rate increased with brood age while provisioning rates of Common and Roseate terns did not change (Species × Brood age interaction: $\chi^2_2 = 23.13$, $p<0.001$, $n = 594$; Figure 4A). In addition, provisioning rate decreased with brood size for all species ($\chi^2_2 = 32.84$, $p<0.001$); chicks from smaller broods had higher provisioning rates than chicks from larger broods (Table 6 in Appendix).

There was a significant effect of brood age on prey length ($\chi^2_1 = 10.80$, $p<0.001$, $n = 511$), suggesting that in general, species delivered larger prey items with increasing brood age (Table 7 in Appendix). With respect to prey length, there was no significant interaction between species and brood age ($\chi^2_2 = 4.36$, $p = 0.11$). Brood size had no effect on prey length ($\chi^2_1 = 0.03$, $p = 0.87$) and Common and Roseate terns continued to feed chicks significantly larger prey items than did Arctic Terns as brood age increased ($\chi^2_2 = 64.56$, $p<0.001$; Figure 4B).

Arctic and Common tern core foraging areas shifted closer to the colony during late chick-rearing, reflecting the increased provisioning rate of Arctic Terns described above (Figures 4A and 5). Late chick-rearing foraging areas were smaller than those of early chick-rearing in both species and, while a high percentage of late chick-rearing foraging ranges were found within those of early chick-rearing, no overlap in core foraging areas between stages was evident in either species (Table 5). However, core

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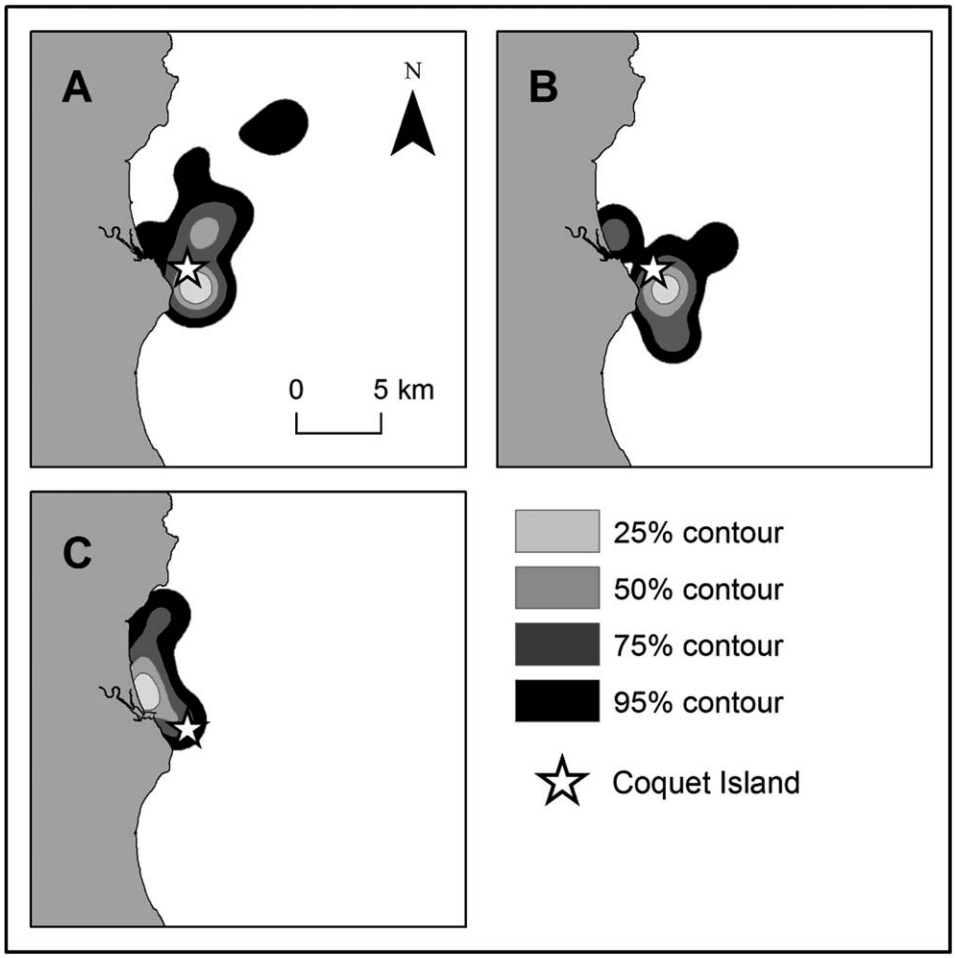


FIGURE 3. Kernel utilization distribution of 394 dive locations (Arctic = 111; Common = 77; Roseate = 206) using tracks from (**A**) 26 Arctic Terns, (**B**) 18 Common Terns, and (**C**) 31 Roseate Terns.

foraging areas of both species overlapped by 40% during late chick-rearing (Figure 5). Although Arctic and Common terns shared similar foraging areas during late chick-rearing, they partitioned resources by varying both prey length and frequency of delivery.

DISCUSSION

Resource competition should favor adaptations that reduce niche overlap (Gause 1934), which may explain species-specific differences in seabird foraging areas and

TABLE 3. Foraging trip characteristics of 3 tern species. Sample size (*n*) is provided for complete and incomplete tracks. Mean maximum foraging distance, total distance traveled, and mean trip duration were calculated using complete tracks; mean bearing on leaving the colony included incomplete tracks. Lower quartiles, medians, upper quartiles, and mean values ± SE are given. Significant differences are indicated in bold.

	Mean maximum foraging distance (km)	Total distance traveled (km)	Mean bearing on leaving colony (degrees where 0° = North)	Mean trip duration (min)
Arctic Tern	1.17, 1.76, 3.39 ($n = 13$)	1.41, 2.35, 4.73 ($n = 13$)	**239.55 ± 20.93 ($n = 25$)**	3.20, 9.88, 15.72 ($n = 13$)
Common Tern	3.35, 3.60, 3.93 ($n = 7$)	4.95, 6.08, 6.72 ($n = 7$)	**267.24 ± 24.04 ($n = 19$)**	9.28, 10.23, 11.07 ($n = 7$)
Roseate Tern	1.22, 1.62, 3.30 ($n = 15$)	1.93, 2.77, 6.23 ($n = 15$)	**101.41 ± 1.70 ($n = 31$)**	3.03, 5.75, 9.38 ($n = 13$)
	Kruskal-Wallis: $\chi^2_2 = 4.45$, $n = 35$, $p = 0.11$	Kruskal-Wallis: $\chi^2_2 = 2.11$, $n = 35$, $p = 0.35$	**Circular ANOVA: $F_{2,74} = 7.34$, $n = 75$, $p = 0.001$**	Kruskal-Wallis: $\chi^2_2 = 1.99$, $n = 35$, $p = 0.37$

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TABLE 4. Foraging range (95% volume contour) and core foraging area (25% volume contour) sizes (km^2) for 3 tern species and percentage of species' foraging areas located within those of Arctic Terns.

	Arctic Tern	Common Tern	Roseate Tern
Foraging range (km^2)	54.10	42.42	36.57
Core foraging area (km^2)	2.91	2.20	2.83
Foraging range shared with Arctic Terns (%)	—	63	41
Core foraging area shared with Arctic Terns (%)	—	94	0

feeding behavior (Rome and Ellis 2004, Lance and Thompson 2005). There are several explanations for how competition facilitates resource partitioning among species. One species may outcompete and directly exclude another from foraging areas, or species may use habitats which suit preferred feeding methods. Even if competition is not currently affecting species interactions, previous competition could have produced interspecific variation in ability to exploit different habitats (Trivelpiece et al. 1987, Wood et al. 2000). Studies have suggested that other seabirds exclude Roseate Terns from feeding flocks and that Roseate Terns forage more efficiently in flocks containing only conspecifics (Duffy 1986, Shealer and Burger 1993). Our results show that Roseate Terns utilize separate foraging areas from other tern species, but it is unclear whether this is caused by a preference for specific foraging conditions or from tern species excluding Roseate Terns from other areas.

Our findings provide direct evidence of resource partitioning by both foraging area and diet composition within a multi-species seabird assemblage. As in previous studies, Common and Roseate terns fed chicks large energy-rich prey items less regularly while Arctic Terns fed a higher proportion of small juvenile fish at a higher rate (Safina et al. 1990, Robinson et al. 2001, Rock et al. 2007).

Roseate Terns fed chicks a high proportion of sandeel and large prey items throughout the chick-rearing period. This species is a dietary specialist over most of its range and relies on few fish species during the breeding season, especially sandeel (Randall and Randall 1980, Nisbet 1981, Safina et al. 1990). This specialization may be a consequence of competition with other species (Duffy 1986, Shealer and Burger 1993) or a preference for specific foraging conditions (Safina 1990a, Shealer 1996). While relatively small, the breeding population of Roseate Terns on Coquet Island is currently stable suggesting there is sufficient food available close to the colony.

Arctic Terns have a limited diving ability and forage more regularly by surface dipping than Common and Roseate terns, which mainly plunge-dive (Shealer 2001,

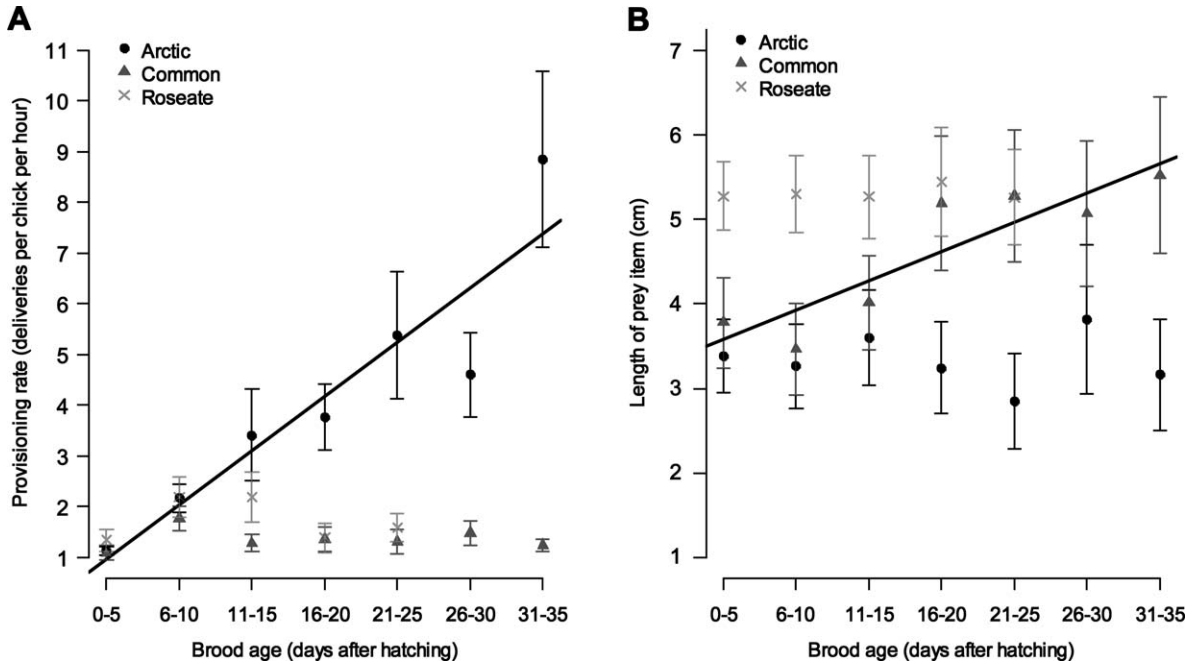


FIGURE 4. (**A**) Mean provisioning rate (deliveries per chick per hour) ± SE for each brood age category (days after hatching). Straight line shows significant linear regression for Arctic Terns ($F_{1,5} = 29.61$, $p = 0.01$, $r^2 = 0.83$). (**B**) Prey length (cm) ± SE for each brood age category with significant linear regression for Common Terns ($F_{1,5} = 20.40$, $p = 0.01$, $r^2 = 0.76$).

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TABLE 5. Foraging range (95% volume contour) and core foraging area (25% volume contour) sizes (km^2) during early (before June 20) and late chick-rearing (from June 20) and percentage overlap between breeding stages.

	Arctic Tern				Common Tern			
	Early chick-rearing (km^2)	Late chick-rearing (km^2)	Overlap (%)	Within early chick-rearing (%)	Early chick-rearing (km^2)	Late chick-rearing (km^2)	Overlap (%)	Within early chick-rearing (%)
Foraging range	92.02	45.92	27	80	108.22	51.56	19	59
Core foraging area	5.44	3.27	0	0	6.16	3.04	0	0

Cabot and Nisbet 2013). Fish larvae and juvenile fish are more likely to congregate near the surface than adult fish, but are smaller than prey usually selected by terns (Rindorf et al. 2000, Cabot and Nisbet 2013). Arctic Terns may have preferentially selected small juvenile fish as they were readily available and easy to catch and transport (Hopkins and Wiley 1972), and delivered them regularly to compensate for their lower energy content. Common and Roseate terns selected larger fish, which may have been in range of their deeper diving capabilities and are easier for these larger-billed tern species to carry (Nisbet 1981, Snow and Perrins 1998, Shealer 2001). Shealer (1996) suggested the limited diet of Roseate Terns was a consequence of foraging habitat specialization. Roseate Tern foraging areas are associated with various biotic and abiotic habitats, including presence of predatory fish (Shealer 1996) and shallow water (Safina 1990a), which affect the availability of sandeel in surface waters. The region in which Roseate Terns were observed foraging around Coquet Island was restricted to depths of <30 m (JNCC personal communication).

Interspecific variation in time spent in specific habitats has been linked to dietary differences, suggesting that dietary segregation is associated with spatial partitioning (Waugh et al. 1999). In our study, Arctic and Common terns foraged over a wider area than Roseate Terns, Arctic Terns concentrating farther north of the colony and Common Terns farther south. There was considerable variation in the mean bearing in which Arctic and Common terns left the colony, while Roseate Terns departed consistently to the northwest. All 3 tern species nested mainly in the southwestern side of the island, so minimizing distance between foraging locations and nest sites is unlikely to have been an important factor. Arctic and Common tern core foraging areas showed some overlap while neither species overlapped with Roseate Tern core foraging areas. However, a large percentage of Common and Roseate tern foraging ranges was found within that of Arctic Terns. Individual variation in foraging area, departure direction, and prey selection was greater in Arctic and Common terns than in Roseate Terns, which foraged mainly on sandeel in a restricted area. Lack of individual variation can have significant effects on species' vulnerability to environmental change (Lomnicki 1978, Safina et al. 1990, Bolnick et al. 2003) and may have important consequences for Roseate Tern conservation.

Extent of foraging areas may explain the greater diversity of prey types and sizes delivered by Arctic and Common terns and the limited diet of Roseate Tern chicks. For Arctic and Roseate terns, dietary segregation coincided with spatial partitioning of foraging areas. However, Arctic and Common terns delivered different prey items while sharing a high percentage of foraging areas. We show that dietary segregation occurs when foraging areas are

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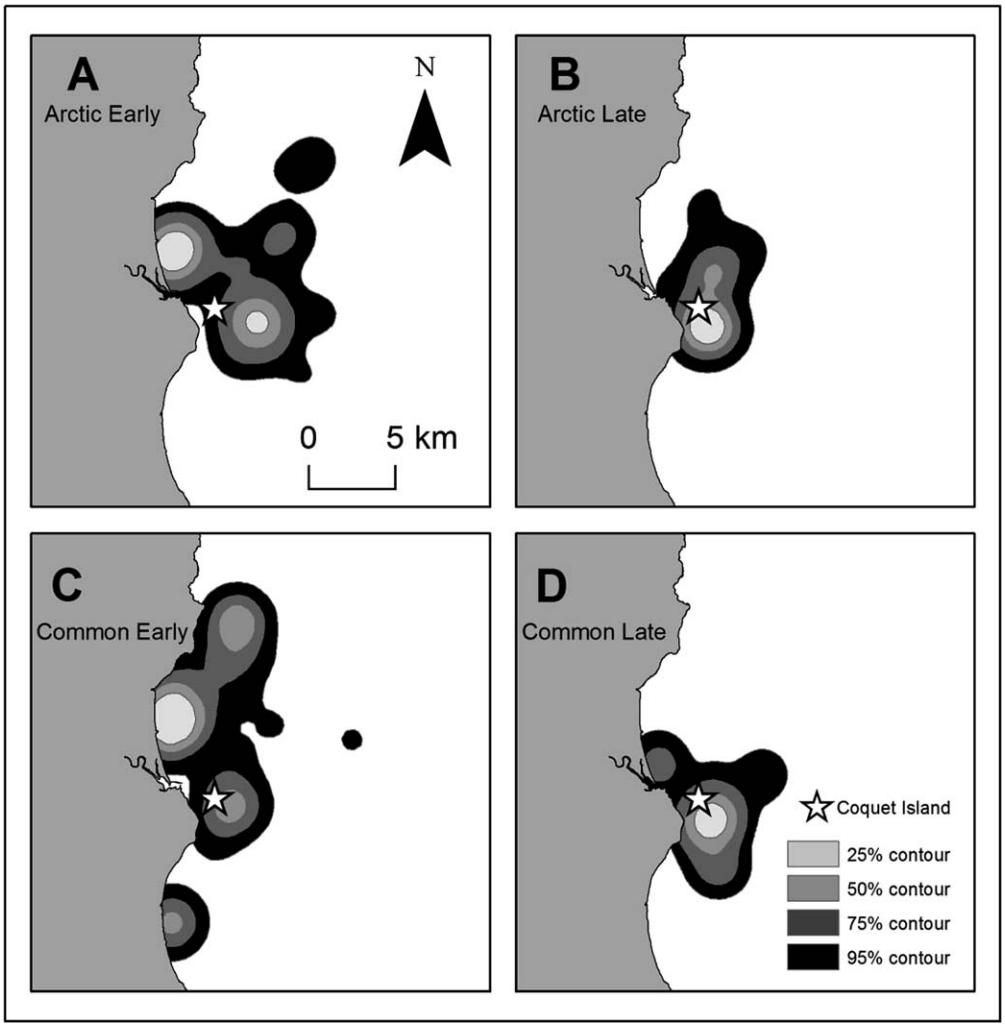


FIGURE 5. Kernel utilization distribution of 470 dive locations during early (<18 days old) and late (>18 days old) chick-rearing for (**A**) Arctic Terns early chick-rearing = 202 locations, 11 tracks; (**B**) Arctic Terns late chick-rearing = 95 locations, 11 tracks; (**C**) Common Terns early chick-rearing = 96 locations, 18 tracks; (**D**) Common Terns late chick-rearing = 77 locations, 7 tracks.

spatially partitioned and also when species forage in similar areas. Similarities in diving ability may explain why Common and Roseate terns, which dive to depths of up to 0.8 m and 1.2 m, respectively, partitioned foraging habitats more completely than Arctic and Common terns, which differ significantly in diving ability (Arctic Terns rarely penetrate more than 0.5 m below the surface [Cabot and Nisbet 2013]). Although our analysis is limited to a single year, visual tracking data from 2009 and 2010 indicate little interannual variation in distributions of all 3 species around Coquet Island (JNCC personal communication).

Species also partition resources by differentially varying foraging behavior in response to increasing brood age (Safina et al. 1990). Chicks require more energy as they approach fledging age (Ricklefs and White 1981), and studies have shown that seabirds increase prey size with brood age, rather than provisioning rate (Wiggins and Morris 1987, Smith 1993). This strategy is more efficient as it requires fewer foraging trips to deliver a given amount of energy. However, there may be costs to delivering larger prey items such as transport, vulnerability to kleptoparasitism, and difficulty in capture (Barrett and Krasnov 1996, Ratcliffe et al. 1997, Dies and Dies 2005). Safina et al. (1990) found that Common Terns fed larger prey items to chicks as the breeding season progressed while Roseate Terns did not.

Arctic Terns in our study responded to increasing chick energy demands by providing more frequent prey deliveries while the average length of prey items remained constant. Common Terns delivered larger prey items as brood age increased while maintaining the same provisioning rates. Arctic and Common tern chicks were similar ages when provisioning observations began, hence changes

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in provisioning rate and prey length were unlikely to have been caused by seasonal effects. Roseate Tern observations started ~11–16 days after those of Arctic and Common terns. Roseate Tern provisioning rates did not change as brood age increased and large prey items were delivered to chicks throughout the chick-rearing period. Although Roseate Tern observations took place when broods were 0–25 rather than 0–35 days old as for Arctic and Common terns, the trend for Roseate Terns to deliver large fish is unlikely to have changed within the last 10 days of chick rearing.

Interspecific variation in foraging behavior with increasing brood age could be explained by changes in foraging areas. Arctic and Common tern foraging ranges and core foraging areas shifted closer to Coquet Island during late chick-rearing. This may have allowed Arctic Terns to increase their provisioning rates, but no corresponding increase was evident in Common Terns; instead, this species fed larger prey with increasing brood age. By foraging closer to the colony, Common Terns may have been able to reduce traveling time and increase time spent selecting larger prey items for chicks. Areas used by Arctic and Common terns during early and late chick-rearing showed some overlap. While species' core foraging areas were slightly different during early chick-rearing, those of both species were located close to the colony during late chick-rearing. Although Arctic and Common terns used the same small foraging area during late chick-rearing, each delivered different prey items. Studies have suggested that partitioning of foraging areas explains interspecific variation in seabird diets (Shealer 1996, Waugh et al. 1999). Our results show that dietary segregation can occur independently of foraging area partitioning and may be due to differences in foraging methods.

Unlike transect-based surveys, visual tracking allows foraging locations of birds of known breeding status and origin to be compared. Our study shows that 3 morphologically similar tern species partition resources using different mechanisms. Arctic and Common terns showed variation in diet, provisioning rate, and response to increasing brood age but shared similar foraging areas, while Roseate Terns differed from other tern species in both diet and foraging area and showed no change in foraging behavior with increasing brood age. We show how studies on multi-species assemblages can effectively compare mechanisms used to partition resources among species breeding sympatrically in a competitive environment, and illustrate the extent to which overlap in diet and foraging areas can vary among morphologically similar species.

We provide strong evidence of 3 sympatric seabird species partitioning resources by diet, foraging area, and response to increasing brood age. Our findings complement those of previous studies comparing diet and foraging area partitioning in 2 seabird species. We show that dietary segregation does not always reflect differential forging area utilization, but that birds foraging in the same area select different prey items.

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APPENDIX

TABLE 6. Results of minimum adequate model fitted using REML explaining variation in log(provisioning rate) with random factor = Nest, $n = 594$.

	Estimate	SE	*t*-value
Intercept	1.08	0.18	5.92
Species			
Arctic	0	—	—
Common	−0.15	0.17	−0.91
Roseate	−0.47	0.17	−2.71
Brood size	−0.32	0.06	−5.76
Brood age	0.02	0.01	3.41
Species × Brood age			
Arctic	0	—	—
Common	−0.04	0.01	−4.77
Roseate	−0.02	0.01	−2.13

TABLE 7. Results of minimum adequate model fitted using REML explaining variation in log(prey length) with random factor = Nest, $n = 511$.

	Estimate	SE	*t*-value
Intercept	1.00	0.05	20.10
Species			
Arctic	0	—	—
Common	0.38	0.05	7.82
Roseate	0.62	0.05	13.24
Brood age	0.07	0.01	3.11

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