

**Foraging ecology and parental care of common terns
(*Sterna hirundo*) nesting in Windermere Basin, Lake Ontario.**

by

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ABSTRACT

The relationships among chick feeding, size and type of prey item, and foraging time away from the brood have not been well studied in seabirds. This study investigated spatial and temporal patterns of foraging and chick-provisioning among 23 radio-tagged male common terns nesting at Hamilton Harbour, Lake Ontario during 1991 and 1992. Telemetry data were collected concurrently with behavioural observations from an elevated blind.

Terns fitted with transmitters did not differ from controls with respect to either brood attendance, patterns of chick mortality, species and size distributions of prey delivered to offspring, or chick-provisioning rates. There was a clear separation of parental roles: males were primarily responsible for feeding chicks while females allocated more time to brood attendance. The prey species most commonly delivered to chicks by adults were rainbow smelt (*Osmerus mordax*) and alewife (*Alosa pseudoharengus*), followed in importance by larval fish, emerald shiner (*Notropis antherinoides*), salmonids, and fathead minnows (*Pimephales promelas*). The relative proportions of various fish species delivered to chicks by males differed over the course of each breeding season, and there was also much variability in species composition of prey between years. Sizes of prey delivered to chicks also differed between sampling periods. The modal size of fish brought to chicks during Peak 1991 was 1.5 bill lengths, while the majority of prey in Late 1991 were small larval fish. The reverse trend occurred in 1992 when small fish were delivered to chicks predominantly during the Peak nesting period. During periods when predominantly small fish were delivered to chicks, the foraging activity of radio-tagged males was concentrated within a two kilometer radius of the colony. The observed variation in prey composition and foraging locations during the study likely reflects temporal variation in the availability of prey in the vicinity of the colony. Males delivered fish to chicks at a constant rate, while females

increased their feeding frequency over the first six to ten brood days. The mean length of fish delivered to chicks by adults increased significantly with increasing chick age.

As a group, within each nesting period, transmitted males either foraged predominantly in the same directional bearing (north during Peak 1991, south during Late 1992), or concentrated foraging activity in the immediate vicinity of the colony (Late 1991, Peak 1992). However, individual radio-tagged males exhibited unique and predictable foraging patterns, often favouring specific locations within these areas and differing in their secondary foraging patterns. Overall, the Lake Ontario shoreline between "CB Bay" (3.5 km south of colony) and the lift bridge canal (4 km north of colony) was the foraging area used most frequently by radio-tagged males during the chick-rearing period.

Foraging patterns of transmitted males at Windermere Basin are similar to patterns of peak-nesting common terns, but differ from those of late-nesters, at a nearby colony (Port Colborne, Lake Erie). Differences between the foraging patterns of late-nesting terns at these colonies likely reflect differences in annual patterns of fish availability between the two locations.

No relationship was found between foraging proficiency of adults and survival of offspring. Stochastic factors, such as predation by black-crowned night-herons (*Nycticorax nycticorax*) and adverse weather conditions during the early stages of chick rearing, may be more important determinants of common tern breeding success than parental quality or fish availability.

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INTRODUCTION

Food supply is believed to play an important role in shaping the reproductive adaptations of seabirds (Lack 1968). Food accessibility may limit colony size (Furness and Birkhead 1984; Birt *et al.* 1987), and influence the evolution of clutch size (Lack 1968), juvenile life histories (Ydenberg 1989), extended parental care, and delayed first breeding (Lack 1968). Proximately, food availability may control timing of egg laying (Becker *et al.* 1985; Safina *et al.* 1988), clutch size and chick survival (Safina *et al.* 1988), and determine the relative allocation by each sex to different parental roles (Pierotti 1981; Wagner and Safina 1989). In instances when prey abundance has been measured, variability in chick growth, feeding patterns, and seasonal breeding success of seabirds have reflected fluctuations in prey availability (Anderson *et al.* 1982; Schaffner 1986; Safina *et al.* 1988)

Most seabirds are central place foragers, and feed well away from the breeding colony. Until recently, biologists have not been able to measure the food resources of off-shore feeding birds, nor to directly observe the foraging behaviour of breeding adults (Anderson and Ricklefs 1987). Measuring prey in aquatic systems has proven particularly difficult because prey are usually highly mobile, patchily distributed and difficult to observe (Safina *et al.* 1988). Instead, characteristics of their food supply have been inferred from stomach contents (Croxall and Prince 1980), the frequency of feeding trips to the nest (Ashmole and Ashmole 1967; Courtney and Blokpoel 1980; Harris 1984; Cairns 1987) and observations of unmarked birds at sea (Gaston and Nettleship 1981; Schneider and Hunt 1982; Tasker *et al.* 1985). None of these methods are able to relate feeding frequency to the location and availability of prey resources. Factors other than food supply, such as risks of predation or intraspecific aggression in crowded colonies, may have selected for the observed breeding adaptations and patterns of chick-provisioning among seabirds. Therefore, food availability of seabirds must

be assessed directly in order to understand its relationship to breeding adaptations (Anderson and Ricklefs 1987).

Fish stocks have proven extremely difficult to assess and subsequently very few studies have addressed this problem directly (but see Safina and Burger 1988, 1989; Safina *et al.* 1988). Three components of seabird foraging ecology that can be assessed are the location, temporal pattern, and success of foraging by breeding adults (Anderson and Ricklefs 1987). Telemetry is an excellent tool that allows researchers to directly investigate some of the relationships between breeding success and foraging behaviour. Radiotelemetry has a history of variable success (negative, Massey *et al.* 1988; positive, Morris and Burness 1992), but is particularly suited for gathering information on the foraging patterns of individual birds (Morris and Black 1980; Jouventin and Weimerskirch 1990; Wanless *et al.* 1990). This technique has revealed considerable variation in foraging patterns among individuals, which could potentially translate into differential breeding success (Morris and Black 1980).

Age-related differences in foraging ability among seabirds are well documented (Dunn 1972; Buckley and Buckley 1974; Burger and Gochfeld 1979, 1981; Porter and Sealy 1982; Greig *et al.* 1983; Maclean 1986; Burger 1987). Buckley and Buckley (1974) compared the feeding behaviour of adult and juvenile royal terns (*Sterna maxima*) and found that adults spent less time foraging, caught more prey per unit time, and dropped fish less frequently, thereby expending less energy per prey item captured than juveniles. These findings are consistent with hypotheses that the limited availability of food resources in the environments in which seabirds live have resulted in the evolution of extended parental care and delayed breeding. Under such conditions it may take a considerable amount of time to learn how to forage efficiently.

Foraging proficiency has also been shown to vary considerably among adult birds. Schaffner (1990) found that provisioning intervals (and thereby feeding

rates) of white-tailed tropicbirds (*Phaethon lepturus*) were more variable than feed masses. While all parents brought back similar amounts of food, some were able to locate and capture prey more rapidly. Several studies have found positive correlations between courtship-feeding rates and chick feeding rates of male common terns (*S. hirundo*, Nisbet 1973; Wiggins and Morris 1986) and herring gulls (*Larus argentatus*, Niebuhr 1981). The observed differences in courtship- and chick-feeding would argue that all males are not equally proficient (or equally motivated) at prey capture, and courtship feeding may be the mechanism by which females can assess male parental quality. Recent studies have also established variation in the foraging locations utilized among individuals breeding at the same colony during the same period of time (Morris and Black 1980; Anderson and Ricklefs 1987; Jouventin and Weimerskirch 1990; Wanless *et al.* 1990). Wanless *et al.* (1990) found that individual, radio-tagged common murrelets (*Uria aalge*) and razorbills (*Alca torda*) used widely separated feeding areas over a short period of time and on any given day birds of the same species foraged in quite different areas. Jouventin and Weimerskirch (1990) used satellite telemetry to follow six male wandering albatrosses (*Diomedea exulans*) during the incubation period, and found a high level of variability among males in duration of foraging trips, and at least some males foraged in different locations. The types of prey fed to chicks has also been shown to influence chick growth. Massias and Becker (1990) found that the quality of chick diet is an important factor influencing growth, but that most chicks were fed a high proportion of lower quality prey items. This may reflect differences in resource availability, or in adult foraging efficiency. It is known that at least some adult common terns do not adjust their fishing in response to a chick's inability to swallow a particular species of fish, and continue to return with these fish even though the chicks are unable to consume them (Burger and Gochfeld 1991).

Despite the overwhelming evidence that there is much variation in individual foraging patterns and/or ability, only a few studies (Morris and Black 1980; Burness 1992) have directly investigated the relationship between foraging patterns and breeding success. Morris and Black (1980) found that radio-tagged herring gulls were predictable, although highly individualistic, in their movement patterns. They also established that there was a clear relationship between movement patterns and eventual brood success of birds studied.

In common terns, as is typical of most seabirds, both pair members exhibit extensive participation in parental care. Previous studies have shown that male and female common terns perform different parental roles during a breeding bout (Nisbet 1978; Wiggins and Morris 1987). At colonies in the Great Lakes, females allocate more time to territorial attendance during incubation and chick-brooding stages than males, who are largely responsible for chick provisioning (Wiggins and Morris 1987; Burness 1992). Common terns feed predominantly on small fish which they capture one at a time by "plunge diving" (Erwin 1977). Prey are carried sideways in the bill and delivered whole to chicks which makes identification and estimation of size easy. In Lake Ontario, alewife and rainbow smelt are the predominant prey species (Gilbertson and Reynolds 1972; Courtney and Blokpoel 1980).

Only one previous study has investigated the foraging patterns of common terns using radio telemetry. Burness (1992) found that individual, radio-tagged common terns exhibited predictable foraging patterns with some degree of inter-individual variability, and also found corresponding differences in chick-provisioning rates. There was little inter-year variability in the foraging patterns of individuals that were tracked for more than one season. These differences in foraging patterns between individual males did not, however, translate into differential breeding success, possibly because stochastic factors (such as predation) played a greater role in chick survival than food availability.

Little is known about the demography, parental care, or foraging ecology of common terns nesting in the Windermere Basin of Hamilton Harbour, Lake Ontario. Since the colony at Windermere Basin was only established in 1989, it is likely that there are differences in foraging and parental care behaviours associated with colony age structure, between common terns nesting at this site and those breeding at older terneries on the Great Lakes. In particular, this study will provide a unique comparative data set with a well-studied (Morris and Hunter 1976; Morris 1986; Wiggins and Morris 1986, 1987; Wiggins 1989; Morris and Burness 1992) colony at Port Colborne, Ontario that has been occupied for 40 years. There may also be differences between these two sites related to colony location. Physical characteristics of the freshwater systems in which these colonies are located (Lakes Erie and Ontario) may create conditions that result in differential prey availability or accessibility, resulting in different types or distributions of prey fish delivered to chicks.

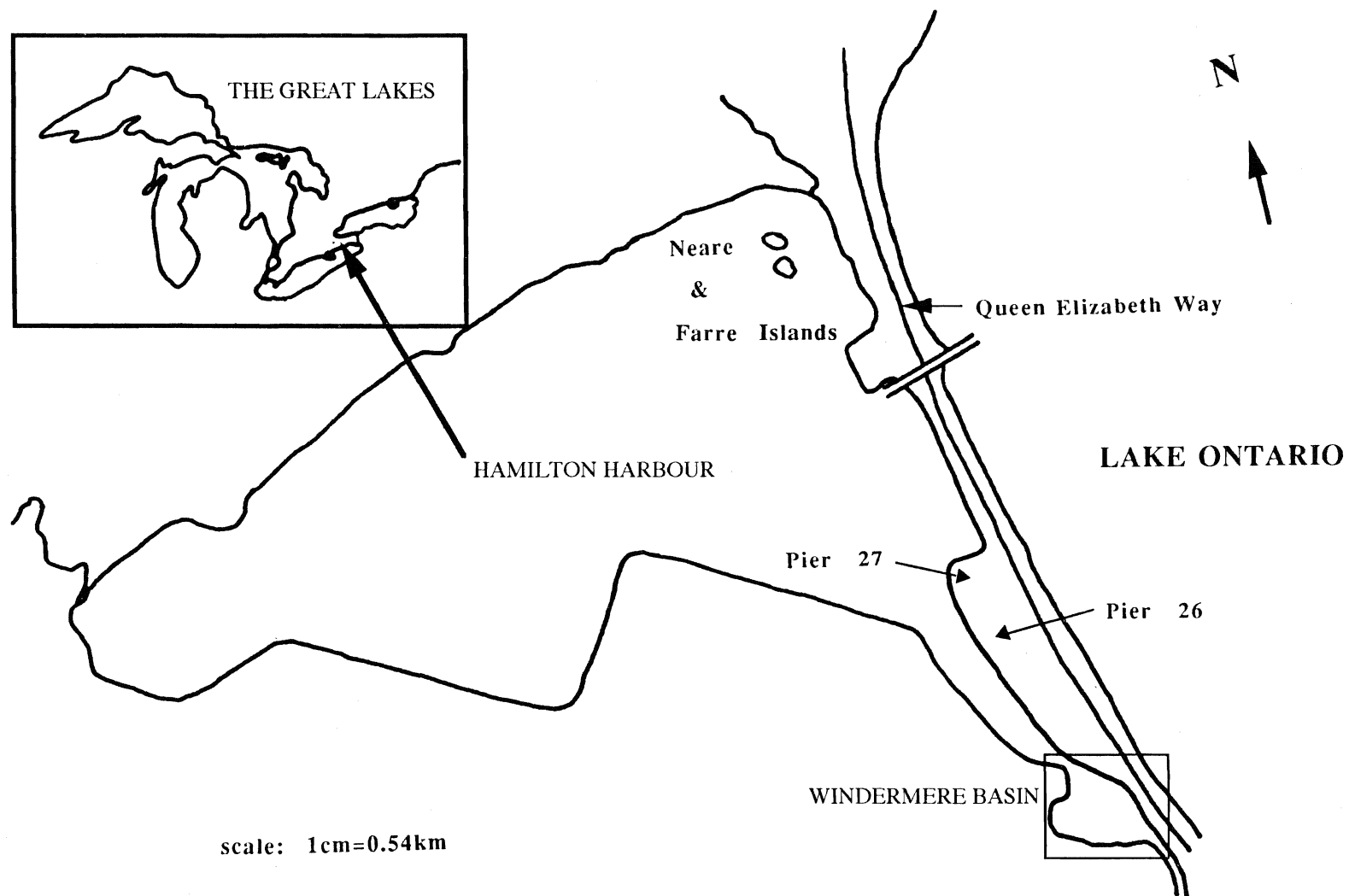
The objectives of this study are to use radio telemetry in concert with behavioural observations from a blind to 1) establish the movement patterns and foraging locations of birds carrying radio transmitters, 2) determine the feeding frequency and types of prey delivered to chicks, 3) determine the relationship between the foraging patterns of adult common terns nesting at Hamilton Harbour and their seasonal breeding success, and 4) compare the results from Windermere Basin with foraging patterns of common terns nesting at a nearby colony in Port Colborne, Lake Erie.

METHODS

2.1 Study location

This study was conducted at Windermere Basin (43°16'24"N, 79°46'46"W), located in the southern-most portion of Hamilton Harbour, at the extreme north-western end of Lake Ontario (Fig. 1). Common terns have nested in Hamilton Harbour since 1961 (Morris *et al.* 1976), but permanent breeding colonies have existed there only since 1982 (Dobos *et al.* 1988). From 1982 until 1988, most of the common terns in Hamilton Harbour were nesting on two small artificial islands, Neare and Farre Islands, and the in eastern part of the Harbour along Pier 27. These sites were abandoned during 1988-89, probably because of competition with ring-billed gulls (*L. delawarensis*) for breeding sites (Weseloh and Bishop 1990). The present colony in the Windermere Basin was established in 1989 after suitable nesting habitat was created there, in the form of a system of man-made dykes and elevated mudflats (Weseloh and Bishop 1990). Nest scrapes were constructed on either a fine gravel or dirt substrata, and depressions were often lined with twigs or small stones. In both years of my study, nesting areas were covered with dense vegetation by the middle of June. While known records are few, the Windermere Basin colony is comprised both of individuals hatched in Hamilton Harbour (N=7 band returns), as well as immigrants from other colonies on the Great Lakes (N=4 band returns; DJM, unpubl. data). This colony is presently the second largest on the Great Lakes (Dobos *et al.* 1988), consisting of an estimated 585 breeding pairs in 1991 and 713 pairs in 1992 (based on clutch counts taken on 24 May of each year). I conducted this study during the 1991 and 1992 breeding seasons, which lasted from late April to mid-August.

**Figure 1. Location of study site at Windermere Basin,
Hamilton Harbour. Inset shows study area in
relation to Great Lakes region.**



2.2 Selection of study pairs

Common terns often exhibit a bimodal distribution of clutch initiation dates over the course of a breeding season. The first mode of this distribution represents a relatively synchronous initiation of clutches by many of the females present at the colony during early May. In late June or early July a second period of breeding activity is initiated by failed breeders or younger, less experienced individuals nesting for the first time (Hays 1978; Nisbet *et al.* 1984). I chose sampling periods to correspond with these "peak" and "late" breeding periods for each of the 1991 and 1992 breeding seasons. Hereafter, these nesting periods are referred to as Peak and Late respectively. In 1991, study clutches were initiated from 9-15 May in the Peak period, while clutch initiation ranged from 29 June to 5 July for the Late period. Clutch initiation dates for Peak and Late in 1992, corresponded to 8-12 May and 11-23 June respectively (Table 1). Clutch initiation dates for the Peak periods are actual dates, while clutch initiation dates for the Late samples are back-dated from known hatching dates.

I visited the study area daily beginning in mid-April (in both 1991 and 1992) to record the arrival of terns, and determine laying chronologies at points across the study area. Daily nest checks confirmed clutch initiation dates and clutch sizes. Scrape locations were identified by numbered nest markers and eggs were individually numbered with a permanent, non-toxic marker in the order of laying sequence. Eggs were weighed, and width/length measurements were recorded. During each study period, I selected a study plot determined from these regular checks to represent the highest nesting density of tern pairs laying during that period. An elevated blind (1.25mX1.25mX1.5m) was erected shortly after clutch completion for the Peak periods (16 May 1991; 12 May 1992), and during late incubation for the Late sampling periods (21 July 1991; 29 June 1992).

Table 1. Clutch initiation dates and clutch size data for common tern study pairs at Windermere Basin, in which one of the pair members was radio-tagged (Transmitter) or neither member of the pair was assigned a transmitter (Control).

Sampling Period	Group (N; Males/Females)	Clutch initiation dates (range)	Clutch size	
			2-egg	3-egg
Peak 1991	Control (8)	09 - 15 May	0	8
	Transmitter (6M/2F)	13 - 14 May	0	8 ¹
Late 1991	Control (9)	29 June -05 July ²	7	2
	Transmitter (4M)	30 June -04 July ²	2	2
Peak 1992	Control (6)	11 -17 May	0	6
	Transmitter (6M) ³	08 -11 May	0	6
Late 1992	Control (6)	10 -23 June ²	0	6 ⁴
	Transmitter (5M/1F)	13 -15 June ²	0	6 ⁴

¹ One 4-egg clutch reduced to a 3-egg clutch.

² Initiation dates based on back dating from hatching of the first egg (assuming a 20 day developmental period).

³ One transmitter was lost on its second day after the male's clutch was predated.

⁴ 2-egg clutches supplemented to produce 3-egg clutches.

Common terns are sexually monomorphic and the sex of an individual can only be determined using behavioural observations, morphological measurements, or by performing a laparotomy. For Peak 1991 and 1992, daily periods of observation were spent in the blind to observe copulations and courtship feeding behaviour for the purpose of establishing the sex of potential study pairs (Morris 1986). Within each potential study pair, at least one pair member was individually recognizable by at least one of the following criteria: the individual was previously banded with a metal ring, had a unique colour pattern on its bill, or was colour-dyed with picric acid. In Peak 1991 and Peak 1992 most study pairs were sexed using sex-specific behavioural acts (N=22). For pairs that could not be distinguished by this method (N=6), sex was later deduced from head-bill measurements when both members of the pair were trapped (see Coulter 1986; Chardine and Morris 1989). In two cases, the determination of sex by head-bill measurements was confirmed later in the breeding season when I observed these individuals performing sex-specific behavioural acts. Since observation blinds were erected during the Late breeding periods after copulation and courtship-feeding activity had largely ceased, only eight pairs were sexed using behavioural criteria. The sex of most pair members (N=17) was determined using head-bill measurements alone. Of the pairs sexed using head-bill measurements, 15 were later confirmed through behavioural observations.

All study pairs were selected such that they were in close proximity to the blind. Blind-to-nest distances were measured for Peak and Late 1992. The mean distance from observer to nest was 8.41 ± 2.1 m (N=23), with no nest greater than 11.2 m from the blind. No difference was found between experimental and control nests in Peak 1992 ($t = 0.16$, d.f.=9, $p > 0.05$) or Late 1992 ($t = 0.34$, d.f.=10, $p > 0.05$) with respect to distance from the blind compared to 1992. Study nests in 1991 were at similar distances from the blind. Nest densities were also similar

among the four sampling periods ($0.100/\text{m}^2$, $0.099/\text{m}^2$, $0.114/\text{m}^2$, $0.111/\text{m}^2$). During both Peak 1991 and Peak 1992, only nests containing three-egg clutches were used as study nests. Terns nesting during Late 1991 had either 3-egg ($N=4$) or 2-egg clutches ($N=8$). Late-nesting females in 1992 laid either 2- or 3-egg clutches, but I supplemented clutches to produce 3-egg clutches in all study nests (Table 1).

Study pairs were captured immediately prior to egg-hatching with a walk-in trap constructed of chicken wire. In all cases, the trapping of adults was completed within a 1-1.5 day period to minimize disturbance. Each captured animal was weighed and head-bill and bill depth (at the gonys) measurements were taken. A unique combination of PVC colour-bands was placed on the legs of each individual tern, and the tail and/or wings were sprayed with picric acid dye to facilitate identification of study birds. Study pairs were assigned to one of two groups; 'experimental' or 'control'. The only difference between these groups was that a transmitter crystal and battery, fused with epoxy to a U.S.F.W.S. aluminum band, was attached in the standard fashion to the leg of each 'experimental' adult (see Morris and Burness 1991 for a description of the transmitter units and details of the procedure). These units weigh approximately 1.28 g and constitute less than 1% of an adult terns body mass (Burness 1992). This is well within the accepted practice that a transmitter should not exceed 5% of a birds body weight (Caccamise and Hedin 1985). These units were previously field tested on common terns, and were found to have no effect on attendance patterns or chick feeding rates (Morris and Burness 1992). Control pairs were used to determine if there was any effect associated with transmitter attachment in this study, and to increase sample sizes for some types of data that were collected. Individuals from 'control' nests and mates of birds receiving transmitters were banded only with a standard metal ring. All study animals were released within 10 minutes following trapping (mean handling time= 6.12 ± 3.12 min.; $N=45$). There was no difference in capture-to-

release time between terns fitted with a transmitter and those receiving only a metal band ($t=1.17$, d. f.=43, $p > 0.05$).

In Peak 1991 six males and two females were fitted with transmitter units, and eight 'control' nests were used. Only males were assigned transmitters during Late 1991 ($N=4$) and Peak 1992 ($N=6$). Control groups consisted of 12 nests for both of these sampling periods. During Late 1992 the transmitter group consisted of five males and one female (Table 1). Over the course of the study, 24 individual common terns were fitted with transmitters, and 26 breeding pairs were used as controls. The majority of transmitter units were attached to males as earlier studies in the Great Lakes found that male contributions to chick feeding are much greater than that of their female partners (Wiggins and Morris 1987, Burness 1992; but refer to Wagner and Safina 1989).

Twice-daily visits were made into each study area during egg pipping and hatching. Investigator disturbance (defined as time spent in the colony, outside of the blind), measured during Peak 1992, was 19.0 ± 10.0 minutes per observation period (excluding the four observation periods when adults were trapped). The amount of time spent in the colony in Peak 1992 is representative of the study as a whole. Brown (1992) found that a similar level of 'normal' investigator disturbance had no effect on the hatching or fledging success of ring-billed gulls. Chicks were color-dyed with picric acid in order of hatching sequence; on the head, chest and rump for the first, second and third-hatched chicks respectively. Study plots were rarely entered after chicks in all study broods hatched, and chick survival was monitored daily from the blind. All study broods were provided with shelters to reduce gull predation (Burness and Morris 1992), except during Peak 1991. Alternatively, these chicks used the dense vegetation that grew in the study plot as shelter.

2.3 Behavioural observations

Six hours were normally spent in the blind each day in two 3-hour periods, after sunrise (0600-0930 hrs) and before sunset (1730-2100 hrs). These time periods were determined from an earlier study to be times of maximum foraging activity (Morris 1986). In total, 325.75 hours of behavioural data were collected over the two years of the study (Table 2). Observations from the blind obtained data on 1) adult attendance patterns during chick brooding, 2) the species and size of fish delivered to chicks, and 3) the feeding frequency by each parent to each chick.

For each study pair, brood attendance (defined as the amount of time spent on territory by each adult, measured in minutes per hour) was measured from the hatching of the last chick (brood age 1) until all chicks from the brood had either fledged or died. Attendance was measured from the hatching of the last chick because during the hatching period adults divide their attention between incubation and chick feeding. Chicks reaching the age of 20 days were considered to have fledged, as they are capable of flight by this time and often move away from their nest sites (Hunter 1976).

Common terns carry fish singly, crosswise in their bills, and deliver them whole to their chicks. This makes possible the identification of fish species and quantification of prey size. Fish size was estimated using the adult's culmen as a template (length = 36.3 ± 1.4 mm, N=42), and recorded to the nearest half bill-length (Wiggins 1984; Wiggins and Morris 1987; Wagner and Safina 1989). At least one specimen of each species of fish delivered to chicks by adults was collected and identified using the classification of Scott and Crossman (1973). Fish species were identified with binoculars (8X40) from the blind, using distinctive morphological features such as color, presence of markings, body shape, scale size and arrangement, and fin shape or position. In cases where a species identification could not be made (N=131; 5.5% of all observations; range = 3.2-9.4% per

Table 2. Hours of behavioural data collected during 1991 and 1992 at Windermere Basin.

Year	Sampling Period	<u>Observation Period</u>			
		<u>Pre-hatch</u>	<u>Post-hatch</u>		
		AM & PM	AM	PM	Total
1991	Peak	54.5	42.5	39.8	82.3
	Late	0	34.8	46.0	80.8
1992	Peak	15.0	23.5	20.5	44.0
	Late	0	25.8	23.5	49.3

breeding period), fish were recorded as either "unknown" (missed by observer) or "unidentified" (a species delivered too infrequently to identify properly). I spent observation periods in the blind prior to chick hatching in both 1991 (54.5 hours) and 1992 (15.0 hours), in order to familiarize myself with the different types of fish and become proficient with the various identification techniques. Feeding frequency was standardized for differences in brood sizes among the control and experimental pairs by dividing the number of feedings per hour by the number of chicks in each brood.

2.4 Radio telemetry

Transmitters (150-152 MHz range; designed and built by Holohill Systems Ltd., Woodlawn, Ontario) and receiving equipment were field-tested in the Windermere Basin area in March 1991 to establish transmitter signal behaviour within that region. Signals were detected using a single-channel receiver connected to a four-element Yagi antennae and held at a height of 1.5 meters. Radio-tracking of all terns began immediately following transmitter attachment (Table 3). Radio telemetry was performed by a field-assistant concurrently with the collection of behavioural data from an observation blind. Watches were synchronized daily so that an accurate record of the birds' movement patterns could be made using both types of data. During the 1991 season, radio-tracking was performed either by boat (N=103.5 hrs) or by car (N=66.25 hrs). Data from telemetry work in 1991 demonstrated that terrestrial-based listening stations were sufficient for establishing common tern movement patterns. Therefore, in 1992 radio tracking was performed exclusively by car (N=108.75 hrs; Table 3).

For each set of birds, a base station was established 100 m directly east of the observation blind (designated as BB in Fig. 17, pg. 94). A second, aquatic base station, located at the Lake Ontario entrance to the Lift bridge canal, was utilized in

Table 3. Hours¹ of radio telemetry data collected during 1991 and 1992 at Windermere Basin.

Year	Sampling Period	Dates	Observation Period				Total
			<u>AM</u>		<u>PM</u>		
			boat	car	boat	car	
1991	Peak	5 - 17 June	21.0	20.5	22.8	18.8	83.0
	Late	21July -2Aug.	32.8	15.5	27.0	11.5	86.8
1992	Peak	1 -11 June	0	34.0	0	24.5	58.5
	Late	6 -18 July	0	25.0	0	25.3	57.3 ²

¹ Defined as number of hours during which the receiver was operating. Telemetry sampling was continuous during these periods, except for the time spent travelling between sampling stations.

² 7.0 hours of telemetry data were also collected during the middle of the day (1100-1600 hrs)

1991 when a boat was used for radio-tracking study subjects. For tracking birds away from the colony, 21 additional sampling stations were established at optimal listening points around the north, west and south shores of Lake Ontario, and along the north and western edges of Hamilton Harbour (Fig. 17). Sampling stations were roughly 2 km apart, distributed over areas where common terns had been observed to forage in years preceding the present study. Previous field-testing showed that transmitters could be detected over a range of 1-1.5 km. Therefore, any signal that was detected could be placed between the sampling station from which it was detected and the adjacent sampling station in the direction of the detected signal. Identical sampling locations were used during 1991 and 1992. Stations were visited in a systematic fashion, that was altered as a consequence of signal information received at each station. Transmitter channels were scanned approximately every 5 minutes during the sampling period, with the exception of time spent moving from one sampling station to another. The mean lifetime of the transmitters used in this study was 11.7 ± 1.9 days ($N=23$; range = 9-16.5 days), excluding one unit that was fitted to a male who abandoned the colony shortly following attachment after its clutch was predated (Table 4). In total, 278.5 hours of radio telemetry data were collected on 24 individual common terns (Table 3). Data collected include details on 1) foraging location, 2) routes taken to and from foraging sites, and 3) variations in frequency and destination of foraging trips away from the colony.

2.5 STATISTICAL ANALYSES

Unless otherwise stated, mean values are reported as the mean plus or minus one standard deviation. For all analyses, the criterion for rejecting the null hypothesis was set at $\alpha=0.05$. Statistical tests, and rational for their use, are described in Zar (1984).

Table 4. Performance of radio transmitters during 1991 and 1992 at Windermere Basin.

Year	Sampling Period	Telemetry Initiated	Telemetry Terminated	Sample Size (N)	Transmitter Life ($\bar{X} \pm 1$ SD days)
1991	Peak	5 June	18 June	8	11.6 ± 1.3
	Late	21 July	7 Aug	4	14.4 ± 2.7
1992	Peak	1 June	11 June	5 ¹	10.1 ± 0.8
	Late	6 July	18 July	6	11.3 ± 0.5

¹ A sixth radio-tagged male deserted the colony and radio telemetry was only performed for three days, as its nest was predated on the evening that the transmitter was attached. This male was excluded from this analysis.

One-way repeated measures ANOVAs were performed for comparisons of both brood attendance and feeding frequency between 1) Transmitter and Control groups, 2) morning and evening observation periods, 3) sexes, and 4) Peak and Late breeding periods. Repeated measures ANOVA procedures were also used to determine if brood attendance or feeding frequency changed with brood age. Brood age, standardized to the hatching of the last chick of a clutch, was used as the repeated measure. All data were pooled into two-day blocks. Repeated measures ANOVAs were also used to compare chick mortality with brood age between Transmitter and Control groups. However, for these analyses, data were not pooled into day blocks. Spearman Rank Correlation was used to determine if a relationship existed between 1) mean feeding frequency and mean size of prey delivered to chicks, and 2) mean feeding frequency during brood ages one to five and offspring survival to a brood age of 15 days. Contingency Table analyses (or Fisher Exact tests) were employed to determine whether there were differences between 1) Transmitter and Control groups, 2) morning and evening observation periods, 3) sexes, and 4) Peak and Late breeding periods, with respect to both the species and size distributions of fish delivered to chicks. Contingency Table analyses were also used to test for homogeneity of signal detections from different sampling stations during each telemetry sampling period. Kendall's Coefficient of Concordance (Siegal and Castellan 1988) was used to determine if there was significant variation between males (within a breeding period) with respect to the foraging locations they favoured.

RESULTS

A. Behavioural observations of parental care

3.1 The behaviour of terns following transmitter attachment

All terns fitted with radio transmitters were released within 10 minutes following trapping (mean handling time = 6.32 ± 2.67 min.; $N=18$). There was no difference in capture-to-release time between terns fitted with a transmitter, and controls receiving only a metal band ($t=1.17$, d. f.=43, $p > 0.05$). During the trapping periods of 1992, I measured the amount of time it took for captured birds to return to their nests upon release (some measurements were also made in 1991). Most radio-tagged individuals returned to their nests within 40 minutes of release (32.1 ± 16.8 , $N=13$), and all but one individual returned within one hour of release. This individual was released at the end of a trapping period and was present at its nest during the next observation period. No significant difference was found between Transmitter and Control groups ($t=0.87$, d.f.=28, $p > 0.05$) with respect to the amount of time taken to return to their nests after release.

The initial reaction of radio-tagged common terns towards their transmitters was to fly out over Windermere Basin and frequently dip into the water. At the colony, terns would peck at the transmitter and antennae, and also trip over the antennae while walking. The frequency of these behaviours varied from individual to individual, but generally ceased after the first day following transmitter attachment.

After an extensive survey in early May, 1992, five of the common terns fitted with transmitters during the 1991 breeding season were observed again at Windermere Basin. All five individuals had intact transmitters although antennas were missing. One of these terns (a female) is known to have also bred in 1992. In contrast, none of the Control birds that were colour-banded during the 1991

breeding season were resighted in 1992. Caution should be used when interpreting these return data with respect to transmitter effects. Notwithstanding, there appear to be no obvious adverse effects associated with transmitter attachment, as the units do not appear to have affected either the winter survival, migration, or site tenacity of these individuals.

3.2 Brood Attendance

3.2.1. Comparisons between Transmitter and Control groups

To determine if there was an effect of radio-tagging on the attendance patterns of study birds, comparisons were made between Transmitter and Control males within each breeding period. These analyses were repeated for females belonging to Control and Transmitter groups. Unless stated otherwise, analyses were performed on data from brood ages one through six, pooled into two-day blocks.

In Peak 1991, there was no significant difference in brood attendance rates between peak-nesting males carrying transmitters ($N=6$) and their non-transmitted male counterparts ($N=8$) during either the morning ($F=0.66$, $d.f.=1, 10$, $p=0.44$) or evening ($F=0.05$, $d.f.=1, 9$, $p=0.84$) observation periods (Table 5). Similarly, no significant difference in brood attendance was observed among the female partners of Transmitter and Control males during the morning ($F=0.12$, $d.f.=1, 10$, $p=0.74$) or evening ($F=1.35$, $d.f.=1, 9$, $p=0.28$; Table 5) in Peak 1991. There were no differences in attendance patterns exhibited by radio-tagged and control males or their female partners during the late-nesting period in 1991. No significant difference was found in brood attendance rates between late-nesting males carrying transmitters ($N=4$) and control males ($N=9$) during either the morning ($F=0.36$, $d.f.=1, 9$, $p=0.56$) or evening ($F=0.14$, $d.f.=1, 9$, $p=0.72$) observation periods (Table 5). Analyses of attendance during the evening

Table 5. Brood attendance ($X \pm 1$ SD min./hr.) for Transmitter and Control groups of common terns nesting during Peak and Late 1991 at Windermere Basin. Only transmittered males and their female partners are included in the Transmitter group. Means were calculated over observed nesting period. Statistical analyses were performed on a subset of the data (see Results section).

Time	Sex	Attendance (X ± 1 SD min./hr.)		Significance F p	
Peak 1991					
		Transmitter (6) ²	Control (8)		
AM (42.5) ¹	Male	11.1 ± 11.9	8.5 ± 10.8	0.66	0.44
	Female	25.6 ± 18.9	29.3 ± 19.0	0.12	0.74
PM (39.75)	Male	4.5 ± 7.0	3.7 ± 5.9	0.05	0.84
	Female	28.3 ± 20.8	30.4 ± 21.1	1.35	0.28
Late 1991					
		Transmitter (4)	Control (9)		
AM (34.75)	Male	14.0 ± 12.3	17.4 ± 13.9	0.36	0.56
	Female	28.2 ± 18.2	24.8 ± 15.6	0.20	0.67
PM (46.0)	Male	9.8 ± 10.7	11.6 ± 13.1	0.14	0.72
	Female	29.5 ± 18.4	23.0 ± 16.4	0.48	0.51

¹ Hours of observation

² Number of study pairs

observation periods of Late 1991 were performed for brood ages one through ten inclusive, pooled into two-day blocks. No significant differences were detected in brood attendance between the female partners of Transmitter and Control males during the morning ($F=0.20$, d.f.=1, 9, $p=0.67$) or evening ($F=0.48$, d.f.=1, 9, $p=0.51$; Table 5) of the late-nesting period in 1991.

Similarly, Transmitter and Control groups did not differ in attendance patterns during either Peak or Late 1992 (Table 6). Sample sizes of five and six radio-tagged males were used during Peak and Late 1992 respectively, complemented with six control pairs during each of these breeding periods. Transmitter and Control males did not differ significantly in brood attendance during either the morning ($F=0.38$, d.f.=1,6, $p=0.56$) or evening ($F=0.11$, d.f.=1,6, $p=0.75$) observation periods of Peak 1992, nor during the morning ($F=0.32$, d.f.=1,6, $p=0.59$) or evening ($F=0.61$, d.f.=1,6, $p=0.46$) in Late 1992 (Table 6). For the evening period of Peak 1992, analyses were performed on brood ages one through three (not pooled into day-blocks) for both males and females. Female partners of radio-tagged and Control males did not differ in brood attendance during either the morning ($F=0.004$, d.f.=1,5, $p=0.95$) or evening ($F=0.18$, d.f.=1,6, $p=0.69$) observation periods of Peak 1992, nor during the morning ($F=0.003$, d.f.=1,6, $p=0.96$) or evening ($F=1.85$, d.f.=1,6, $p=0.22$) in Late 1992 (Table 6). It is clear from analyses of brood attendance patterns during 1991 and 1992 that transmitters had no effect on the behaviour of radio-tagged males or their female partners. Accordingly, in all analyses that follow Transmitter and Control groups are pooled.

Table 6. Brood attendance ($X \pm 1$ SD min./hr.) for Transmitter and Control groups of common terns nesting during Peak and Late 1992 at Windermere Basin. Only transmitted males and their female partners are included in the Transmitter group. Means were calculated over observed nesting period. Statistical analyses were performed on a subset of the data (see Results section).

Time	Sex	Attendance (X ± 1 SD min./hr.)		Significance Fp	
Peak 1992					
		Transmitter (5) ²	Control (6)		
AM (23.5) ¹	Male	21.2 ± 10.6	18.6 ± 12.6	0.38	0.56
	Female	39.7 ± 10.6	42.6 ± 14.1	0.00	0.95
PM (20.5)	Male	12.9 ± 10.9	15.0 ± 11.0	0.11	0.75
	Female	42.9 ± 16.1	45.4 ± 12.0	0.18	0.69
Late 1992					
		Transmitter (6)	Control (6)		
AM (25.8)	Male	19.3 ± 20.0	20.7 ± 17.3	0.32	0.59
	Female	36.8 ± 21.4	31.3 ± 23.2	0.00	0.96
PM (23.5)	Male	11.0 ± 10.8	11.9 ± 14.4	0.61	0.46
	Female	36.0 ± 19.6	44.9 ± 12.6	1.85	0.22

¹ Hours of observation

² Number of study pairs

3.2.2. Sex differences in brood attendance patterns

Comparisons were made to determine if there was significant within-sex variation in brood attendance patterns between the morning and evening observation periods, or if there were differences in the amount of time allocated to brood attendance by males and females within each nesting period. Unless stated otherwise, all ANOVA procedures used data for brood ages one through six, pooled into two-day blocks.

Males spent significantly more time in brood attendance in the morning compared to evening during both Peak 1991 ($F=24.78$, d.f.=1, 21, $p<0.001$; Table 7), and Late 1991 ($F=16.3$, d.f.=1, 20, $p=0.001$; Table 7). In contrast, the amount of time spent by females in brood attendance did not differ significantly between morning and evening observation periods for either Peak 1991 ($F=2.23$, d.f.=1, 21, $p=0.15$; Table 7) or Late 1991 ($F=0.03$, d.f.=1, 20, $p=0.87$; Table 7). Brood attendance was also consistent between morning and evening observation periods for both males and females during 1992. Data were pooled into 2-day blocks and analyzed for brood ages one through four, and one through eight for Peak and Late 1992 respectively. There was no significant difference in male brood attendance between morning and evening observation periods during either Peak 1992 ($F=1.26$, d.f.=1, 16, $p=0.28$; Table 7) or Late 1992 ($F=1.08$, d.f.=1, 8, $p=0.99$; Table 7). No significant differences in female brood attendance were found between the morning or evening observation periods during either Peak 1992 ($F=0.24$, d.f.=1, 16, $p=0.63$; Table 7) or Late 1992 ($F<0.01$, d.f.=1, 8, $p=0.99$; Table 7). In all subsequent analyses of brood attendance patterns, morning and evening observations have been pooled for males and females for all periods, except 1991 males, as they spent significantly more time in brood attendance during the morning.

Table 7. Brood attendance ($X \pm 1$ SD min./hr.) of male and female common terns between morning and evening observation periods, during the Peak and Late breeding periods of 1991 and 1992 at Windermere Basin. Means were calculated over observed nesting period. Statistical analyses were performed on a subset of the data (see Results section).

Sex	Period	Attendance ($X \pm 1$ SD min./hr.)		Significance	
		A.M.	P.M.	F	p
Male	Peak 1991	9.9 \pm 11.4	4.1 \pm 6.5	24.78	< 0.001 *
	Late 1991	16.3 \pm 13.5	11.0 \pm 12.4	16.02	< 0.001 *
	Peak 1992	20.0 \pm 11.5	13.7 \pm 10.8	1.26	0.28
	Late 1992	19.9 \pm 18.8	11.4 \pm 12.2	1.08	0.33
Female	Peak 1991	27.4 \pm 19.0	29.3 \pm 20.9	2.23	0.15
	Late 1991	25.9 \pm 16.4	25.1 \pm 17.2	0.03	0.87
	Peak 1992	38.9 \pm 15.3	43.8 \pm 14.7	0.24	0.63
	Late 1992	34.6 \pm 22.1	39.2 \pm 17.8	0.00	0.99

* Denotes significant result

There were sharp contrasts in the amount of time allocated to brood attendance between the sexes for both Peak and Late periods in 1991 and 1992; during all sampling periods, females spent significantly more time attending the brood than their mates (Table 8). During the initial stages of chick brooding in Peak 1991, the majority of a females time budget (approximately 45 minutes/hour) was allocated to brood attendance compared to a mean attendance rate of approximately 10 minutes/hour among males (Fig. 2A). During Peak 1991 females spent significantly more time engaged in brood attendance than their mates in both the morning ($F=23.8$, d.f.=1, 22, $p<0.001$) and evening ($F=140.45$, d.f.=1, 20, $p<0.001$) observation periods. Brood attendance by females decreased rapidly with increasing brood age ($F=11.36$, d.f.=2, 44, $p<0.001$; Fig. 2A). Attendance by males also decreased significantly with increasing brood age in both the morning ($F=14.98$, d.f.=2, 22, $p<0.001$) and evening ($F=4.85$, d.f.=2, 20, $p=0.02$; Fig. 2A), although the decrease was more rapid during the morning. Both males and females spent negligible amounts of time in attendance by brood ages of 10 and 14 days respectively.

Brood attendance patterns in Late 1991 were similar to those observed during the peak-nesting period. Shortly after hatching, late-nesting females spent approximately 40 minutes/hour in nest attendance, approximately two times that allocated by their mates in both the morning ($F=23.65$, d.f.=1, 20, $p<0.001$) and evening ($F=28.08$, d.f.=1, 20, $p<0.001$; Fig. 2B). The amount of time late-nesting males spent in brood attendance decreased with increasing brood age during the morning observation periods ($F=10.23$, d.f.=2, 20, $p=0.001$) but not during the evening ($F=2.45$, d.f.=2, 20, $p=0.11$; Fig. 2B). Female attendance rates did not change significantly ($F=0.98$, d.f.=2, 42, $p=0.38$) over the first six brood days, but do appear to decrease over the longer period of brood ages one through 16 (Fig. 2B). By brood age 15, late-nesting males and females were each spending

Table 8. Brood attendance ($X \pm 1$ SD min./hr.) between male and female common terns, during the Peak and Late observation periods of 1991 and 1992 at Windermere Basin.

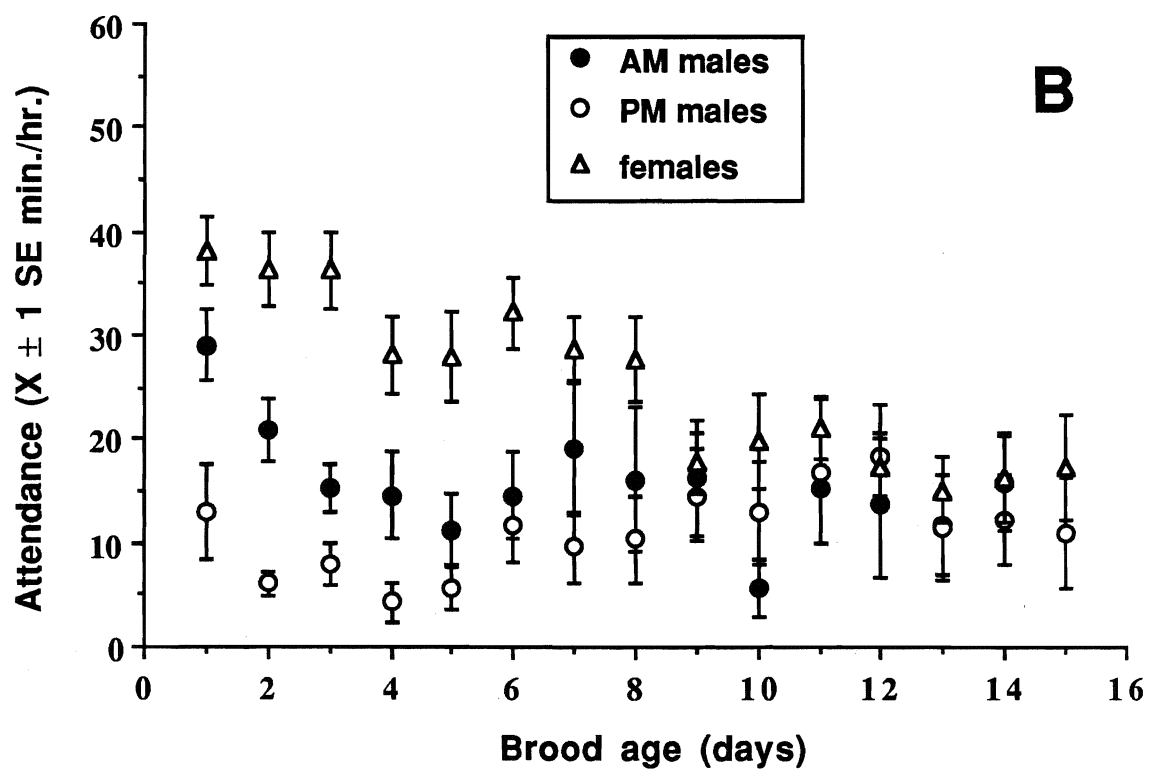
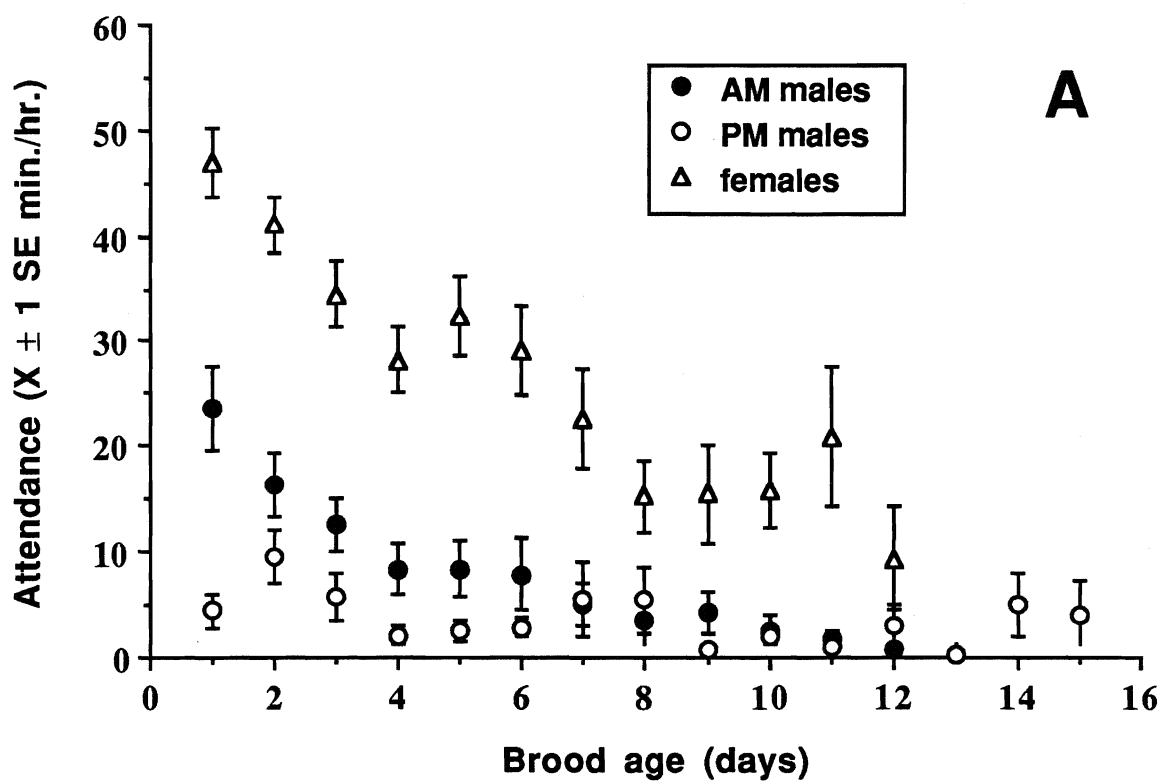
Year	Period	Attendance ($X \pm 1$ SD min./hr.)		Significance	
		Male	Female	F	p
1991	Peak ¹	7.0 \pm 9.7	28.4 \pm 20.0	48.65	< 0.001 *
	Late ¹	13.5 \pm 13.2	25.5 \pm 16.9	40.74	< 0.001 *
1992	Peak	17.3 \pm 11.6	41.0 \pm 15.1	75.0	< 0.001 *
	Late	15.8 \pm 16.5	36.8 \pm 20.3	11.8	0.006 *

¹ Significant differences were found between morning and evening brood attendance among males in both Peak and Late 1991 (Table 7). In order to make comparisons within- and between breeding periods I have pooled morning and evening periods for 1991 males.

* Denotes significant difference

Figure 2A. Brood attendance ($X \pm 1SE$ min./hr.) patterns of male and female common terns during morning and evening observation periods of Peak 1991 at Windermere Basin.

Figure 2B. Brood attendance ($X \pm 1 SE$ min./hr.) patterns of male and female common terns during morning and evening observation periods of Late 1991 at Windermere Basin.



approximately 20 minutes/hour at the nest site, during both the morning and evening observation periods.

During 1992, females spent significantly more time in brood attendance than males (approximately 2.3 times more) in both the Peak ($F=75.0$, d.f.=1,14, $p<0.001$) and Late (brood ages 1-8, $F=11.8$, d.f.=1, 10, $p=0.006$) breeding periods (Table 8). Male attendance rates during Peak 1992 were initially 20 minutes/hour, and remained constant over the following four brood days ($F=1.39$, d.f.=2, 20, $p=0.27$; Fig. 3A). Female attendance declined significantly ($F=3.54$, d.f.=2, 18, $p=0.05$) during the same period, from approximately 50 to approximately 40 minutes/hour (Fig. 3A). During Late 1992, male attendance rates differed significantly ($F=3.46$, d.f.=3, 27, $p=0.03$) over brood ages one through eight, but attendance neither increased nor decreased as chick age increased (Fig. 3B). In contrast, during the late-nesting period of 1992, females spent significantly less time with older chicks (brood ages 1-8, $F=4.60$, d.f.=3, 27, $p=0.01$) than they spent with their broods immediately after hatching (Fig. 3B).

3.2.3. Seasonal patterns of brood attendance

Comparisons were made to determine if there was significant variation in brood attendance patterns between Peak and Late periods within a breeding season, and also between years of the study. Analyses were performed on attendance data for brood ages one through six (unless stated otherwise), pooled into two-day blocks.

Female attendance patterns during Late 1991 were not significantly different ($F=0.002$, d.f.=1, 43, $p=0.96$; Table 9) from those exhibited by females earlier during the breeding season. There was no significant difference ($F=3.79$, d.f.=1, 21, $p=0.07$; Table 9) between peak- and late-nesting males during the morning in 1991, with respect to the amount of time spent attending their broods. However,

Figure 3A. Brood attendance ($X \pm 1$ SE min./hr.) patterns of male and female common terns during morning and evening observation periods of Peak 1992 at Windermere Basin.

Figure 3B. Brood attendance ($X \pm 1$ SE min./hr.) patterns of male and female common terns during morning and evening observation periods of Late 1992 at Windermere Basin.

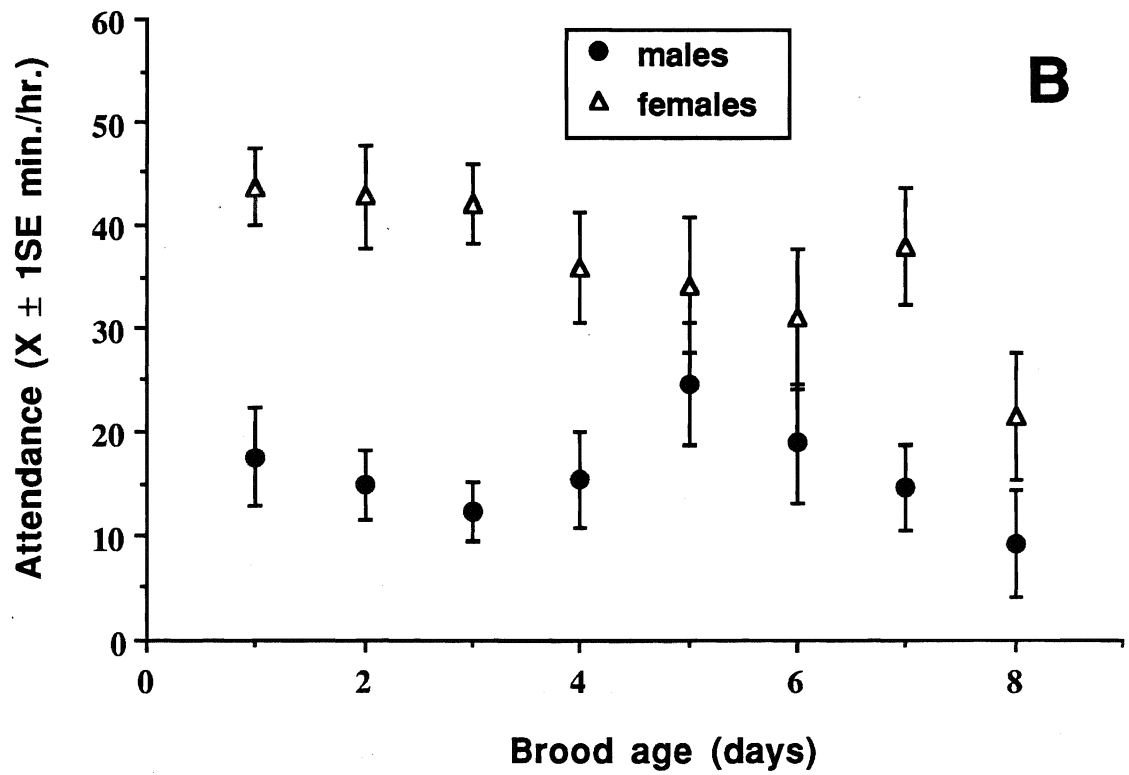


Table 9. Brood attendance ($X \pm 1$ SD min./hr.) for male and female common terns, between Peak and Late observation periods in 1991 and 1992 at Windermere Basin.

Year	Sex	Time ¹	Attendance ($X \pm 1$ SD min./hr.) ²		Significance F p	
			Peak	Late		
1991	Male	AM	11.4 \pm 9.3	16.8 \pm 10.6	3.79	0.07
		PM	4.2 \pm 5.3	7.6 \pm 6.2	7.60	0.01 *
	Female		34.1 \pm 16.5	31.9 \pm 14.7	0.002	0.96
1992	Male		17.3 \pm 10.3	17.7 \pm 12.4	0.05	0.83
	Female		40.2 \pm 11.1	39.0 \pm 13.5	0.03	0.87

¹ Morning and evening observations are pooled unless indicated as otherwise.

² All attendance times are calculated for brood ages 1-6 inclusive, except males during the evening for Peak and Late 1991 which are compared over brood ages 1-10.

* Denotes significant difference.

there was a significant difference in evening attendance rates over the first 10 brood days ($F=7.6$, d.f.=1, 17, $p=0.01$; Table 9) between peak- and late-nesting males in 1991. During 1992, no significant differences were observed between Peak and Late breeding periods for either males ($F=0.05$, d.f.=1,14, $p=0.83$) or females ($F=0.03$, d.f.=1,14, $p=0.87$; Table 9). In general, both males and females nesting during 1992 spent more time in brood attendance than their counterparts nesting in 1991 (Table 9).

3.3 Chick Mortality

Analyses were performed to determine whether there were differences in the patterns of chick mortality between Transmitter and Control groups. As hatching among study nests occurred over as much as a six day period (Table 1) the age of each brood was standardized to the hatching date of the last chick, designated as brood age 1. During 1991, losses of whole broods throughout the observation period were common. Numbers of broods within Transmitter and Control groups remained relatively even, and more than half of the broods in each group still had chicks, until brood ages of 19 (Peak) and 10 (Late) days, respectively. To avoid the statistical problems associated with missing data, samples were truncated at brood ages of 19 and 10 days for Peak and Late 1991 respectively. Formal analyses were not performed on Peak 1992 data as chicks in most study broods (8 of 11) were predated during a single evening. During Late 1992, most broods (9 of 13) failed by a brood age of 5 days. Thereafter these broods were supplemented with foster chicks of similar brood ages to maintain chick feeding and telemetry samples. Consequently, comparisons of chick attrition between Control and Transmitter broods in Late 1992 have been limited to brood ages one through five.

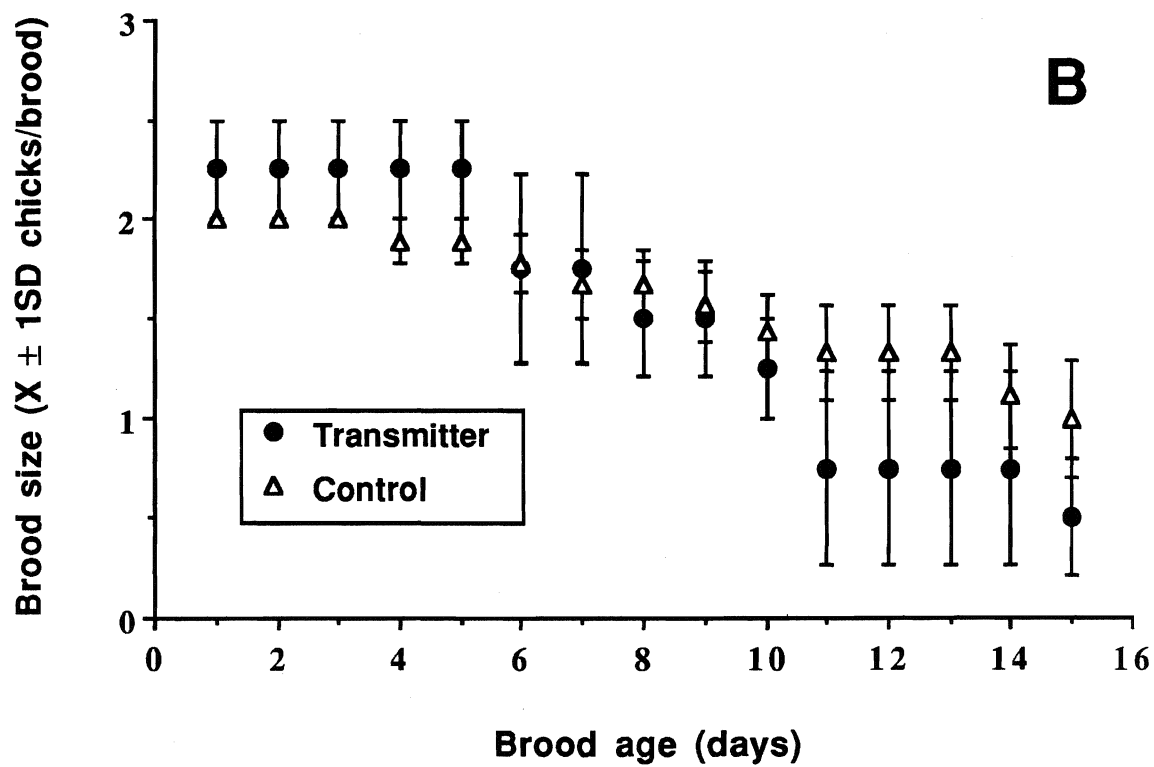
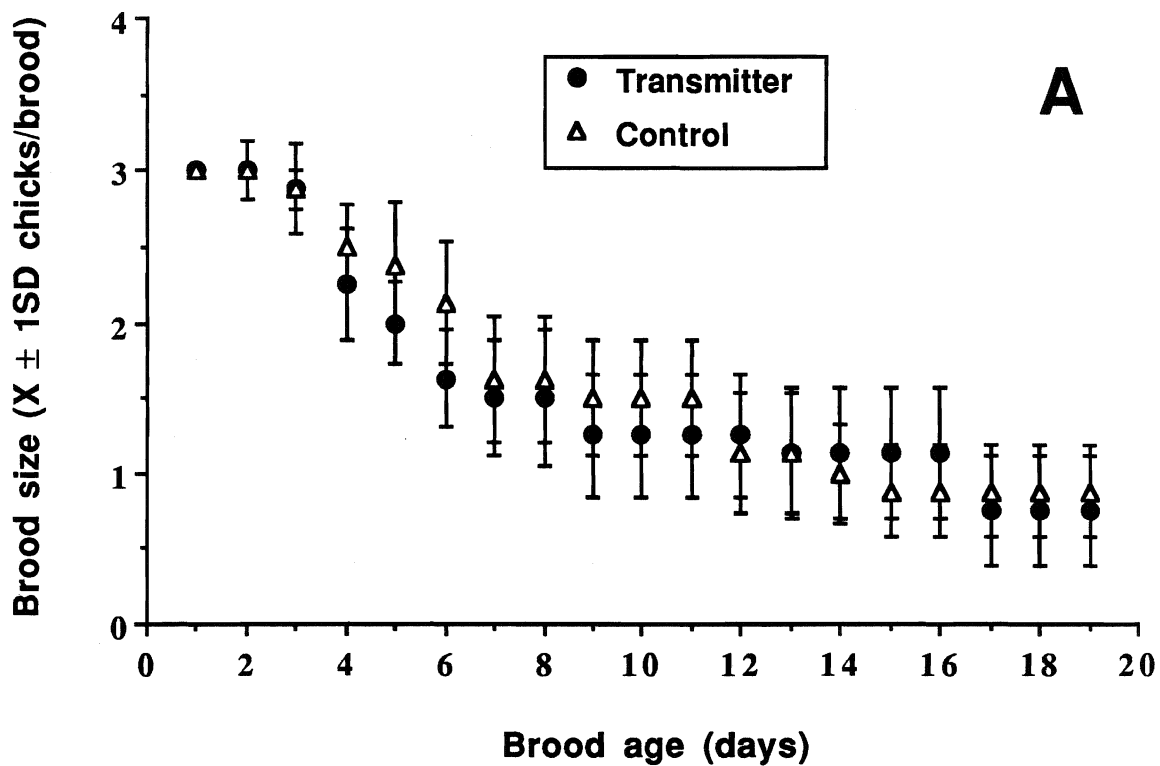
3.3.1. Chick mortality with brood age

As there was no significant difference in the pattern of chick loss (mean brood size per group per day) between Transmitter and Control broods in either Peak 1991 ($F=0.06$, d. f.=1,14, $p=0.82$), Late 1991 ($F=0.25$, d. f.=1,11, $p=0.63$), or Late 1992 ($F=0.05$, d. f.=1,11, $p=0.82$), groups were pooled for all analyses of chick mortality. There was a significant, linear decrease ($F=20.27$, d.f.=17, 255, $p<0.001$) in mean brood size of Peak broods in 1991 with increasing brood age, indicating that chick loss occurred at a constant rate over the brooding period (Fig. 4A). Chick losses were attributed to either dead chicks found in the vicinity of the nest ($N=9$, 26% of total losses) or to chicks that wandered away from their nest and were never observed again ($N=26$, 74% of total losses). No chick predation was observed during Peak 1991. Overall, the fledging success (chicks surviving to at least a brood age of 20 days) of Peak pairs in 1991 ($N=16$) was 0.81 ± 0.91 chicks/brood. Total brood failure occurred in 50% of study nests. Among nests that fledged at least one chick ($N=7$), the mean number of chicks fledged per brood was 1.63 ± 0.52 chicks.

A similar, significant ($F=13.75$, d.f.=14, 168, $p<0.001$) decrease in mean brood size with increasing brood age occurred during Late 1991 (Fig. 4B). Data for most broods were collected up to a brood age of 15 days, and therefore the fledging success of late-nesting study pairs is not known. Total brood failure by a brood age of 15 days occurred in 38% ($N=5$) of Late 1991 study nests, compared to total failure of 44% ($N=7$) of broods for the same brood age during the peak-nesting period. Most chicks losses occurred when chicks wandered away from their nests ($N=15$, 71% of total losses) or when chicks were found dead in the vicinity of their nest ($N=4$, 19% of total losses), but at least two chicks are known to have been predated. These chicks were probably killed by a great-horned owl (*Bubo virginianus*), as owl feathers were found at the nests and the corpses of chicks

Figure 4A. Patterns of chick mortality ($X \pm 1$ SD chicks/brood) for broods of male common terns belonging to Transmitter and Control groups during Peak 1991 at Windermere Basin.

Figure 4B. Patterns of chick mortality ($X \pm 1$ SD chicks/brood) for broods of male common terns belonging to Transmitter and Control groups during Late 1991 at Windermere Basin.

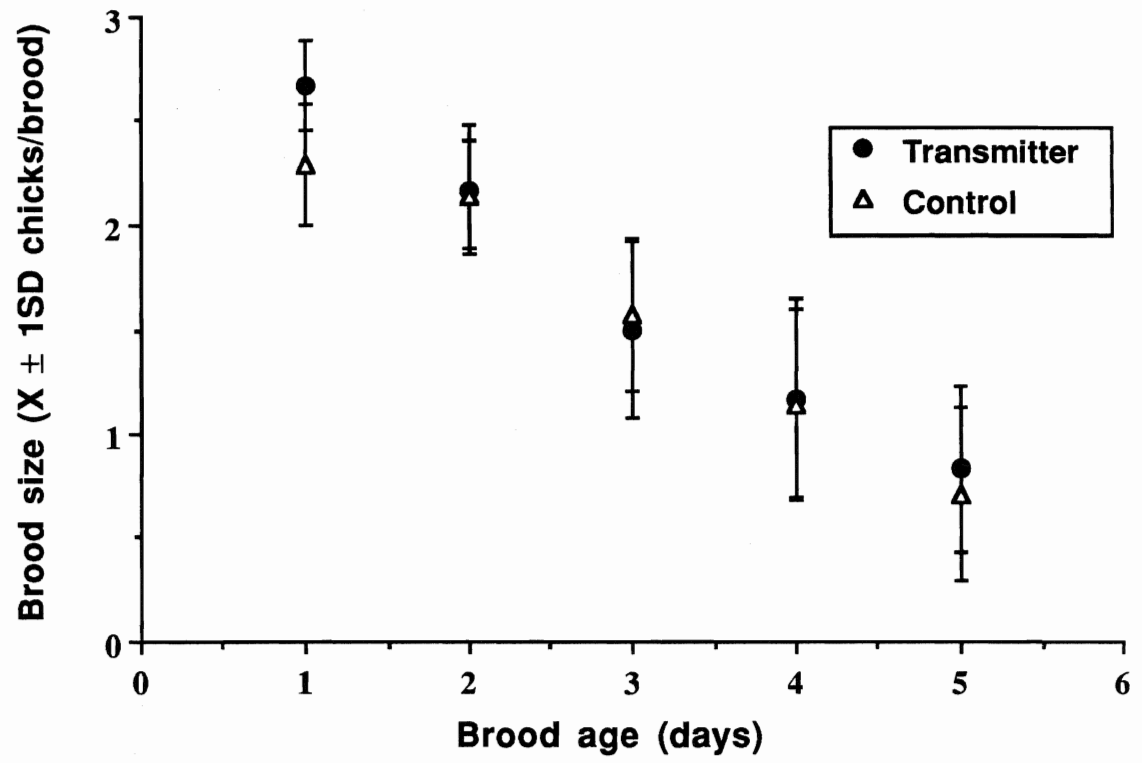


were consistent with patterns of predation exhibited by owls. Among nests with chicks still alive at a brood age of 15 days ($N=7$), the mean number of chicks per brood was 1.38 ± 0.52 . There was no significant difference ($U=92.5$, d. f.=1, $p=0.59$) in the number of chicks per brood at a brood age of 15 days between Peak and Late periods in 1991.

On the evening of 10 June 1992, all Control broods ($N=6$) and three out of five Transmitter broods were predated by black-crowned night-herons. Eight out of the 11 study broods were between the brood ages of four and six days (5.0 ± 1.79 days, $N=11$) when the predation event occurred. All study broods had three chicks at brood age 1, and no losses of chicks occurred from any of the Transmitter or Control broods prior to the black-crowned night-heron predation. Accordingly, there was no difference in the patterns of chick mortality between Transmitter and Control broods during Peak 1992.

A significant, linear decrease ($F=23.49$, d.f.=9, 108, $p<0.001$) in brood size with increasing brood age was observed for Late broods in 1992 (Fig. 5). Chick mortality during Late 1992 was high, with nine of 13 broods failing by a brood age of five days. For the Late 1992 sample of study nests as a whole, the mean brood size at brood age 10 (the final observation period) was 0.31 ± 0.63 chicks/brood. For broods surviving to at least a brood age of 10 days the mean brood size was 1.75 ± 0.96 chicks/brood. One chick was killed by a conspecific adult, while another was predated by an adult ring-billed gull. However, the majority ($N=40$, 66.7% of total losses) were found dead in the vicinity of the nest or missing ($N=19$, 31.7% of total losses). Many dead chicks were observed in the previous sampling period, either wet or cold to the touch, and often outside of the nest scrape.

Figure 5. Patterns of chick mortality ($X \pm 1$ SD chicks/brood) for broods of male common terns belonging to Transmitter and Control groups during Late 1992 at Windermere Basin.



3.4 Size and species of food items delivered to chicks by adults

The frequency of chick-feedings, and the types and sizes of prey items delivered to chicks were recorded for all study broods. Measurements of breeding, adult male and female common tern culmen (upper mandible) lengths (N= 42) revealed a mean of 36.3 ± 1.4 mm with relatively little inter-individual variability (C.V.= 3.8%). In common terns, therefore, bill length is a suitable template for estimating prey sizes as the template remains constant among subjects. Data were pooled into two day age blocks, and unless stated otherwise, ANOVA procedures were performed on brood ages one through six inclusive.

3.4.1. Types of prey delivered to chicks by adults

A variety of prey species was delivered to chicks during the course of this study (Table 10). Considerable variation was observed between the different nesting periods with respect to the frequency of each fish species that were delivered to chicks. The rank order of importance for each fish species was not consistent among sampling periods, and during some nesting periods the importance of a particular food type increased dramatically (for example, fathead minnow during Peak 1992; Table 10). In general, the species (or types) of fish most commonly delivered to chicks by adults (in order of overall importance) were rainbow smelt, alewife, unidentified larval fish, emerald shiner, salmonid parr (*Salmo gairdneri*, *S. trutta*, *Salvelinus namaycush*, or *Oncorhynchus tshawytscha*), and fathead minnow.

Table 10. Types and rank order of prey delivered to chicks by peak- and late-nesting common terns in 1991 and 1992. (the most frequently delivered fish type = 1)

Common name	Nomenclature	Rank Order				
		Peak 1991	Late 1991	Peak 1992	Late 1992	Over -all

<u>Fish</u>						
rainbow smelt	<i>Osmerus mordax</i>	1	4	2	2	1
alewife	<i>Alosa pseudoharengus</i>	3.5	2	3	1	2
emerald shiner	<i>Notropis antherinoides</i>	2	3	5	6	4
rainbow trout	<i>Salmo gairdneri</i>					
brown trout	<i>Salmo trutta</i>					
lake trout	<i>Salvelinus namaycush</i>					
chinook salmon	<i>Oncorhynchus tshawytscha</i> ²	3.5	6.5	4	9.5	5
larval fish ¹		5	1	6	3	3
fathead minnow	<i>Pimephales promelas</i>	8.5	9.5	1	5	6
trout perch	<i>Percopsis omiscomaycus</i>	8.5	6.5	7.5	4	7
three-spined stickleback	<i>Gasterosteus aculeatus</i>	6	8	7.5	7	8
bluegill sunfish	<i>Lepomis macrochirus</i>	8.5	5	9.5	9.5	9
<u>Arthropods</u>						
field cricket	<i>Gryllus pennsylvanicus</i>					
June beetles	<i>Phyllophaga sp.</i>	8.5	9.5	9.5	8	10

¹ Unidentified larval fish (0.5 to 1.0 bill lengths).

² These four Lake Ontario salmonid species cannot be distinguished by an observer from a blind, and are grouped as "salmonid parr".

i) **Comparisons between Transmitter and Control groups**

Chi-square analyses were performed to determine whether there were differences between Transmitter and Control males, or between the female partners of Transmitter and Control males with respect to the species composition of prey items delivered to chicks. In 1991, no significant differences were found between Transmitter or Control males in the distribution of prey species delivered to chicks during either the morning ($X^2=4.5$, d.f.=4, $p=0.35$) or evening ($X^2=3.7$, d.f.=4, $p=0.44$) observation periods of the Peak period, or during the morning ($X^2=3.2$, d.f.=5, $p=0.68$) or evening ($X^2=4.1$, d.f.=4, $p=0.40$) in the Late period. During Peak 1991, no significant differences were detected between the female partners of Transmitter and Control males in the distribution of prey species delivered to chicks during the morning ($X^2=6.8$, d.f.=5, $p=0.23$) or evening ($X^2=2.3$, d.f.=4, $p=0.68$) observation periods. In Late 1991, the distribution of prey species delivered to chicks did not differ between the female partners of Transmitter and Control males during the morning ($X^2=8.3$, d.f.=4, $p=0.08$). The single significant difference, was in the proportions of different prey species delivered to chicks by the female partners of Transmitter and Control males during the evening observation period ($X^2=8.6$, d.f.=3, $p=0.04$).

No difference was detected between Transmitter and Control males during the morning ($X^2=4.0$, d.f.=2, $p=0.13$) or evening ($X^2=4.4$, d.f.=2, $p=0.11$) in Late 1992. Similarly, no difference existed between the female partners of Transmitter and Control males with respect to the distribution of prey delivered to chicks during either the morning ($X^2=5.1$, d.f.=2, $p=0.08$) or evening (Fisher, $p=0.14$) in Peak 1992, nor during the morning (Fisher, $p=0.27$) or evening (Fisher, $p=0.23$)

observation periods of Late 1992. However, during Peak 1992, there were consistent differences between Transmitter and Control males with respect to the distributions of fish delivered to their chicks. Significant differences were found between experimental and control males during both the morning ($X^2=18.0$, d.f.=4, $p<0.001$) and evening ($X^2=17.1$, d.f.=3, $p<0.001$) observation periods of Peak 1992. Approximately 60% of the fish delivered to chicks by Control males were fathead minnows, while Transmitter males delivered more smelt and salmonid parr to chicks than Control males. For all analyses that follow, feeding data for Transmitter and Control groups have been pooled (except for morning and evening observations of males during Peak 1992, and evening observations for females in Late 1991).

Comparisons of types of fish delivered to chicks by males during Peak 1991 revealed that there was no significant difference ($X^2=10.9$, d.f.=6, $p=0.09$) in the distribution of fish species between the morning and evening observation periods. Similarly, there was also no difference ($X^2=10.3$, d.f.=6, $p=0.11$) between morning and evening in the distribution of fish types delivered to chicks by females. Similar patterns also emerged during Late 1991: no significant difference was detected in the species delivered to chicks between morning and evening for males ($X^2=6.4$, d.f.=6, $p=0.38$) or females ($X^2=7.6$, d.f.=6, $p=0.27$). During 1992, no differences were detected between the morning and evening sampling periods with respect to the types of fish delivered to chicks by adults. The distributions of fish delivered to chicks during Peak 1992 were not significantly different between morning and evening observation periods for either Transmitter males ($X^2=6.9$, d.f.=4, $p=0.14$) or Control males ($X^2=3.8$, d.f.=2, $p=0.15$). Males during Late 1992 did not differ significantly between morning and evening observation periods ($X^2=1.2$, d.f.=4, $p=0.89$) in the types of fish they delivered to their chicks. Females delivered similar prey distributions to chicks during the morning and evening observation periods of Peak 1992 ($X^2=2.4$, d.f.=2, $p=0.31$) and Late 1992 ($X^2=0.47$, d.f.=2, $p=0.79$).

ii) **Male and female chick-provisioning patterns: species of fish.**

Some sex-related patterns were observed with respect to the quantities and types of fish delivered to chicks. In all sampling periods during the study, male common terns delivered at least two times more fish to chicks than their female partners ($t = 7.2$, $d.f. = 3$, $p < 0.005$; Fig. 6). During 1991, 65.6% ($N = 481$ of 733) and 65.2% ($N = 653$ of 1001) of all fish were delivered by males during Peak and Late periods, respectively. Males were responsible for a higher proportion of chick provisionings in 1992, contributing 71.6% of all feedings ($N = 416$) during the Peak and 77.4% of the total fish delivered ($N = 310$) during the Late nesting period (Fig. 6).

Males and females also differed significantly in the proportions of different types of fish they delivered to their young in Peak 1991 ($X^2 = 17.8$, $d.f. = 6$, $p = 0.007$; Fig. 7A), but did not differ ($X^2 = 8.4$, $d.f. = 6$, $p = 0.21$; Fig. 7B) in the late period of the same year. During Peak 1991 the major differences between the sexes were that males delivered relatively more rainbow smelt and emerald shiner, but a lower proportion of alewife and salmonid parr than females. Also, fish belonging to the "other" category, such as trout perch (*Percopsis omiscomaycus*), three-spined sticklebacks (*Gasterosteus aculeatus*), and sunfish (*Lepomis macrochirus*), were delivered to chicks more frequently by females (Fig. 7A).

During Peak 1992, there were significant differences in the distribution of fish delivered to chicks between females (pooled Transmitter and Control) and Transmitter males ($X^2 = 33.4$, $d.f. = 4$, $p < 0.0001$; Fig. 8A), and between females (pooled) and Control males ($X^2 = 45.6$, $d.f. = 3$, $p < 0.0001$; Fig. 8A). Females delivered higher proportions of smelt and alewife (40% and 35% respectively) than males. In addition, only 10% of fish delivered by females were fathead minnows,

Figure 6. Proportions of fish delivered to chicks by male and female common terns during the Peak and Late nesting periods of 1991 and 1992 at Windermere Basin. Numbers above bars represent the total numbers of fish delivered by each group.

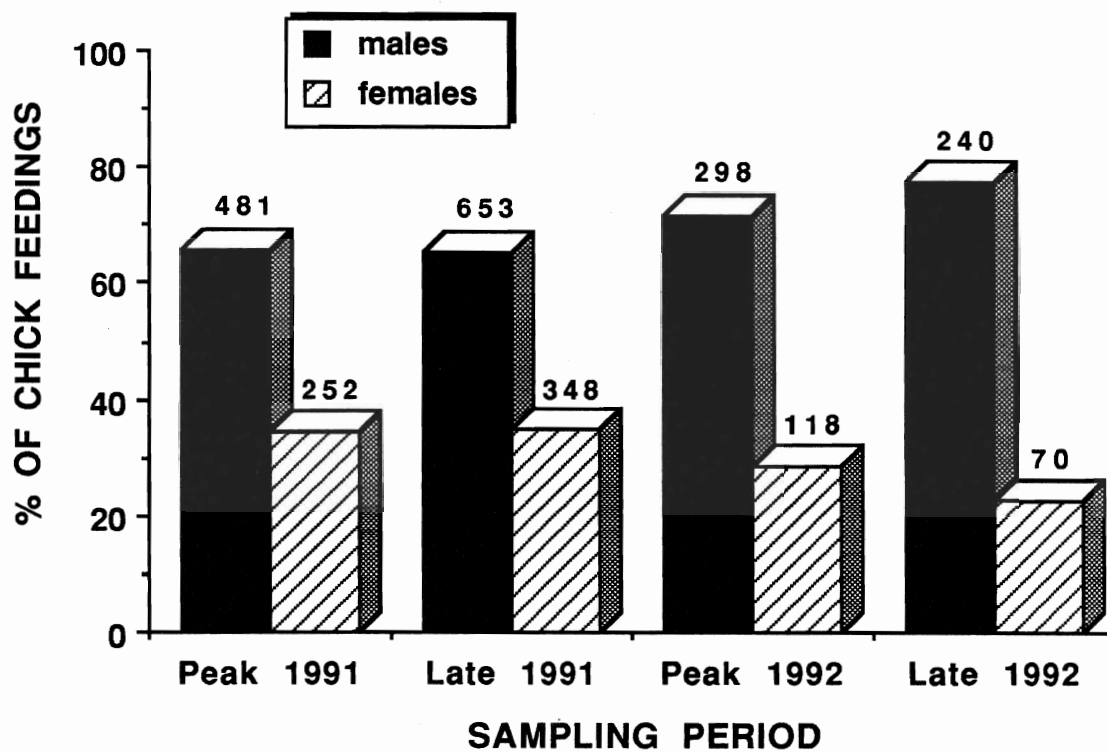


Figure 7A. Proportion of prey types delivered to chicks by male and female common terns during Peak 1991 at Windermere Basin. The "other" category includes fish of species delivered at low frequencies (fathead minnows, trout-perch, three-spined stickleback, sunfish, and unknown species). Instances when a feeding occurred but the fish was not identified are grouped as "missed".

Figure 7B. Proportion of prey types delivered to chicks by male and female common terns during Late 1991 at Windermere Basin. The "other" category includes fish of species delivered at low frequencies (fathead minnows, trout-perch, three-spined stickleback, sunfish, and unknown species). Instances when a feeding occurred but the fish was not identified are grouped as "missed".

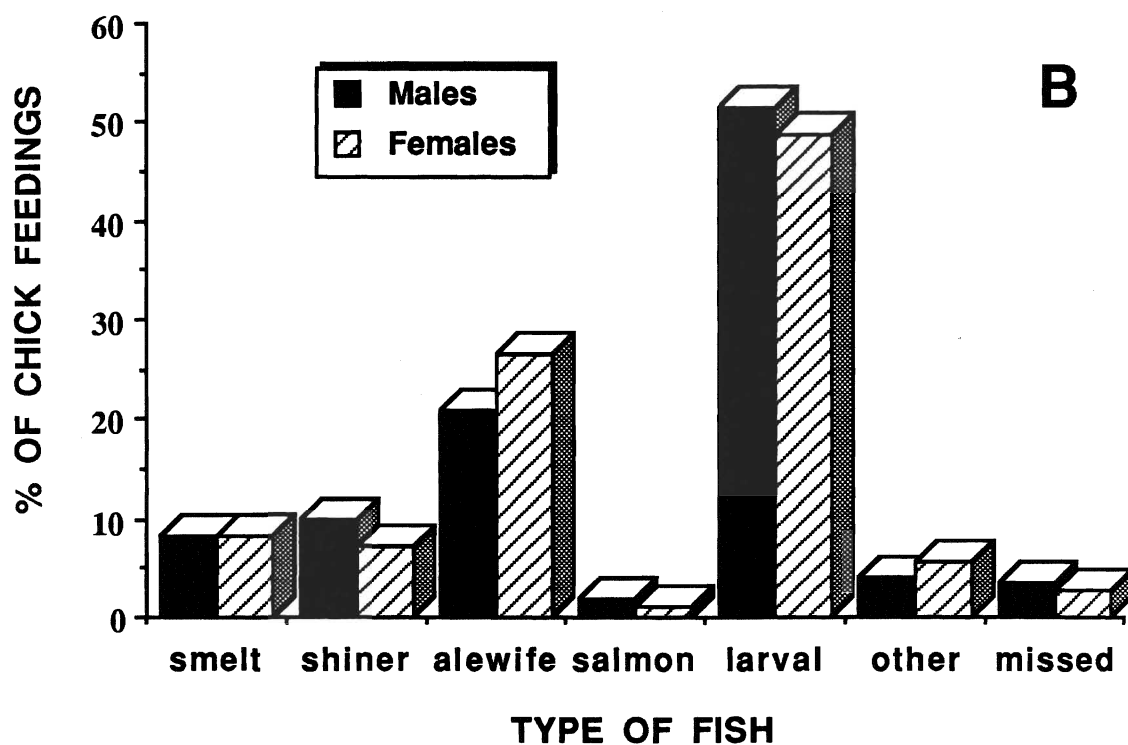
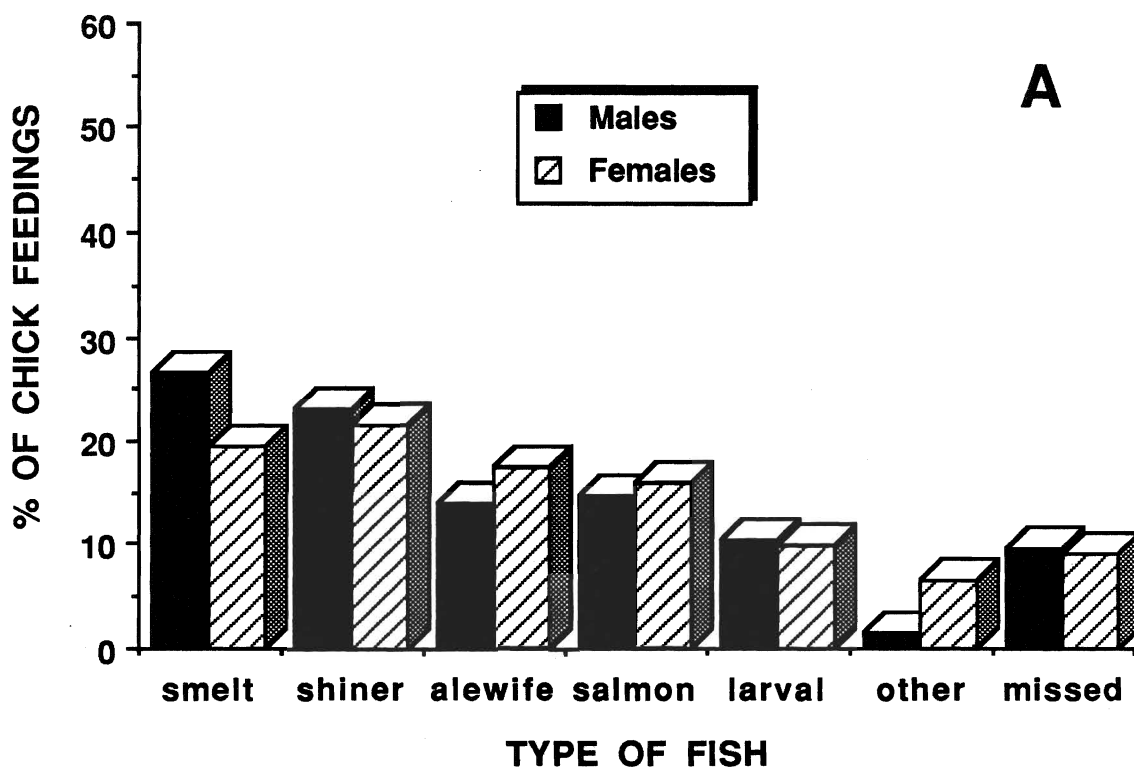
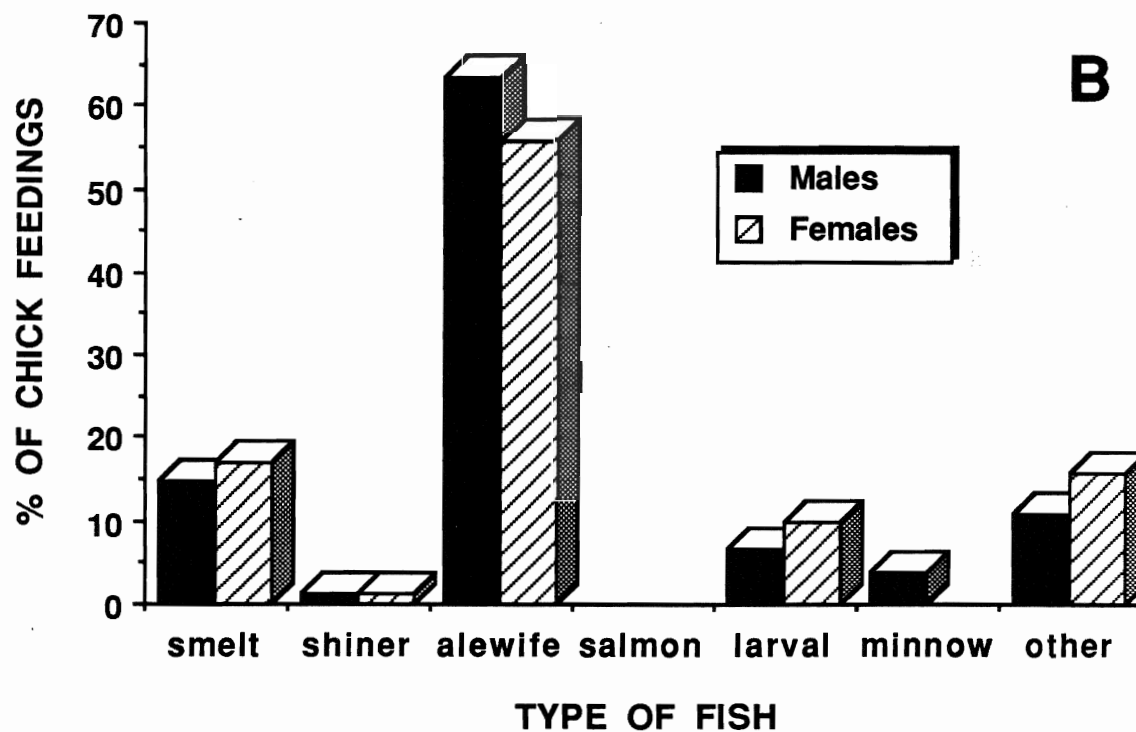
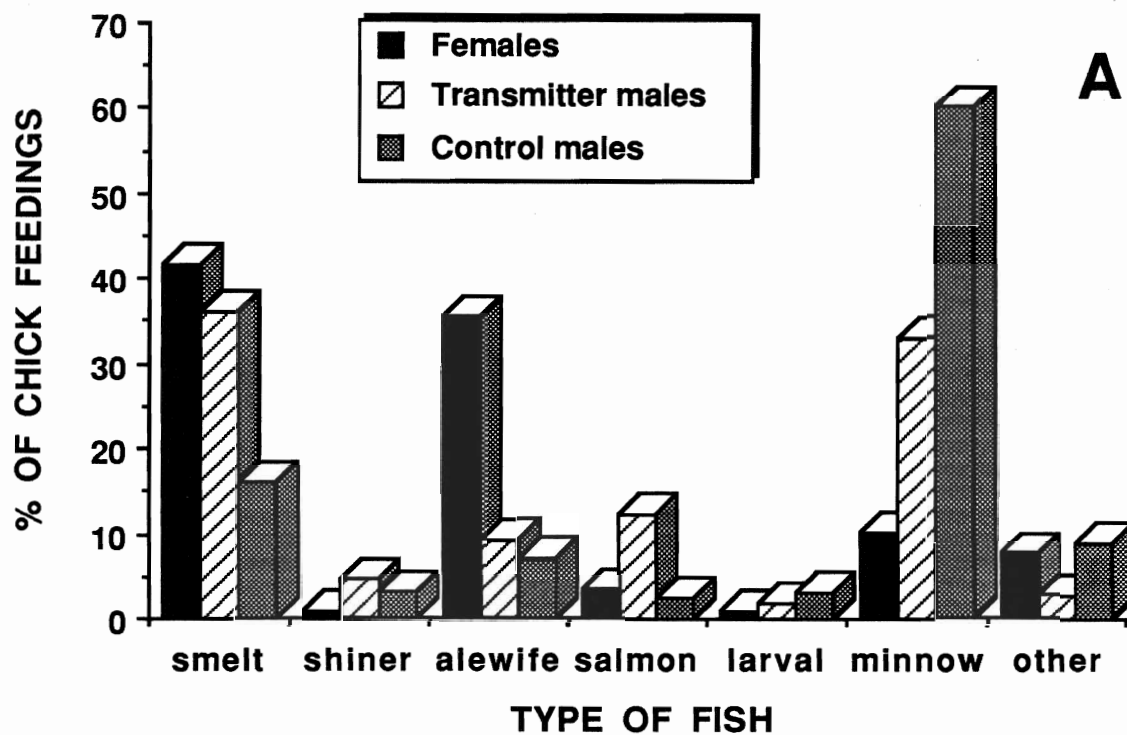


Figure 8A. Proportion of prey types delivered to chicks by Transmitter male, Control male, and female common terns during Peak 1992 at Windermere Basin. The "other" category includes fish of species delivered at low frequencies (trout-perch, three-spined stickleback, sunfish, and unknown species) and instances when a feeding occurred but the fish was not identified.

Figure 8B. Proportion of prey types delivered to chicks by male and female common terns during Late 1992 at Windermere Basin. The "other" category includes fish of species delivered at low frequencies (trout-perch, three-spined stickleback, sunfish, and unknown species) and instances when a feeding occurred but the fish was not identified.



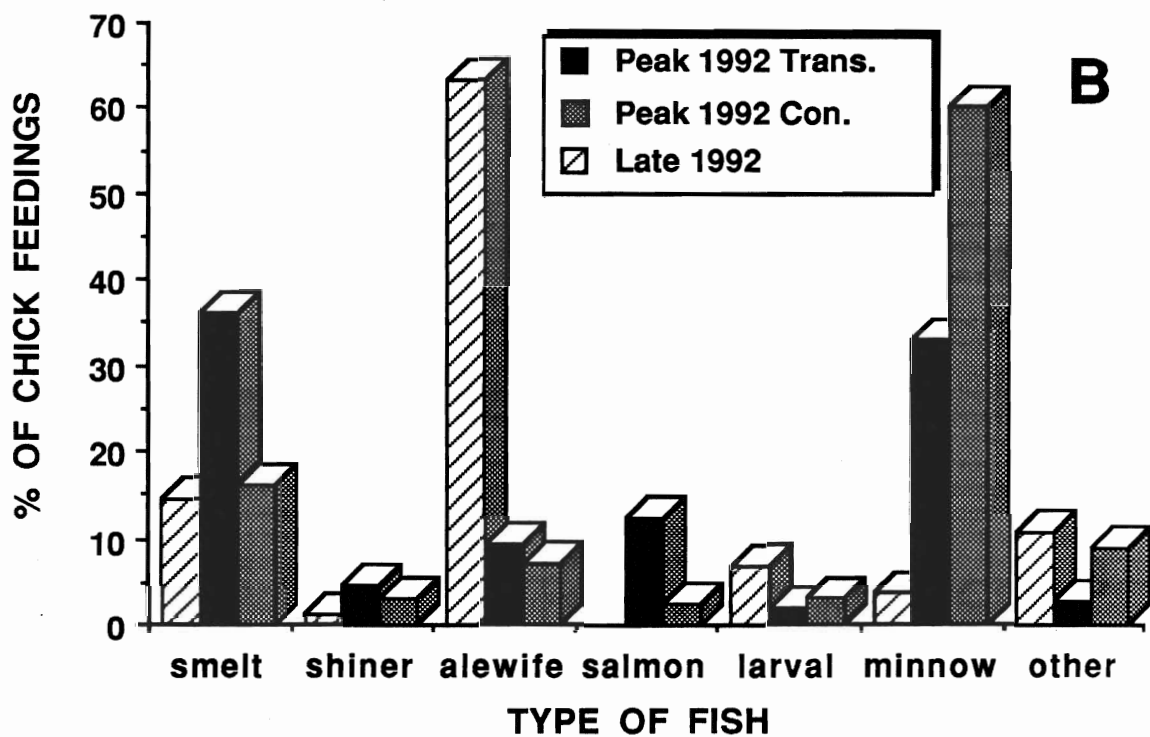
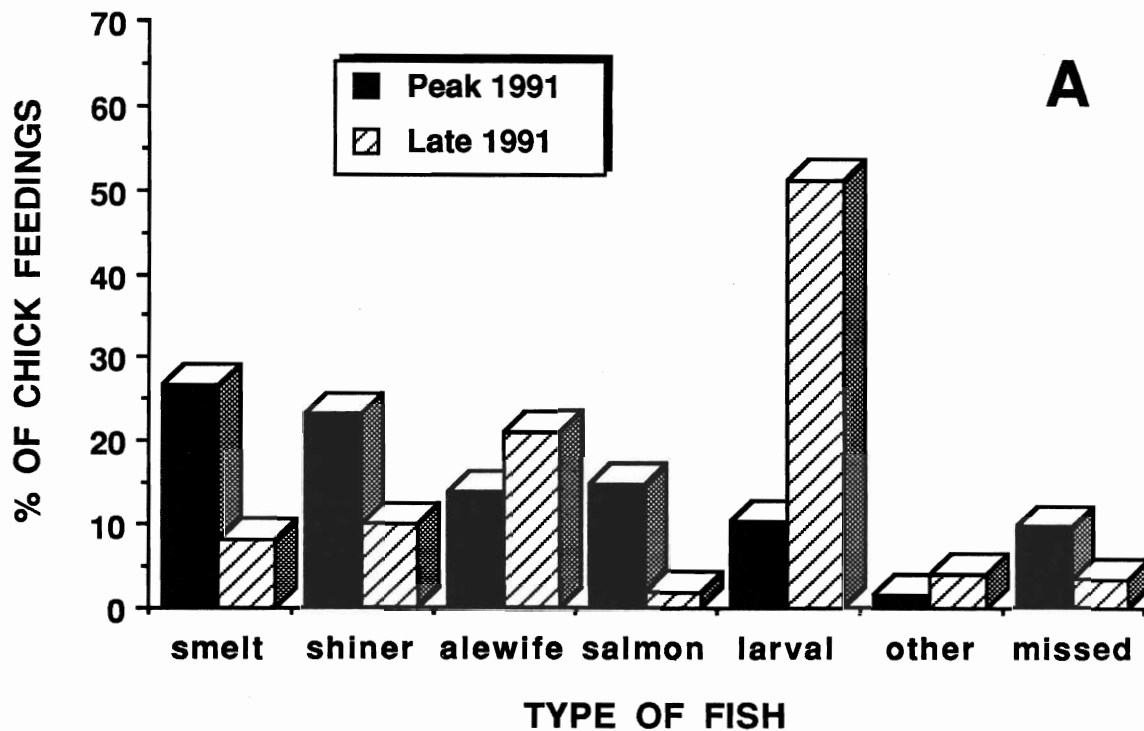
compared with minnow deliveries of 35% and 60% for Transmitter and Control males respectively. Similar to the pattern observed during Late 1991, there was no difference ($X^2=8.0$, d.f.=4, $p=0.09$) between males and females in the proportion of different fish species that were delivered to chicks during Late 1992 (Fig. 8B).

iii) Seasonal patterns in the species of fish delivered to chicks.

The frequency distribution of species delivered to chicks was significantly different between the Peak and Late nesting periods of 1991 for both males ($X^2=318.3$, d.f.=6, $p<0.0001$) and females ($X^2=168.1$, d.f.=6, $p<0.0001$; Fig. 9A). During the peak period, approximately 75% of all deliveries were of four main fish species, whereas during the late period, these species comprised only 40% of deliveries to chicks. Rainbow smelt and emerald shiner were common food types during the peak period, whereas small (<1.0 bill lengths), unidentified larval fish predominated during the late period. There was also a greater proportion of alewife delivered during Late 1991 compared to Peak 1991. The trend for the types of fish delivered to chicks to change over the course of a breeding season (from Peak to Late) was also observed during 1992. As the result of differences between Transmitter and Control males during Peak 1992, these groups were compared separately to pooled Late 1992 males. The species distribution of fish delivered to chicks was significantly different between the Peak and Late nesting periods of 1992 for both Transmitter males ($X^2=160.7$, d.f.=5, $p<0.0001$; Fig. 9B), Control males ($X^2=178.1$, d.f.=5, $p<0.0001$; Fig. 9B), and females ($X^2=21.8$, d.f.=3, $p<0.0001$). During Peak 1992 the predominant fish species delivered to chicks by males were fathead minnow (45%) and smelt (27%). In contrast, during the late-nesting period of 1992 the majority (65%) of fish delivered to chicks was alewife (Fig. 9B).

Figure 9A. Distribution of prey types delivered to chicks by male common terns during Peak and Late 1991 at Windermere Basin. The "other" category includes fish of species delivered at low frequencies (fathead minnows, trout-perch, three-spined stickleback, sunfish, and unknown species). Instances when a feeding occurred but the fish was not identified are grouped as "missed".

Figure 9B. Distribution of prey types delivered to chicks by male common terns during Peak and Late 1992 at Windermere Basin. The "other" category includes fish of species delivered at low frequencies (trout-perch, three-spined stickleback, sunfish, and unknown species) and instances when a feeding occurred but the fish was not identified.



In summary, the proportions of different fish species delivered to chicks changed over the course of the breeding season, in both 1991 and 1992. There was also considerable variation between the two years of the study with respect to the quantities of different fish types delivered to chicks (Figs. 9A & 9B). Each sampling period was dominated by only one or two fish species, while no other species delivered during that period individually consisted of more than 15% of the total number of fish. Consequently, the rank order of importance for each fish species delivered during the study also changed between sampling periods (Table 10).

Although the quantities delivered and relative importance of each fish species differed among nesting periods, there were some consistent trends in prey delivery between 1991 and 1992. Both the pattern and magnitude of smelt delivery remained constant between 1991 and 1992 (Figs. 9A & 9B). In both years, smelt comprised one quarter of fish delivered to chicks during the Peak period, whereas this proportion dropped to 10-15% of the total number of fish delivered during both Late nesting periods. Similar trends (although differing in magnitude between years) occurred with shiner and salmonid parr (Figs. 9A & 9B). Higher proportions of these fish were delivered to chicks during the Peak periods of both years compared to the Late nesting periods. In contrast, alewife and larval fish were delivered to chicks more frequently during the Late nesting periods of both 1991 and 1992 (Figs. 9A & 9B).

3.4.2. The size of prey delivered to chicks by adults

i) Comparisons between Transmitter and Control groups

Chi-square analyses were performed to determine whether there were differences between Transmitter and Control males, or between the female partners of Transmitter and Control males with respect to the size class distributions of prey items delivered to chicks.

During the Peak and Late nesting periods of 1991, no significant difference in the size class distributions of fish delivered to chicks were found between Transmitter and Control males, nor between the female partners of Transmitter or Control males, in either the morning or evening observation periods (Appendix I). However, significant differences in the sizes of fish delivered to chicks were detected between Transmitter and Control males in both the morning ($X^2=26.6$, d.f.=4, $p<0.0001$) and evening ($X^2=21.6$, d.f.=3, $p<0.0001$) observation periods of Peak 1992. In both observation periods, Control males delivered fish of predominantly one bill length while Transmitter males delivered a higher proportion of larger fish to their chicks. During this period, there were no differences detected between the female partners of Control and Transmitter males (Appendix I). Comparisons between Transmitter and Control groups of males, and female partners of Transmitter and Control males during Late 1992, revealed no significant differences in either the morning or evening observation periods (Appendix I).

There was no tendency for males ($X^2=5.3$, d. f.=5, $p=0.39$) or females ($X^2=3.3$, d. f.=5, $p=0.66$) to deliver different size classes of fish to chicks between morning and evening observation periods during Peak 1991. Similarly, no

significant difference was found between morning and evening in Late 1991 with respect to the size classes of fish delivered to chicks among males ($X^2=0.55$, d. f.=5, $p=0.99$) or females ($X^2=6.7$, d. f.=5, $p=0.25$). The size of fish delivered to chicks by males in 1992 was not dependent on the time of day, as no significant differences were found between morning or evening observation periods for Transmitter males ($X^2=2.4$, d. f.=4, $p=0.67$), or Control males ($X^2=6.3$, d. f.=4, $p=0.18$) during the Peak period, or among Late-nesting males ($X^2=2.63$, d. f.=4, $p=0.62$). Similarly, size class distributions of fish delivered to chicks by females did not differ significantly between morning and evening observation periods during either the Peak ($X^2=4.9$, d. f.=4, $p=0.30$) or Late ($X^2=2.12$, d. f.=2, $p=0.35$) nesting periods of 1992. Transmitter and Control data (for all groups except Peak 1992 males), and morning and evening data are pooled for all further analyses of prey size.

ii) **Male and female chick-provisioning patterns: sizes of prey**

During Peak 1991 there was no significant difference ($X^2=8.38$, d. f.=5, $p=0.14$) between males and females in the sizes of fish they delivered to chicks (Fig. 10A). However, in the late-nesting period of 1991 a significant difference ($X^2=17.8$, d. f.=5, $p=0.003$) was detected between males and females in the distribution of size classes of prey they delivered to chicks (Fig. 10B). During this breeding period male common terns tended to deliver smaller sizes of fish to chicks than females. Sixty-five percent of the fish males fed to chicks were one bill length or less, whereas only 55% of the fish brought to the nest by females belonged to this size class. During Peak 1992, no difference ($X^2=8.0$, d. f.=4, $p=0.09$) was detected between Transmitter males and study females (the female partners of Transmitter and Control males pooled) with respect to the frequency at which different sizes of fish were delivered to chicks (Fig. 11A). However, a

Figure 10A. Size (bill lengths) distribution of prey items delivered to chicks by male and female common terns during Peak 1991 at Windermere Basin.

Figure 10B. Size (bill lengths) distribution of prey items delivered to chicks by male and female common terns during Late 1991 at Windermere Basin.

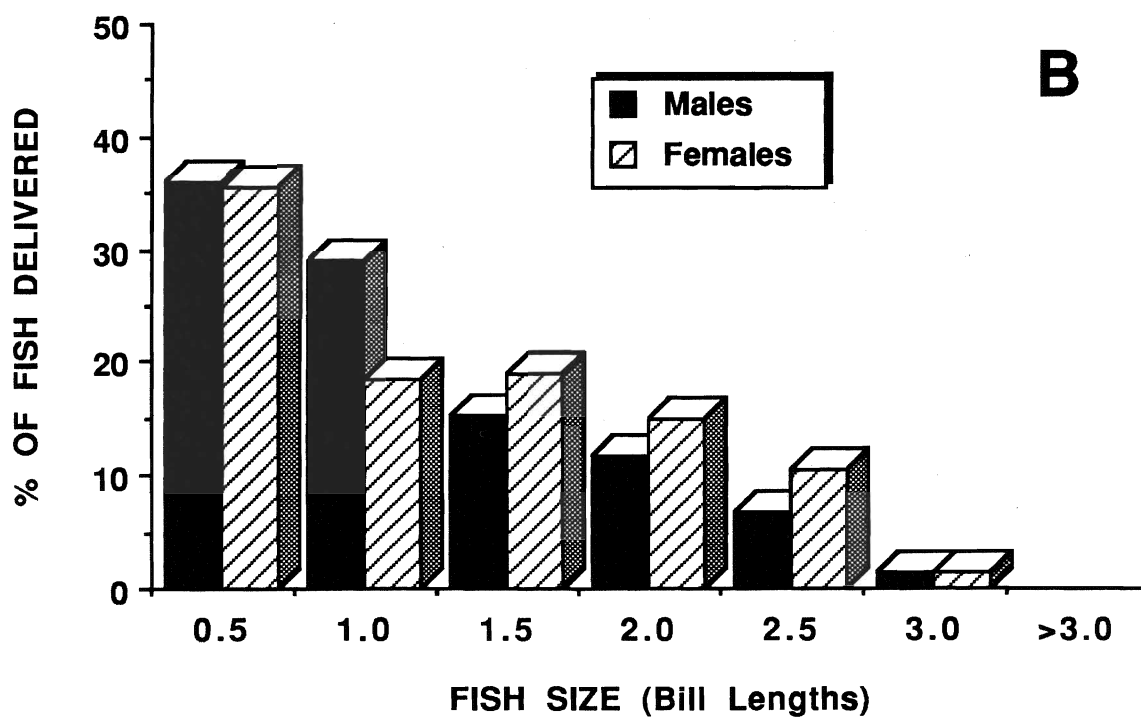
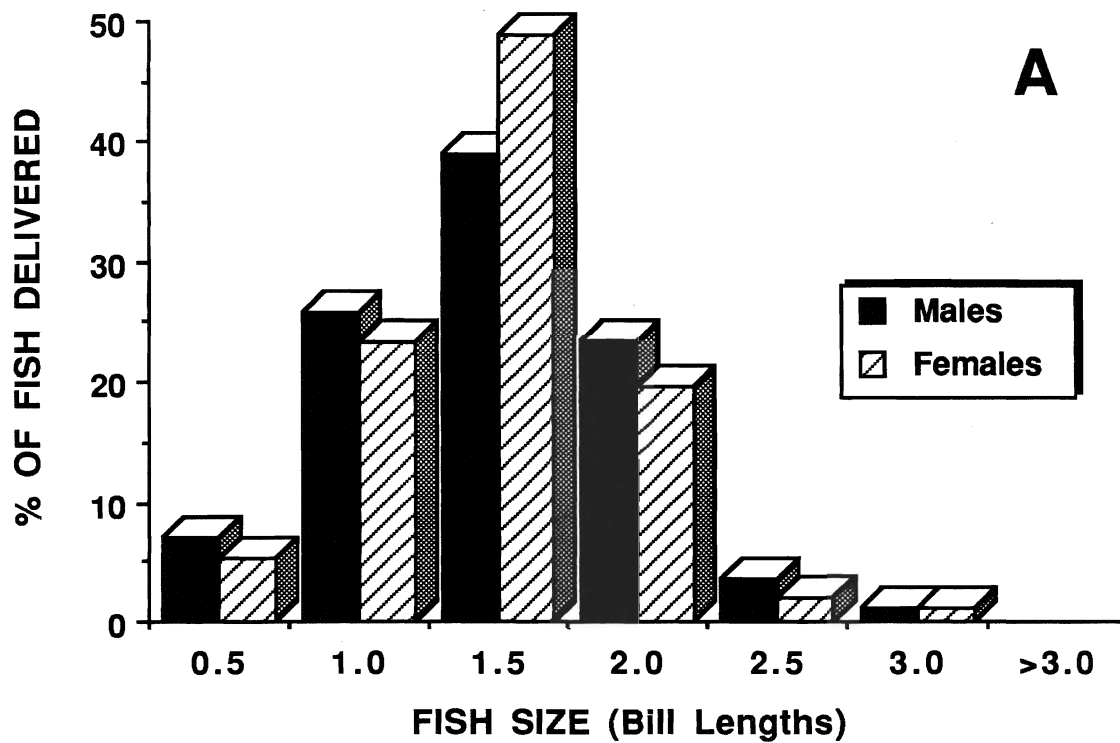
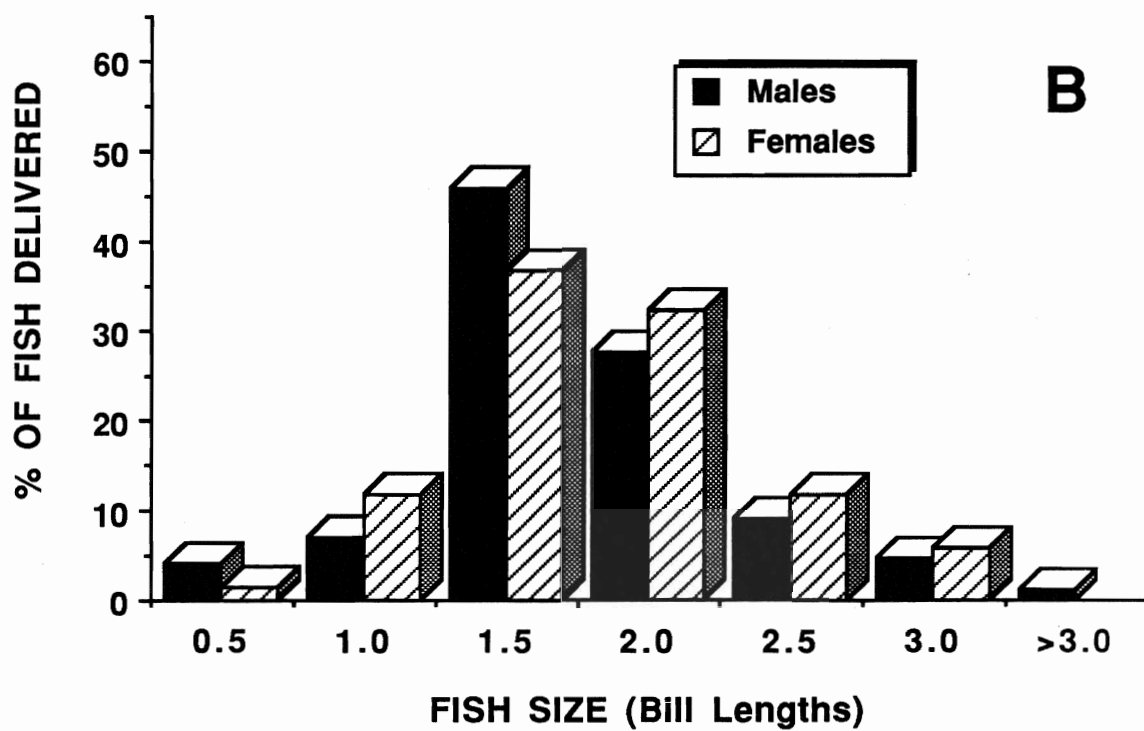
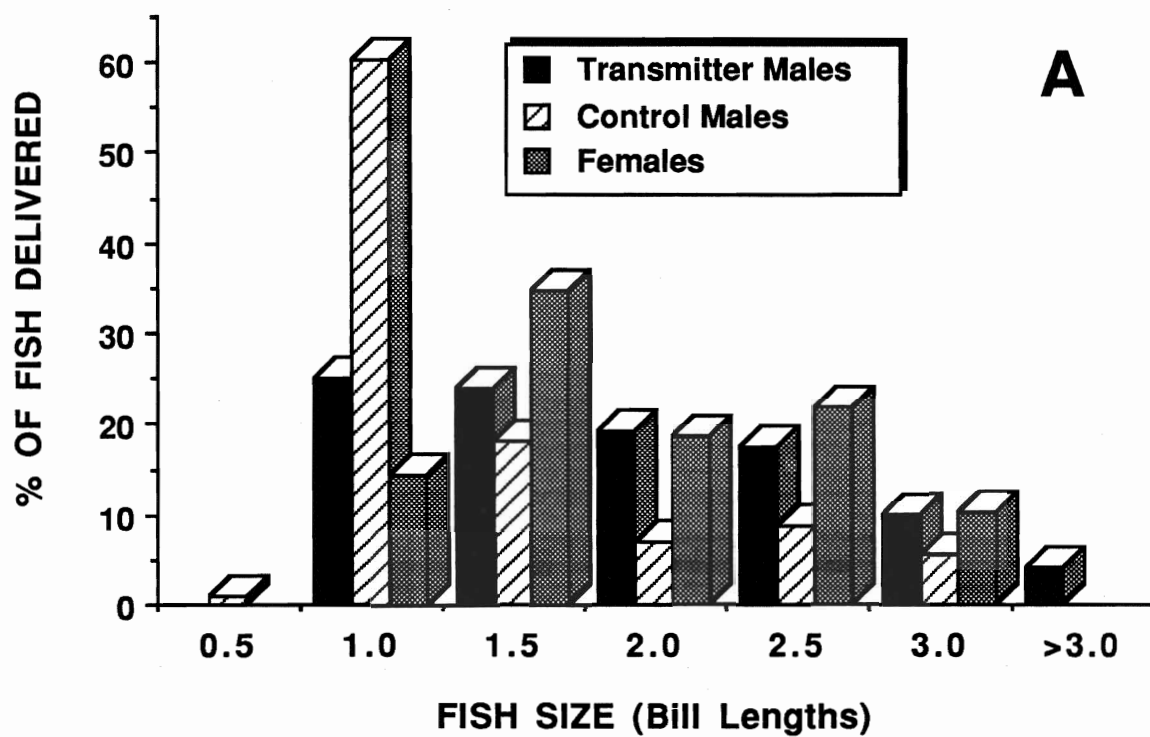


Figure 11A. Size (bill lengths) distribution of prey items delivered to chicks by male and female common terns during Peak 1992 at Windermere Basin.

Figure 11B. Size (bill lengths) distribution of prey items delivered to chicks by male and female common terns during Late 1992 at Windermere Basin.



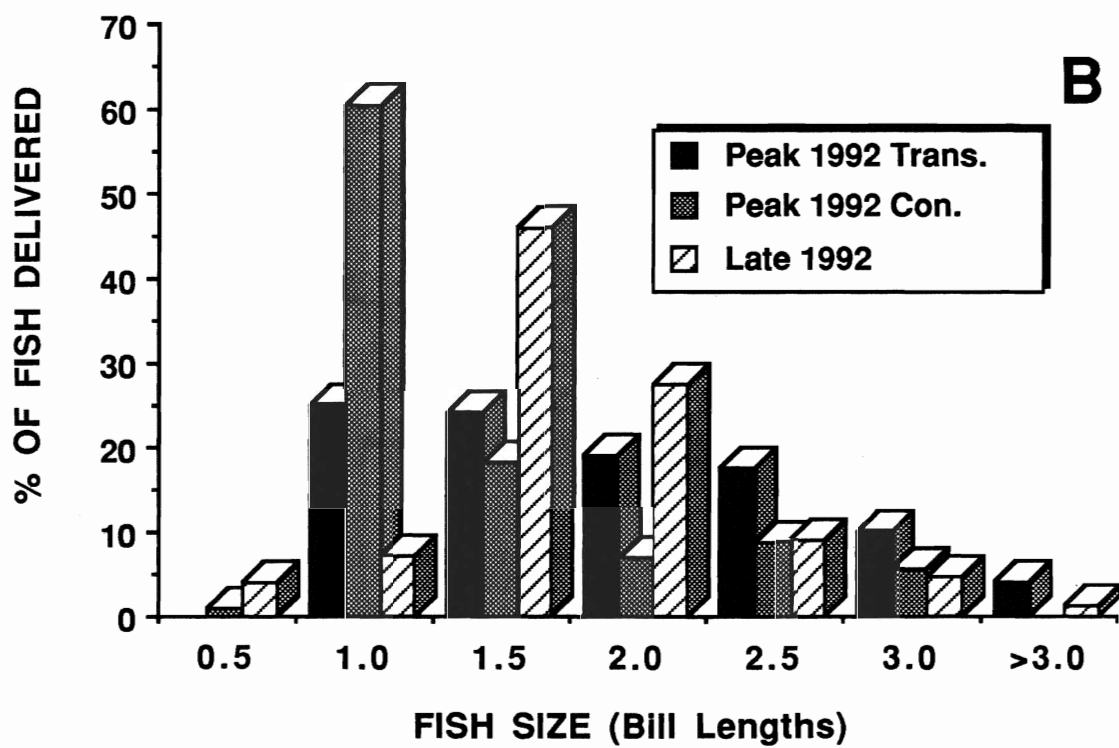
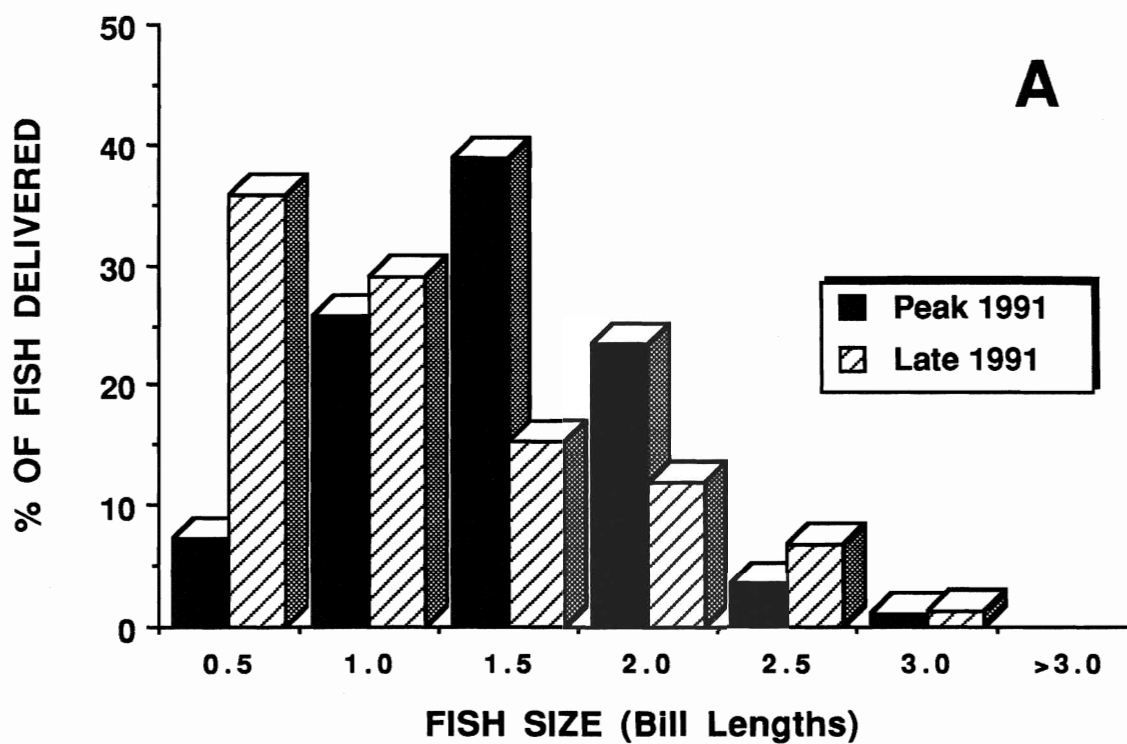
significant difference was found between Control males and study females (female partners of Transmitter and Control males pooled; $X^2=58.5$, d. f.=4, $p<0.0001$) in the size distribution of fish delivered to chicks. Control males tended to deliver fish of the one bill length size class more frequently than females (Fig. 11A). There was no difference ($X^2=2.0$, d. f.=4, $p=0.74$) in the size of fish delivered to broods between late-nesting males and females in 1992 (Fig. 11B).

iii) Seasonal patterns in the sizes of fish delivered to chicks

As there were differences between Peak and Late 1991 and 1992 with respect to the species of fish delivered to chicks, differences in the size class distributions of fish would also be predicted. Significant differences in the size class distributions of fish fed to chicks were detected between Peak and Late sampling periods among males ($X^2=251.7$, d. f.=5, $p<0.0001$) and females ($X^2=90.3$, d. f.=5, $p<0.0001$). During Peak 1991, the modal prey size delivered to chicks by study males was 1.5 bill lengths (Fig. 12A). However, the predominance of larval fish delivered to chicks during Late 1991 shifted the distribution of prey sizes toward fishes of one bill length or less (Fig. 12A). The reverse trend occurred in 1992, as males delivered small fish to chicks predominantly during the Peak nesting period, while the modal prey size during the Late period was 1.5 bill lengths (Fig. 12B). Both Peak-nesting Transmitter males ($X^2=39.1$, d. f.=4, $p<0.0001$), and Control males ($X^2=108.3$, d. f.=4, $p<0.0001$) delivered a significantly higher proportion of smaller prey than late-nesting males (pooled Transmitter and Control; Fig. 12B). However, no difference ($X^2=6.9$, d. f.=4, $p=0.14$) was found between Peak and Late females in 1992 with respect to the size class distributions of fish they delivered to chicks (Fig. 12B).

Figure 12A. Size (bill lengths) distribution of prey items delivered to chicks by male common terns during Peak and Late 1991 at Windermere Basin.

Figure 12B. Size (bill lengths) distribution of prey items delivered to chicks by male common terns during Peak and Late 1992 at Windermere Basin.



iv) **Relationship between chick age and size of fish delivered to chicks by adults.**

One-way, repeated measures ANOVAs were employed to determine whether a relationship existed between the size of fish delivered to chicks and the chicks' stage of development. No analyses were performed on the sizes of prey delivered to chicks by females during 1992, as sample sizes were too small to employ repeated measures analysis of variance procedures. Data were pooled into two-day blocks, except data for males during Late 1991 and Peak 1992 which were analyzed on a daily basis. Analyses were performed on brood ages one through eight unless stated otherwise.

During Peak 1991, there was a significant increase in the size of fish delivered to chicks with increasing brood age for both males (brood ages 1-10, $F=9.48$, d.f.=4, 28, $p<0.001$) and females (brood ages 1-12, $F=2.87$, d.f.=5, 25, $p=0.04$; Fig. 13A). A similar trend was observed during the Late nesting period in 1991, when the size of fish delivered to chicks by adults increased significantly as chicks grew older (males, $F=9.19$, d.f.=7, 42, $p<0.001$; females, $F=6.54$, d.f.=3, 21, $p=0.003$; Fig. 13B). Significant increases in prey size with increasing chick age were also observed among study males during the Peak (brood ages 1-5, $F=5.49$, d.f.=4, 32, $p=0.002$; Fig. 14A) and Late ($F=11.42$, d.f.=3, 12, $p=0.001$; Fig. 14B) nesting periods of the 1992 breeding season. Changes in the size of fish delivered to chicks by females as a function of chick age are displayed in Figs. 14A (Peak 1992) and 14B (Late 1992).

Figure 13A. Change in the size ($X \pm 1$ SE bill lengths) of fish delivered to chicks by male and female common terns, from brood ages one through twelve, during Peak 1991 at Windermere Basin.

Figure 13B. Change in the size ($X \pm 1$ SE bill lengths) of fish delivered to chicks by male and female common terns, from brood ages one through fourteen, during Late 1991 at Windermere Basin.

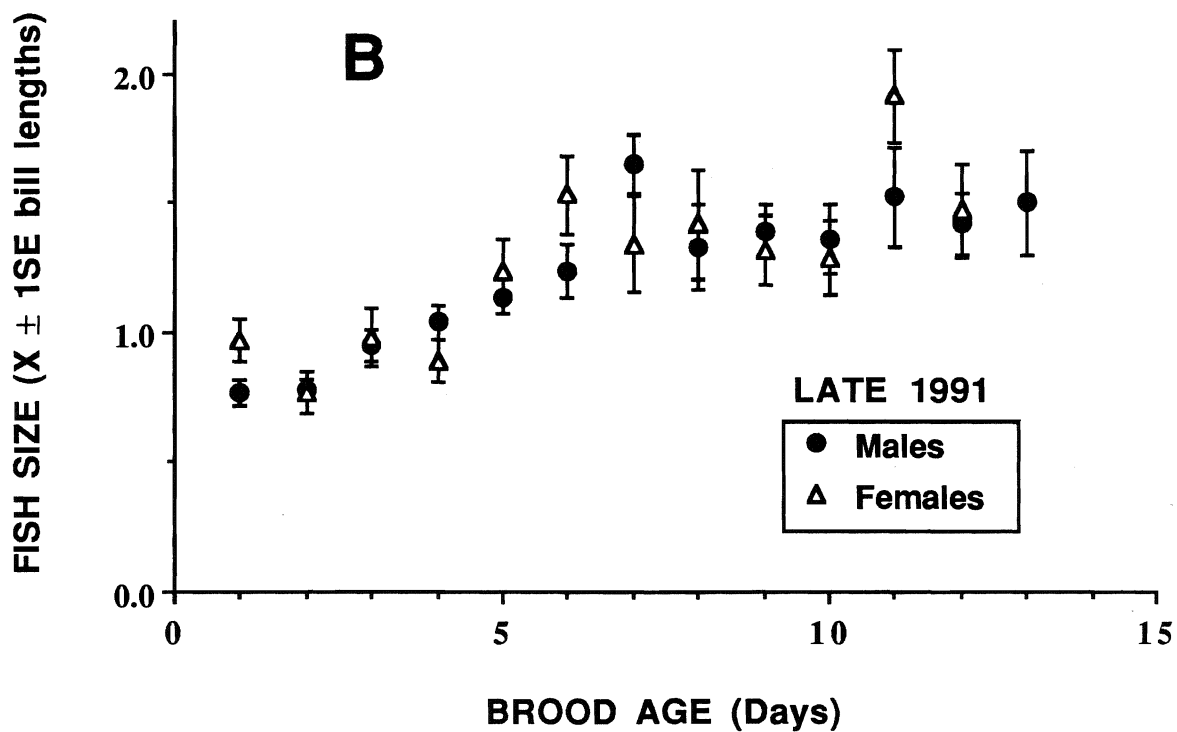
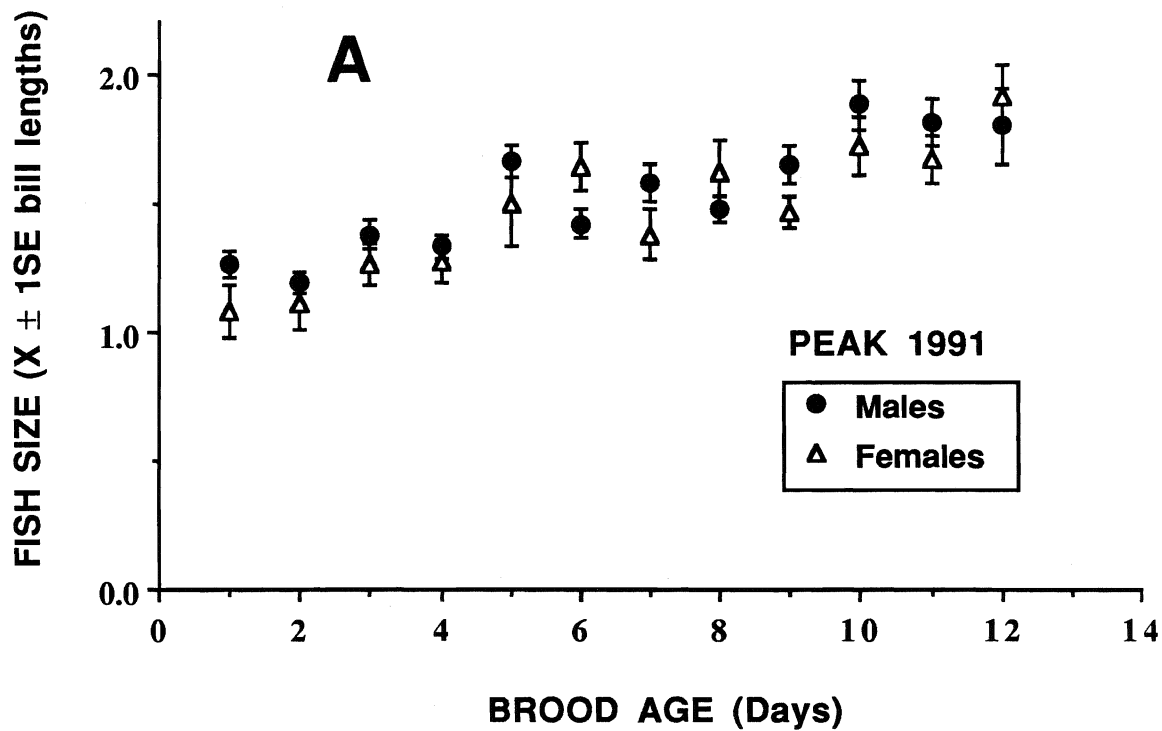
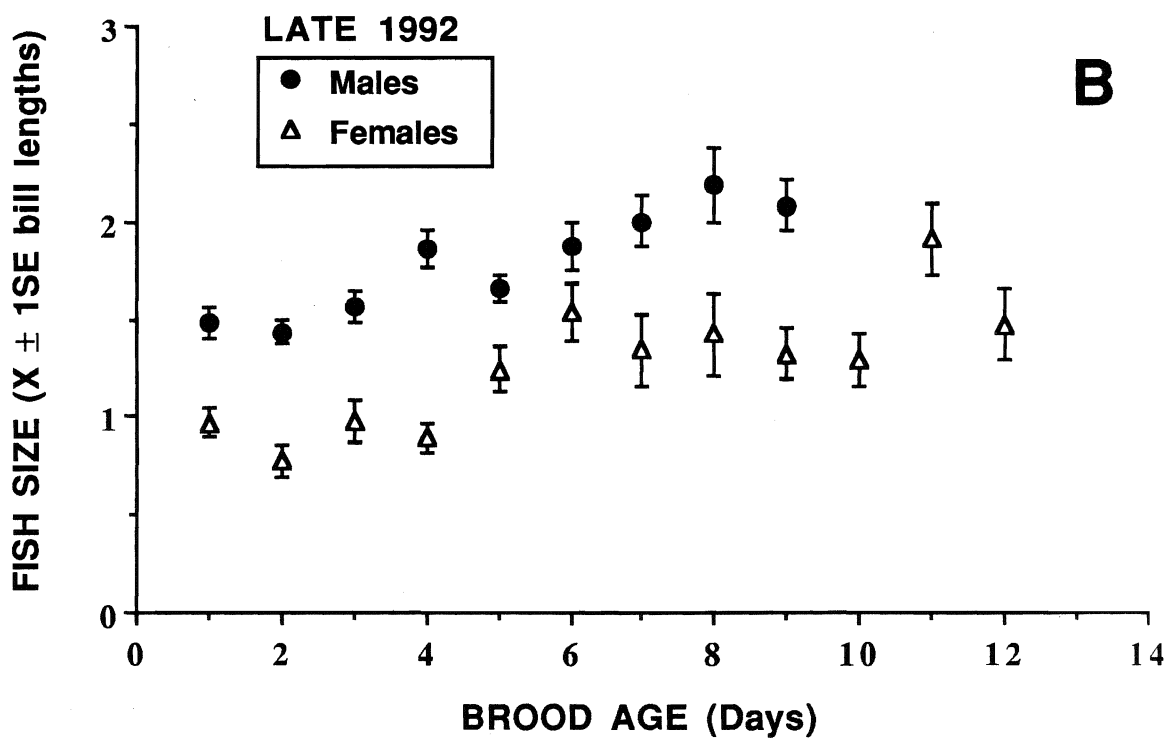
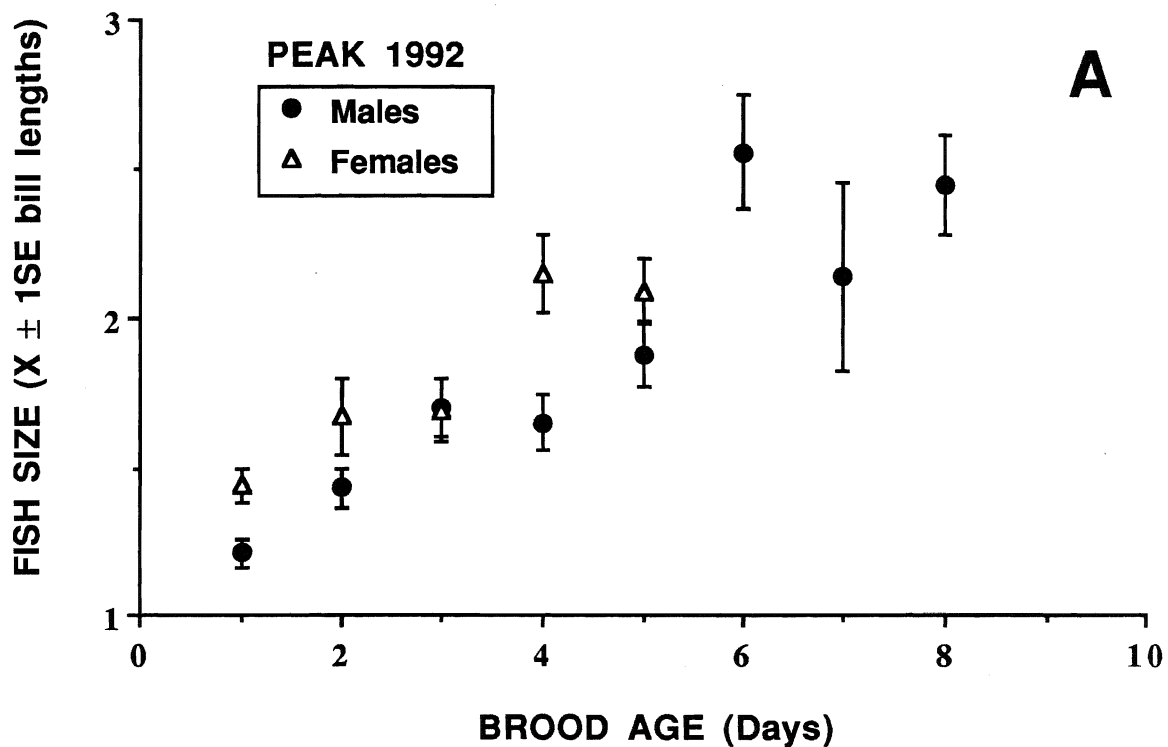


Figure 14A. Change in the size ($X \pm 1$ SE bill lengths) of fish delivered to chicks by male and female common terns, from brood ages one through eight, during Peak 1992 at Windermere Basin.

Figure 14B. Change in the size ($X \pm 1$ SE bill lengths) of fish delivered to chicks by male and female common terns, from brood ages one through ten, during Late 1992 at Windermere Basin.



3.5. Feeding Frequency

3.5.1. Comparisons between Transmitter and Control groups.

Comparisons were made between Transmitter and Control males, and between the female partners of experimental and control males, to determine if there were differences in the rates at which these groups delivered fish to their chicks. Comparisons between Transmitter and Control groups were performed using repeated measures ANOVAs, with brood age (standardized to the hatching of the last chick in a brood) as the repeated measure. Feeding frequency data were pooled into two-day blocks, and unless stated otherwise analyses were performed over the first eight days post-hatching of the third chick.

No significant differences were found between Transmitter and Control males, or between the female partners of Transmitter and Control males, with respect to the rate at which fish were delivered to chicks during either the morning or evening observation periods of either the Peak or Late nesting periods of 1991 or 1992 (Appendix 2). Transmitter and Control groups are pooled for all further analyses of chick-provisioning rates.

Comparisons of feeding frequencies between males and females revealed no difference in the rates of food delivery between morning and evening observation periods during the study. During Peak 1991, there were no significant differences in feeding frequency between the morning and evening observation periods for either males (brood ages 1-10; $F=0.19$, d.f.=1, 9, $p=0.68$) or females (brood ages 1-10; $F=0.66$, d.f.=1, 10, $p=0.44$). Similarly, no significant differences were detected between the morning and evening observation periods for either males (brood ages 1-10; $F=4.71$, d.f.=1, 12, $p=0.051$) or females (brood ages 1-10; $F=0.004$, d.f.=1, 12, $p=0.95$) during the Late nesting period of 1991. No differences

were found between morning and evening feeding frequencies in either Peak 1992 (brood ages 1-6; males, $F=2.45$, d.f.=1, 8, $p=0.16$; females, $F=0.07$, d.f.=1, 8, $p=0.81$) or Late 1992 (males, $F=0.32$, d.f.=1, 7, $p=0.59$; females, $F=2.18$, d.f.=1, 7, $p=0.18$). Hereafter, morning and evening observation periods have also been pooled.

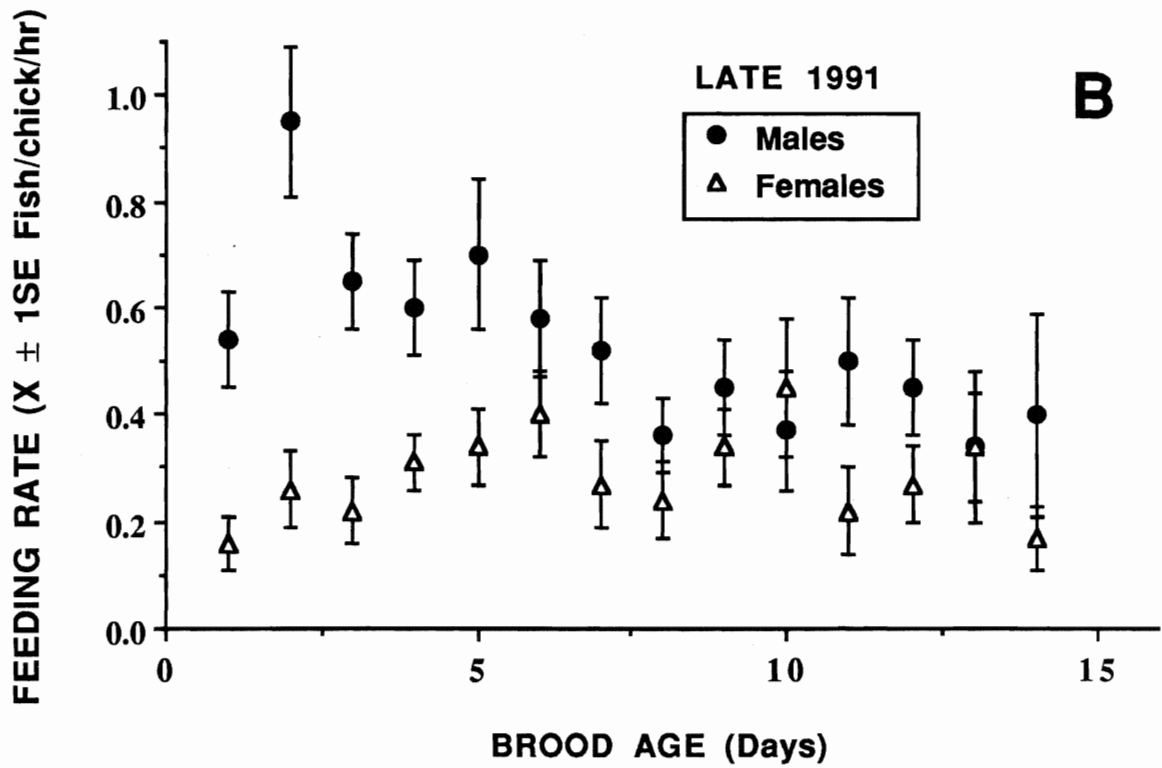
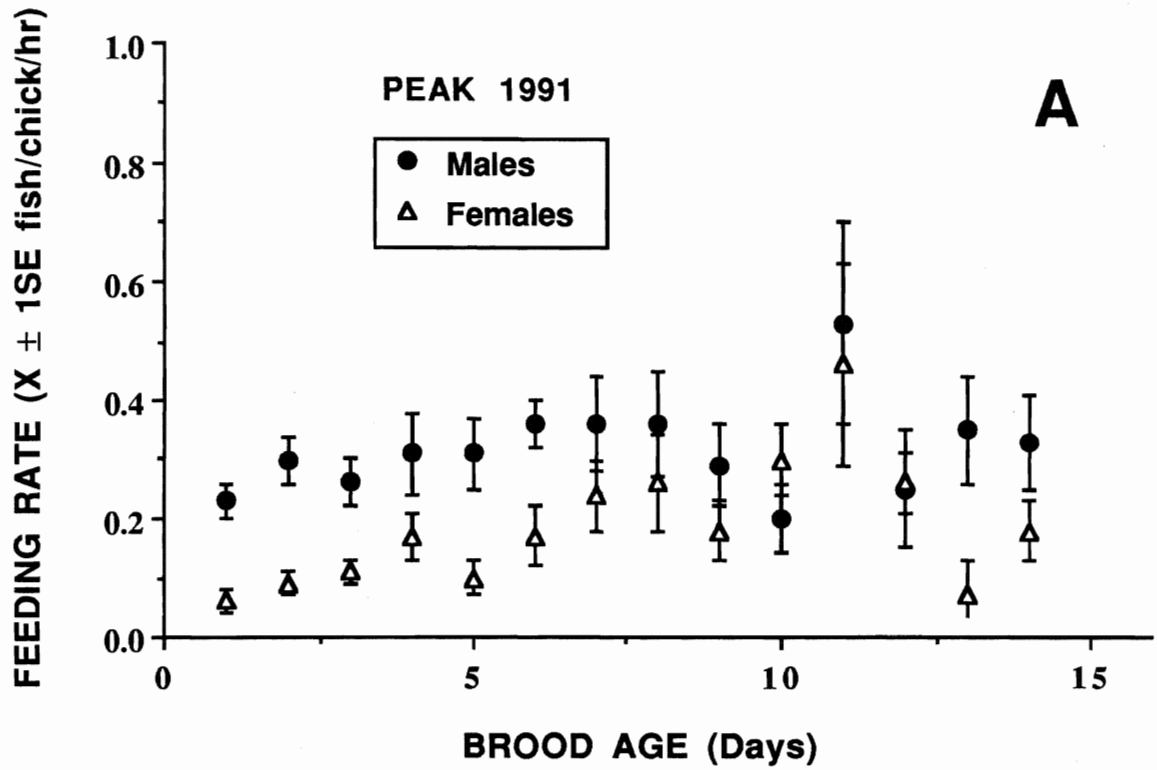
3.5.2. Male and female chick-provisioning patterns: rates of fish delivery.

It was established earlier that male common terns at Windermere Basin delivered at least two times more fish to chicks than did females. Therefore, it is not surprising that males also delivered fish at higher rates than females in all sampling periods during this study. Males delivered fish to chicks at significantly higher rates in both the Peak (brood ages 1-8, $F=12.8$, d.f.=1,26, $p=0.001$) and Late (brood ages 1-10, $F=25.8$, d.f.=1,27, $p<0.001$) breeding periods of 1991. This trend was also observed during 1992, as males delivered food packages to chicks at a higher frequency than their mates during both the Peak (brood ages 1-4, $F=57.9$, d.f.=1,32, $p<0.001$) and Late (brood ages 1-8, $F=50.1$, d.f.=1,16, $p<0.001$) nesting periods.

During Peak 1991, male feeding frequencies were constant over the observed period (brood ages 1-10, $F=1.79$, d.f.=4, 36, $p=0.15$) at a rate of approximately 0.3 fish/chick/hour (Fig. 15A). In contrast, female feeding frequencies increased significantly (brood ages 1-10, $F=3.8$, d.f.=4, 40, $p=0.01$) as chicks grew older, from 0.05 fish/chick/hour at brood age one to 0.28 fish/chick/hour by brood age 10 (Fig. 15A). Trapping adults during the Late nesting period of 1991 interfered with the collection of behavioural data over the first two brood days for three of the Control broods. To increase the sample size for analyses of feeding rates during Late 1991, brood days one and two have been excluded (in repeated measures

Figure 15A. Feeding frequencies ($X \pm 1$ SE fish/chick/hour) of male and female common terns, from brood ages one through fourteen, during Peak 1991 at Windermere Basin.

Figure 15B. Feeding frequencies ($X \pm 1$ SE. fish/chick/hour) of male and female common terns, from brood ages one through fourteen, during Late 1991 at Windermere Basin.



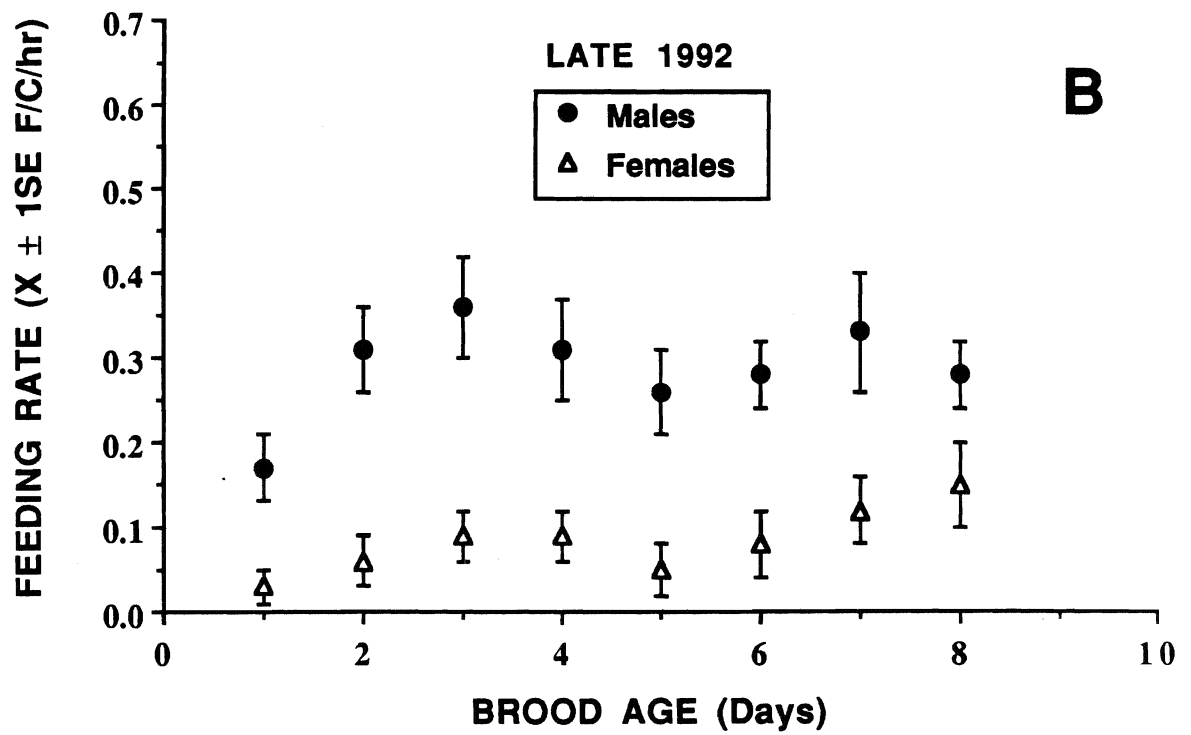
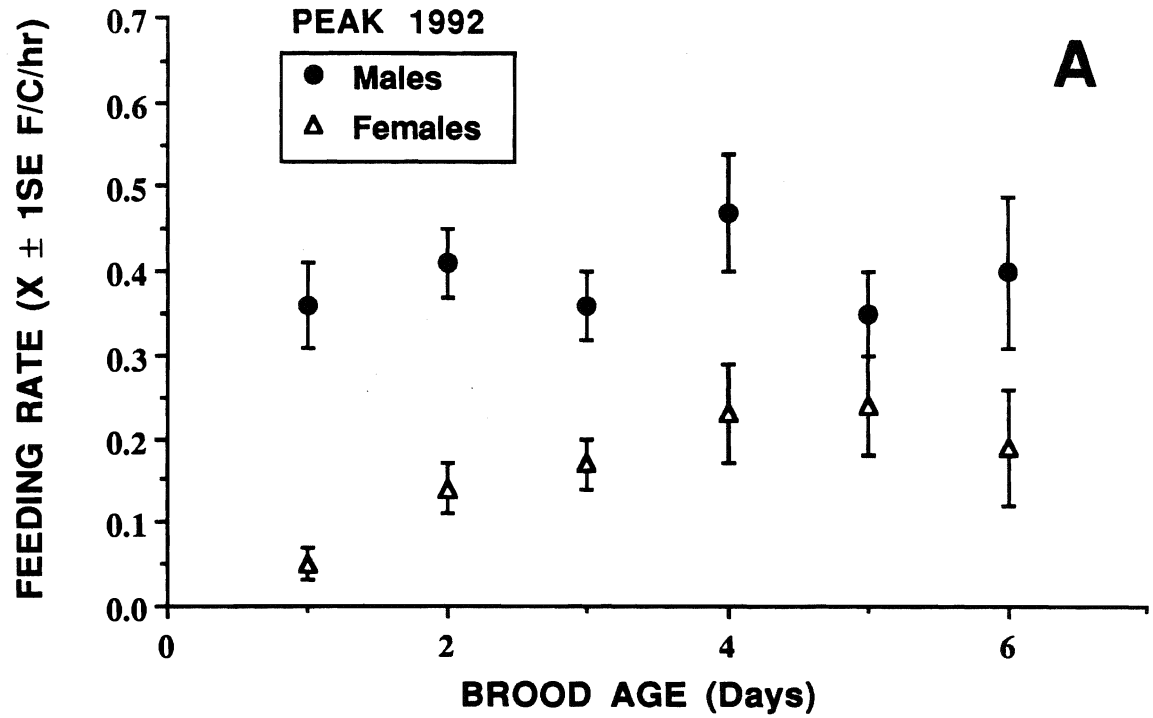
ANOVAs, subjects are eliminated from an analysis if there are any missing data points). During the Late nesting period of 1991, male feeding rates decreased significantly (brood ages 3-10, $F=3.2$, $d.f.=3$, 48, $p=0.03$) until a brood age of eight to ten days, and remained constant thereafter at a feeding frequency of approximately 0.4 fish/chick/brood (Fig. 15B). Female feeding frequencies remained constant (brood ages 3-10, $F=1.5$, $d.f.=3$, 45, $p=0.23$) during this nesting period at a rate between 0.2 and 0.3 fish/chick/hour (Fig. 15B).

Male chick-feeding rates did not change significantly over the course of the breeding season during either Peak 1992 (brood ages 1-6, $F=0.23$, $d.f.=2$, 16, $p=0.80$; Fig. 16A) or Late 1992 (brood ages 1-8, $F=0.60$, $d.f.=3$, 21, $p=0.63$; Fig. 16B). Feeding rates were approximately 0.4 and 0.3 fish/chick/hour for Peak and Late 1992, respectively. Similar to the fish delivery patterns observed among females in Peak 1991, the rate at which females provisioned their chicks during 1992 increased significantly with increasing chick age in both the Peak (brood ages 1-6, $F=3.88$, $d.f.=2$, 16, $p=0.04$; Fig. 16A) and Late (brood ages 1-8, $F=4.67$, $d.f.=3$, 21, $p=0.01$; Fig. 16B) nesting periods. Feeding frequencies increased from 0.05 to approximately 0.25 fish/chick/hour for females during the Peak nesting period. Feeding rates increased more slowly for females during Late 1992, from 0.05 to approximately 0.15 fish/chick/hour over the first eight brood days.

In general, males delivered fish to chicks at a higher, but constant rate over the observed sampling periods, while females increased their feeding frequencies over the first six to ten brood days (Figs. 15A & B, Fig. 16A & B). The Late nesting period of 1991 was an exception for both males and females (Fig. 15B). Initially, male feeding frequencies were high compared to other sampling periods, but after a brood age of eight to ten days males were delivering fish to chicks at constant rates. The fish delivery rates of females during this period did not increase as their chicks developed, as had occurred in the other sampling periods.

Figure 16A. Feeding frequencies ($X \pm 1$ SE fish/chick/hour) of male and female common terns, from brood ages one through six, during Peak 1992 at Windermere Basin.

Figure 16B. Feeding frequencies ($X \pm 1$ SE fish/chick/hour) of male and female common terns, from brood ages one through eight, during Late 1992 at Windermere Basin.



3.5.3. Seasonal patterns in the rate of fish delivery to chicks.

Chick-provisioning rates were significantly higher (brood ages 1-10, $F=14.75$, $d.f.=1$, 24 , $p=0.001$) for males during Late 1991 compared to feeding frequencies of males during the Peak period of the same year (Figs. 15A & B). Females also delivered fish to chicks at significantly higher rates (brood ages 1-10, $F=4.84$, $d.f.=1$, 24 , $p=0.04$) during Late 1991 than they did during the Peak nesting period of 1991 (Figs. 15A & B).

During 1992, the chick-feeding rates of males did not differ significantly (brood ages 1-6, $F=1.84$, $d.f.=1$, 21 , $p=0.19$) between the Peak and Late nesting periods (Figs. 16A & B). Among females however, fish delivery rates were significantly higher during Peak 1992 (brood ages 1-6, $F=10.68$, $d.f.=1$, 21 , $p=0.004$) than they were during Late 1992, by a magnitude of approximately two times (Figs. 16A & B). For males and females combined, feeding frequencies were highest during Late 1991 compared with Peak 1991, while the reverse was true during 1992.

There was no relationship between mean feeding frequencies of males and the mean size of fish delivered to offspring for either Peak 1991 ($r=0.02$, $N=12$, $p=0.94$), Peak 1992 ($r=-0.23$, $N=6$, $p=0.60$), or Late 1992 ($r=0.26$, $N=9$, $p=0.46$). However, during Late 1991, there was a significant negative correlation between mean fish size and rate of delivery by males ($r=-0.63$, $N=12$, $p=0.04$). Late 1991 was the period when the predominant prey species delivered to chicks was larval smelt.

3.6 Relationship between feeding frequency and breeding success.

There was no correlation between the mean feeding frequency of individual males over brood days one through five and the number of offspring still surviving by a brood age of 15 days, for either Peak 1991 ($r=0.01$, $N=16$, $p=0.97$) or Late

1991 ($r=0.17$, $N=11$, $p=0.56$). Sample sizes were too small to perform correlations on data from Peak and Late 1992.

B Movement patterns established using radio telemetry

All telemetry sessions were performed concurrently with the collection of behavioural observations from the blind, to permit a detailed commentary on daily movements of the birds carrying transmitters as they moved to and from the colony securing food for offspring. The locations of telemetry sampling stations and generalized common tern foraging areas around Hamilton Harbour and the western shores of Lake Ontario are designated on Figure 17. Descriptions of the designated foraging areas are given in Table 11.

3.6 Peak 1991

During the Peak nesting period of 1991, six male and two female Common Terns were fitted with radio transmitters. The number of listening hours per subject (both the time spent collecting 5-minute telemetry samples and time spent moving among sampling stations) varied from a minimum of 57.0 hours to a maximum of 74.5 hours, primarily as a function of differences in the life span of transmitter units (Table 12). The two females were detected at the colony at a much higher frequency than males. Female 669 was present at the colony during 93 of the 130 (71.5%) of the five-minute sampling periods collected from the colony base sampling station, located 200 meters east of the study plot. Female 630 was present at the colony for all of the telemetry samples collected from the colony base station ($N=130$), and was never detected away from the colony. In contrast, males spent the majority of their time away from the colony, presumably securing food for their offspring. Transmittered males were only detected at the colony in 10.8 to

Figure 17. Map of Hamilton Harbour and northwestern Lake Ontario showing permanent telemetry sampling stations (A-T) and designated foraging locations (1-16).

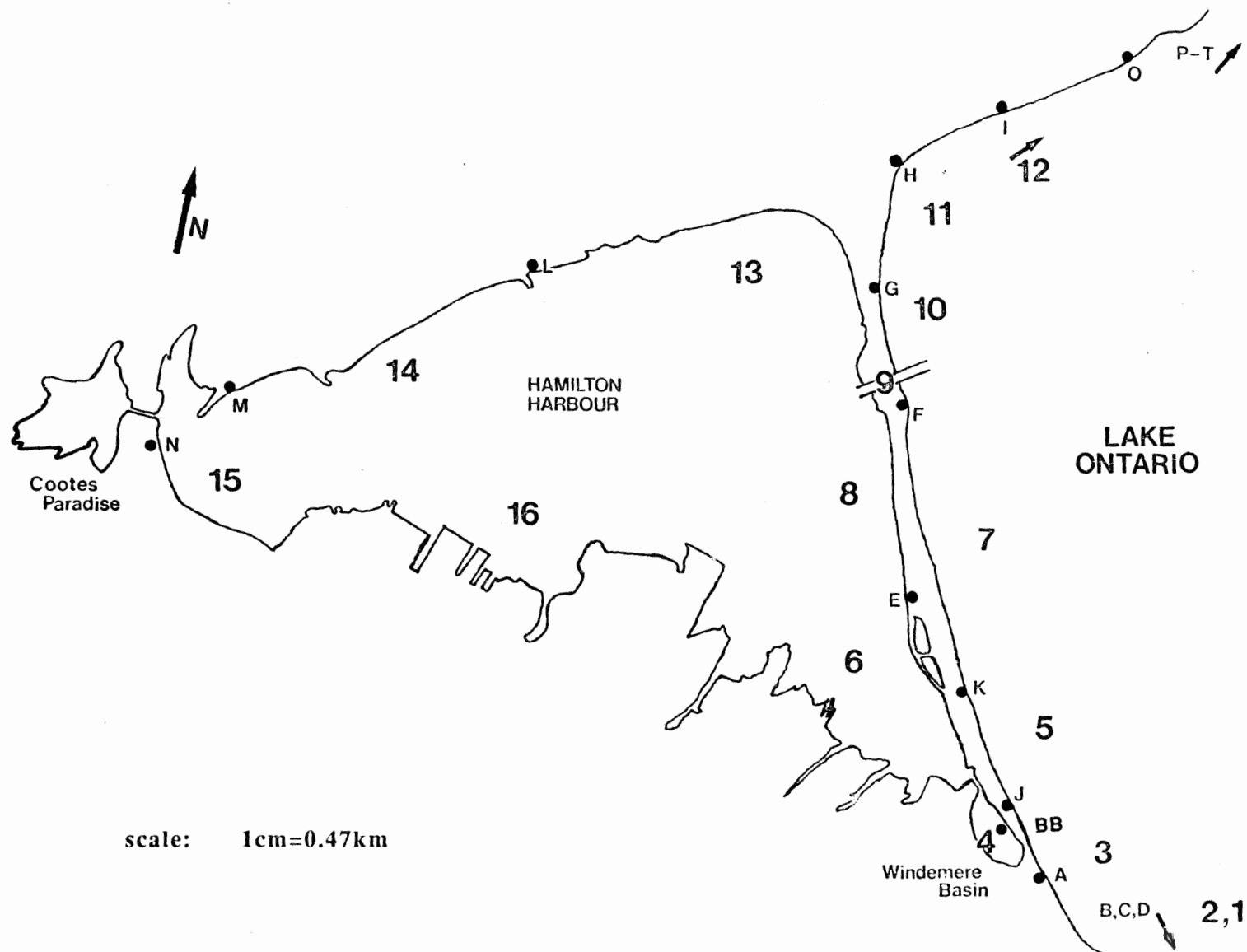


Table 11. Generalized foraging locations used by radio-tagged common terns during Peak and Late nesting periods of 1991 and 1992 at Windermere Basin.

Location	Description
<u>Lake Ontario</u>	
1	South-east of station Charlie along shore (including 50 Pt. Conservation Area.
2	CB Bay (bay between stations Brava and Charlie)
3	Between stations Juliette and Brava, including Van Wagner's Pond
5	Between stations Juliette and cormorant colony (station Echo)
7	Between cormorant colony and Burlington Canal (Lift bridge)
9	In or around Burlington Canal (Lift bridge)
10	Between Burlington Canal and station Golf
11	Between stations Golf and Hotel (CP Bay; bay at City Park, Burlington)
12	North-east of station Hotel along north shore of Lake Ontario, up to Bronte Creek (Burlington/Oakville border)
<u>Hamilton Harbour</u>	
4	Windermere Basin
6	Windermere Channel (between Windermere Basin and station Echo)
8	Between station Echo and Burlington Canal (lift bridge)
13	Between station Lima and the C.C.I.W. (area of Neare and Farr Islands)
14	Along north shore of Hamilton Harbour between stations Lima and Mike
15	Extreme eastern end of Hamilton Harbour (near Cootes Paradise)
16	The southern shore of Hamilton Harbour (closest to the heavily industrialized area)

Table 12. Movement data summary for radio-tagged common terns nesting during Peak 1991 at Windermere Basin.

Bird ¹	Sex	Transmitter hours ²	Detection frequency ³		Visuals ⁵ (N)	% time at colony ⁶
			base ⁴	away		
630	female	60.0	130	0	0	100.0
669	female	65.5	93	37	1	71.5
651	male	74.5	21	75	3	16.2
691	male	68.5	14	92	4	10.8
709	male	68.5	45	74	4	34.6
729	male	60.0	27	25	2	20.7
768	male	57.0	35	54	4	26.9
812	male	74.5	24	64	2	18.5

¹ Number based on last three digits of transmitter frequency (in MHz).

² Number of hours in which telemetry sampling was conducted, from transmitter attachment to transmitter death. All transmitters were attached by 08:30, 6 June 1991 and birds were monitored daily through the evening of 19 June 1991.

³ The number of 5 minute listening periods over the transmitter lifetime when a signal was detected.

⁴ Blind base: located approximately 200 m east of Windermere colony site.

⁵ Visual sightings of transmitted birds from listening stations.

⁶ Proportion of five minute sampling periods during which a signal was detected at the colony. A total of 130 samples was collected from the colony base station.

34.6% ($21.3 \pm 8.4\%$) of all five minute samples from the colony base station (Table 12).

There was not an even distribution of signals detected from the 22 sampling stations over the period of monitoring (Table 13). As the number of telemetry samples collected from each sampling station was not equal during Peak 1991 (Appendix 3), this alone might account for the patchy distribution of signal detections observed during this period. However, if a correction is made for the uneven sampling distribution, there is still significant heterogeneity ($\chi^2=397.1$, d.f.=3, $p \leq 0.0001$) in the distribution of observed signal detections (grouped into the general areas: north, south, in the vicinity of the colony, or Hamilton Harbour) compared to the pattern that would be expected if radio-tagged terns were foraging at random. Signal detections away from the colony were most frequent along the Lake Ontario shoreline, opposite the colony and south-east along that shoreline (stations BB, A, and B, Fig. 17), and along the shoreline in front of or within the lift bridge canal (stations F and G, Fig. 17). These two areas (five sampling stations) accounted for 67.4% of all signals detected away from the colony. With the exception of female 630 who was never detected away from the colony, signals detected from each of the other birds were concentrated in one or both of these principal locations (Table 13). For example, birds 669, 691, and 812 were detected approximately equally at both locations, whereas signal detections from other terns were concentrated predominantly in either the vicinity of the colony (males 651 and 729) or the area of the lift bridge (males 709 and 768). Female 669 showed the least amount of signal concentration of all radio-tagged terns.

Detection of a signal at a particular sampling location does not automatically imply that the bird was foraging at that site. In fact many of the signals detected in the immediate vicinity of the colony result from birds leaving or returning to the colony on route to or from a foraging area. In addition, simply assigning a signal to

Table 13. Number of five-minute sampling periods during which signals of radio-tagged common terns were detected from specific listening stations located around Hamilton Harbour and the western shores of Lake Ontario during Peak 1991. Only one signal detection per individual per five-minute sampling period was included.

Bird ¹	Detection location ²														
	D	C	B	A	BB ³	J	K	E	F	G	H	I-T	L	M	N
<u>female</u>															
630	0	0	0	0	130 (0)	0	0	0	0	0	0	0	0	0	0
669	1	0	1	8	97 (4)	0	1	0	9	4	0	0	9	0	0
<u>male</u>															
651	0	1	16	18	36 (15)	0	4	0	10	4	2	0	4	1	0
691	2	0	7	16	32 (18)	2	8	0	27	8	0	0	0	4	0
709	0	0	6	7	54 (9)	5	2	0	22	8	6	8	0	0	1
729	0	3	4	3	41 (14)	0	0	0	1	0	0	0	0	0	0
768	0	1	6	1	36 (1)	2	5	1	13	10	11	0	1	2	0
812	0	1	5	6	34 (10)	0	8	0	19	2	0	9	2	0	0
total⁴	2	6	44	51	460 (71)	9	27	1	92	32	19	17	7	7	1
grand total = 775															

¹ Bird transmitter codes and number of transmitter hours are as in Table 12.

² Refer to Figure 17 for locations of listening stations.

³ Telemetry sampling station approximately 200 m east of colony (Blind base). Numbers in column are total signal detections from this station, while numbers in brackets represent instances when an individual was detected from the colony base station but not placed at the colony.

⁴ Total for males only

the particular sampling station it was detected from results in the loss of any directional information associated with that signal. Therefore, a subset of the signal detection data was used to differentiate whether transmitted birds were actually foraging at a given location or simply traveling through it.

The decision about placing a bird at a particular location involved assessment of signal data accumulated from several listening stations over a relatively short period of time on a particular day. Accordingly, from field notes associated with each signal detection, conclusions were drawn about the most probable location of the bird when a signal was heard (Table 14). A common tern was presumed to be foraging at a given location if 1) a signal was detected at a designated foraging location from a particular sampling station for two or more consecutive five-minute sampling periods, 2) a signal was detected from two adjacent sampling stations and determined to be between them, or 3) the subject was observed while it was foraging. If a detected signal met any of these criteria it could be assigned to one of the 16 designated foraging locations (Fig. 17), defined using telemetry sampling stations and existing landmarks (Table 11). During Peak 1991, the majority (88%) of all presumed foraging bouts of transmitted males were along the shoreline of Lake Ontario, both in the immediate vicinity (within a two kilometer radius) and to the north of the colony (Table 14). Foraging activity was concentrated in two specific locations; 35% of presumed foraging bouts occurred in the areas adjacent to the colony (locations 3 and 5, Fig. 17), while approximately a quarter of all presumed foraging occurred between the lift bridge (location 9, Fig. 17) and "CP Bay" (location 11, Fig. 17; Table 14). A Kendall's Coefficient of Concordance test revealed that there was significant association ($W=0.58$, $N=4$, $k=6$, $p\leq 0.01$) among transmitted males with respect to their relative use of the colony vicinity as a foraging area, and the directional bearings (north, south, or Hamilton Harbour) of their presumed foraging trips away from the colony.

Table 14. Number of five-minute sampling periods during which radio tagged common terns were detected at presumed foraging locations around Hamilton Harbour and the western shores of Lake Ontario during Peak 1991. Only one signal detection per individual per five-minute sampling period was included.

Bird ¹	Designated locations ²														
	<u>South</u>		<u>Vicinity</u>				<u>North</u>					<u>Harbour</u>			
	1	2	3	4	5	6	7	9	10	11	12	8	13	14	15 ³
<u>female</u>															
630	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
669	0	1	4	2	9	5	4	4	0	0	1	4	4	0	0
<u>male</u>															
651	1	5	24	0	14	2	14	4	2	3	1	2	6	0	0
691	1	1	9	2	27	12	12	16	2	4	1	8	2	0	0
709	0	0	7	0	10	4	9	5	3	3	25	0	2	0	0
729	3	4	9	0	4	6	1	0	0	0	0	0	0	0	0
768	2	3	2	0	1	1	4	5	9	23	1	2	0	1	0
812	2	1	13	1	13	3	4	8	0	4	10	1	0	0	0
total⁴	9	14	64	3	69	28	44	38	16	37	38	13	10	1	0
	23		164				173					24			

¹ Bird transmitter codes and number of transmitter hours are as in Table 12.

² Refer to Figure 17 and Table 11 for designated locations. Locations are grouped into four general areas: south of the colony along the Lake Ontario shoreline, within a 2 km radius of the colony (vicinity), north of the colony along the Lake Ontario shoreline, and Hamilton Harbour.

³ Designated foraging areas 15 and 16 pooled.

⁴ Total for males only.

Although all males foraged predominantly in the same directional bearing (north), each of the six transmitted males that were detected away from the colony favoured specific foraging locations falling within that compass bearing (Table 14). Four of the transmitted birds (651, 691, 709, and 812) favoured the Lake Ontario shoreline opposite the colony, southeast along that shoreline, and in the vicinity of the lift bridge (locations 3,5,7,9, Fig. 17). Birds 651 and 691 foraged almost exclusively in the areas adjacent to the colony and at the lift bridge, whereas the other two terns also utilized secondary foraging locations. In addition to foraging extensively between the colony and lift bridge, males 709 and 812 had 41.2% and 23.3% of their foraging trips respectively, occur in or to the north-east of "CP Bay" (location 11, Fig. 17). The remaining two subjects exhibited unique foraging patterns. Bird 729 was only detected once to the north of the colony, and foraged predominantly in the vicinity of the colony or in a southerly compass bearing along the Lake Ontario shoreline (Table 14). Alternatively, male 768 foraged predominantly to the north of the colony and somewhat to the south, but relatively few foraging bouts occurred in the immediate vicinity of the colony. The single location that it visited most often (43% of total) was "CP Bay" (location 11, Fig. 17). In contrast to her male counterparts, female 669 foraged between the colony and lift bridge in both Hamilton Harbour and along the shore of Lake Ontario, showing no preference for any particular foraging location (Table 14).

In summary, during the Peak nesting period of 1991 common terns foraged almost exclusively along the Lake Ontario shoreline (82.0%) compared with Hamilton Harbour, and the overwhelming majority (92.7%) of foraging trips on Lake Ontario occurred either adjacent to or north of the colony.

3.7 Late 1991

Data for the four males that carried radio transmitters during the late-nesting period of 1991 are presented in Tables 15, 16, and 17. The number of telemetry sampling hours ranged from a minimum of 59.8 hours to a maximum of 86.8 hours as a function of differential transmitter life span (Table 15). Males during this period spent anywhere from 55.6 to 80.8% ($71.0 \pm 10.8\%$) of their time away from the colony, presumably foraging (Table 15). The number of five-minute samples collected from each of the 22 telemetry sampling stations is reported in Appendix 3.

The pattern of signal detections observed during Late 1991 was compared to the pattern that would be expected if radio-tagged common terns were foraging randomly (corrected for the differential sampling effort from the various telemetry stations). A significant degree of heterogeneity ($X^2=54.0$, d.f.=3, $p \leq 0.0001$) among the different areas (north, and south of the colony, colony vicinity, and Hamilton Harbour) was associated with the observed distribution of signal detections. Four sampling stations (stations BB, K, L, and F; Fig. 17) accounted for approximately two-thirds (68.8%) of all signal detections during the Late nesting period of 1991 (Table 16). As it had in Peak 1991, the Lake Ontario side of the lift bridge (station F, Fig. 17) accounted for the highest number of signal detections (25.1%). The number of signal detections from the other two stations (K, L, Fig. 10) increased dramatically during Late 1991, together accounting for 38.1% of signal detections compared with 8.8% during the Peak nesting period. In addition, there was a four-fold increase (to 21.0% from 3.9%) in the proportion of signals detected from stations within Hamilton Harbour, most specifically at station L (Table 16, Fig. 17). Signals from three of the four males (851, 889, and 931) were most frequently detected from stations BB, K and F, while the fourth male (971) exhibited a signal distribution concentrated at stations adjacent to the colony and southeast to "CB Bay" (stations BB, J, A, B, and C, Fig. 17).

Table 15. Movement data summary for radio-tagged male common terns nesting during Late 1991 at Windermere Basin.

Bird ¹	Sex	Transmitter hours ²	Detection frequency ³		Visuals ⁵ (N)	% time at colony ⁶
			base ⁴	away		
851	male	86.8	141	233	6	44.4
889	male	86.8	82	121	9	25.8
931	male	68.8	41	205	8	19.2
971	male	59.8	49	70	1	26.6

¹ Number based on last three digits of transmitter frequency (in MHz).

² Number of listening hours from transmitter attachment to transmitter death. All transmitters were attached by 19:30, 21 July 1991 and birds were monitored daily through the evening of 6 August 1991.

³ The number of 5 minute listening periods over the transmitter lifetime in which a signal was detected.

⁴ Blind base: located approximately 200 m east of Windermere colony site.

⁵ Visual sightings of transmitted birds from listening stations.

⁶ Proportion of five minute sampling periods during which a signal was detected at the colony. A total of 317 samples was collected from the colony base station.

Table 16. Number of five-minute sampling periods during which signals of radio-tagged, male common terns were detected from specific listening stations located around Hamilton Harbour and the western shores of Lake Ontario during Late 1991. Only one signal detection per individual per five-minute sampling period was included.

Bird ¹	Detection location ²														
	D	C	B	A	BB ³	J	K	E	F	G	H	I-T	L	M	N
851	0	1	9	9	171 (30)	5	35	13	61	19	0	0	25	5	6
889	0	0	2	11	119 (37)	3	21	10	14	8	0	0	11	3	1
931	0	0	0	11	71 (30)	10	32	4	70	3	0	0	13	7	4
971	0	10	12	8	64 (15)	8	5	1	4	0	0	1	5	1	0
total	0	11	23	39	425 (112)	26	93	28	149	30	0	1	54	16	11
grand total = 906															

¹ Bird transmitter codes and number of transmitter hours are as in Table 15.

² Refer to Figure 17 for location of listening stations.

³ Telemetry sampling station approximately 200 m east of colony (Blind base). Numbers in column are total signal detections from this station, while numbers in brackets represent instances when an individual was detected from the colony base station but not placed at the colony.

The four designated foraging locations within a two kilometer radius of the colony (locations 3, 4, 5, and 6, Fig. 17) accounted for over half (54.5%) of the presumed foraging locations of the four male common terns carrying radio transmitters during Late 1991 (Table 17). As with the Peak nesters, males in Late 1991 also foraged along the shoreline of Lake Ontario toward and in the immediate vicinity of the lift bridge (16.4% of total; locations 7 and 9, Fig. 17). However, unlike the birds in Peak 1991, they rarely (3.1% of presumed foraging activity) ventured past the lift bridge and along the northwest shoreline of Lake Ontario (locations 10-12, Fig. 17; Table 17). There was significant concordance ($W=0.70$, $N=4$, $k=4$, $p \leq 0.05$) among the four radio-tagged males with respect to the foraging patterns they exhibited, although individual differences were evident in the secondary locations favoured by these males (Table 17). Terns 851 and 889 favoured Hamilton Harbour as a secondary foraging location, predominantly in the area of the Hydro Islands (location 13, Fig. 17). While male 931 foraged most intensively in the vicinity of the colony, 65.5 % of its remaining foraging activity occurred in or around the lift bridge canal (locations 7, 9, and 10, Fig. 17; Table 17). Tern 971 differed from the other transmitted males in that one quarter of its presumed foraging activity occurred to the south of the colony, and only on one occasion was it found along the Lake Ontario north of the colony.

The trend in Late 1991 compared to the Peak nesting period of the same year, was the increased importance of the colony vicinity and Hamilton Harbour as foraging areas, with a corresponding decrease in the number of foraging trips to the northern shore of Lake Ontario beyond the lift bridge. The area to the south of the colony was not extensively used in either Peak or Late 1991.

Table 17. Number of five-minute sampling periods during which signals of radio-tagged, male common terns were detected at presumed foraging locations around Hamilton Harbour and the western shores of Lake Ontario during Late 1991. Only one signal detection per individual per five-minute sampling period was included.

Bird ¹	Designated locations ²														
	<u>South</u>		<u>Vicinity</u>				<u>North</u>					<u>Harbour</u>			
	1	2	3	4	5	6	7	9	10	11	12	8	13	14	15 ³
851	1	1	27	29	24	29	9	30	2	3	2	29	43	11	10
889	0	0	10	24	22	27	5	2	1	0	0	24	10	4	7
931	0	1	37	1	40	23	27	27	5	2	3	1	13	8	3
971	9	7	20	8	9	5	1	0	0	0	0	8	0	3	2
total	<u>10</u>	<u>9</u>	<u>94</u>	<u>62</u>	<u>95</u>	<u>84</u>	<u>42</u>	<u>59</u>	<u>8</u>	<u>5</u>	<u>5</u>	<u>27</u>	<u>66</u>	<u>26</u>	<u>22</u>
	19		335				119					141			

¹ Bird transmitter codes and transmitter hours are as in Table 15.

² Refer to Figure 17 and Table 11 for designated foraging locations. Locations are grouped into four general areas: south of the colony along the Lake Ontario shoreline, within a 2 km radius of the colony (vicinity), north of the colony along the Lake Ontario shoreline, and Hamilton Harbour.

³ Designated foraging areas 15 and 16 pooled.

3.8 Peak 1992

Movement pattern and foraging data for the six radio-tagged males nesting during Peak 1992 are presented in Tables 18, 19, and 20. The number of telemetry sampling hours ranged from a minimum of 53.3 hours to a maximum of 59.0 hours as a function of transmitter life span (Table 18). The clutch of male 2/12 was predated on the day following transmitter attachment, and this tern subsequently abandoned the colony. Therefore, male 2/12 was excluded from any further analyses. During this period males were detected in 22.4 to 43.8% ($32.6 \pm 8.0\%$) of telemetry samples collected from the colony base station (Table 18). The number of five-minute samples collected from each of the 22 telemetry sampling stations during Peak 1992 are reported in Appendix 3.

The pattern of signal detections observed during Peak 1992 exhibited significant heterogeneity ($X^2=156.2$, d.f.=3, $p \leq 0.0001$) when compared to a random detection pattern adjusted for the differential sampling effort from each station. Two sampling stations (A and BB, Fig. 17) accounted for 69.7% of all signal detections during the Peak nesting period of 1992 (Table 19). Most signal detections were concentrated in the vicinity of the colony, and only 6.4% of all signal detections occurred either to the south of "CB Bay" (station B, Fig. 17) or north of the lift bridge (station F, Fig. 17; Table 19).

The distribution of presumed foraging locations used by transmitted males during Peak 1992 closely resembles the pattern established from signal detections. Three-quarters of all foraging activity during Peak 1992 occurred within a two kilometer radius of the colony (Table 20). The second most heavily used foraging area (10.6% of total) was located to the north of the colony, specifically along the shoreline between the colony and lift bridge (location 7, Fig. 17). Foraging locations to the south of the colony, to the north of the lift bridge, and in Hamilton Harbour were rarely used during this period (Table 20). There was significant

Table 18. Movement data summary for radio-tagged male common terns nesting during Peak 1992 at Windermere Basin.

Bird ¹	Sex	Transmitter hours ²	Detection frequency ³		Visuals ⁵ (N)	% time at colony ⁶
			base ⁴	away		
2/10	Male	59.0	43	42	3	22.4
2/11	Male	59.0	56	52	2	29.2
2/12	Male	22.3	16	11	0	n/a
3/1	Male	59.0	60	55	1	31.3
3/2	Male	54.8	67	29	2	43.8
3/3	Male	53.3	51	26	1	36.4

¹ The frequency channel assigned to each transmitter.

² Number of listening hours from transmitter attachment to transmitter death. All transmitters were attached by the evening of 01 June 1992 and birds were monitored daily through 11 June 1992.

³ The number of 5 minute listening periods over the transmitter lifetime when a signal was detected.

⁴ Blind base: located approximately 200 m east of Windermere colony site.

⁵ Visual sightings of transmittered birds from listening stations.

⁶ Proportion of five-minute sampling periods during which a signal was detected at the colony. A total of 192 samples was collected from the colony base station for males 2/10, 2/11, and 3/1; 153 five-minute samples for male 3/2; and 140 for male 3/3.

Table 19. Number of five-minute sampling periods during which signals of radio-tagged common terns were detected from specific listening stations located around Hamilton Harbour and the western shores of Lake Ontario during Peak 1992. Only one signal detection per individual per five-minute sampling period was included.

Bird ¹	Detection location ²														
	D	C	B	A	BB ³	J	K	E	F	G	H	I-T	L	M	N
2/10	0	0	3	7	64 (21)	2	0	7	2	0	0	0	0	0	0
2/11	0	0	6	9	83 (27)	1	3	1	2	0	0	0	0	3	0
2/12	3	1	0	5	19 (3)	1	1	0	0	0	0	0	0	0	0
3/1	1	0	0	10	84 (24)	1	4	8	3	1	1	0	0	2	0
3/2	0	0	1	17	75 (8)	2	0	0	1	0	0	0	0	0	0
3/3	1	1	1	11	61 (10)	1	0	1	0	0	0	0	0	0	0
total	5	2	11	59	386 (93)	8	8	17	8	1	1	0	0	5	0
grand total = 511															

¹ Bird transmitter codes and number of transmitter hours are as in Table 18.

² Refer to Figure 17 for location of listening stations.

³ Blind base: telemetry sampling station approximately 200 m east of colony. Numbers in column are total signal detections from this station, while numbers in brackets represent instances when an individual was detected from the colony base station but not placed at the colony.

Table 20. Number of five-minute sampling periods during which radio tagged common terns were detected at presumed foraging locations around Hamilton Harbour and the western shores of Lake Ontario during Peak 1992. Only one signal detection per individual per five-minute sampling period was included.

Bird ¹	Designated locations ²														
	<u>South</u>		<u>Vicinity</u>				<u>North</u>					<u>Harbour</u>			
	1	2	3	4	5	6	7	9	10	11	12	8	13	14	15 ³
2/10	0	0	11	0	2	13	2	0	0	0	0	0	0	0	0
2/11	0	2	11	5	1	11	4	0	0	1	0	0	0	1	2
2/12	0	3	0	0	3	0	2	0	0	0	0	0	0	0	0
3/1	0	1	4	0	0	15	5	3	0	2	0	2	2	0	0
3/2	0	0	15	0	0	0	1	0	0	0	0	0	0	0	0
3/3	0	0	7	1	0	0	0	0	0	0	0	0	0	0	0
total	<u>0</u>	<u>6</u>	<u>48</u>	<u>6</u>	<u>6</u>	<u>39</u>	<u>14</u>	<u>3</u>	<u>0</u>	<u>3</u>	<u>0</u>	<u>2</u>	<u>2</u>	<u>1</u>	<u>2</u>
	6		99				20					7			

¹ Bird transmitter codes and number of transmitter hours are as in Table 18.

² Refer to Figure 17 and Table 11 for designated locations. Locations are grouped into four general areas: south of the colony along the Lake Ontario shoreline, within a 2 km radius of the colony (vicinity), north of the colony along the Lake Ontario shoreline, and Hamilton Harbour.

³ Designated foraging areas 15 and 16 pooled.

association ($W=0.68$, $N=4$, $k=5$, $p \leq 0.01$) among radio-tagged males with respect to the general foraging locations they utilized (north, south, colony vicinity, and Hamilton Harbour) during the Peak 1992 telemetry sampling period. The five males followed during this nesting period exhibited the least amount of individual variability of any period during the study (Table 20).

In summary, during the Peak nesting period of 1992 the majority (75%) of foraging activity by transmittered males occurred within a two kilometer radius of the colony. There was little individual variability exhibited compared with other sampling periods during the study.

3.9 Late 1992

Movement pattern and foraging data for one female and five male common terns fitted with radio transmitters during the Late nesting period of 1992 are presented in Tables 21, 22, and 23. Battery durations among the six transmitters were almost identical, and telemetry ranged from a minimum of 57.8 hours to a maximum of 58.8 hours (Table 21). During this period individual males spent from 25.6 to 57.5% ($39.0 \pm 11.5\%$) of their time at the colony, as determined from the proportion of times they were detected in telemetry samples from the colony base station (Table 21). The high affinity for the colony exhibited by male 3/6 (detected in 57.5% of samples collected from the colony base station) was an anomaly during Late 1992, as all other males during this period were detected at the colony in less than 40% of five-minute telemetry samples. Furthermore, this male had the highest detection rate from the colony base station of any male monitored during the study, by at least 13%. Alternatively, female 3/5b was detected at the colony much less frequently than the two females transmittered during Peak 1991 (39.7% of five-minute samples collected from the colony base station, compared to 71.5% and 100% for each of the females in 1991).

Table 21. Movement data summary for radio-tagged common terns nesting during Late 1992 at Windermere Basin.

Bird ¹	Sex	Transmitter hours ²	Detection frequency ³		Visuals ⁵ (N)	% time at colony ⁶
			base ⁴	away		
3/5b	female	57.8	58	10	0	39.7
2/10	male	57.8	65	46	0	38.7
3/2	male	58.8	62	26	1	36.9
3/4	male	58.8	61	34	1	36.3
3/5a	male	58.8	43	48	3	25.6
3/6	male	57.8	84	31	0	57.5

¹ The frequency channel assigned to each transmitter.

² Number of listening hours from transmitter attachment to transmitter death. All transmitters were attached by 09:00, 7 July 1992 and birds were monitored daily through the morning of 17 July 1992.

³ The number of 5 minute listening periods over the transmitter lifetime when a signal was detected.

⁴ Blind base: located approximately 200 m east of Windermere colony site.

⁵ Visual sightings of transmittered birds from listening stations.

⁶ Proportion of five minute sampling periods during which a signal was detected at the colony. A total of 146 samples were collected from the colony base station for birds 3/5b and 3/6, and a total of 168 samples were collected for all other individuals.

There was not an equal number of five-minute samples collected from each of the 22 telemetry sampling stations during Late 1992 (Appendix 3). The distribution of signal detections of transmitted males in Late 1992 exhibited significant heterogeneity ($X^2 = 65.4$, d.f. = 3, $p \leq 0.0001$) compared to the pattern expected if these terns were moving throughout the study area at random (adjusted for the differential sampling effort from various telemetry stations). During Late 1992, the majority (79.4%) of signals was detected along the shore of Lake Ontario between "CB Bay" and the shoreline adjacent to the colony (stations C, B, A, BB, and J, Fig.17; Table 22). Very few signal detections were made from sampling stations north of the colony or in Hamilton Harbour, and the majority (69.0%) that were detected in these areas can be attributed to male 2/10. The signal detections for all other transmitted individuals were clumped in the vicinity of and to the south of the colony (Table 22).

Late 1992 was a unique period compared with the previous three, in that 46.5% of all presumed foraging activity occurred to the south of the colony (Table 23). During foraging trips to the south of the colony, radio-tagged terns concentrated their foraging activity in two specific locations: approximately 3.5 kilometers from the colony in "CB Bay" (location 2, between stations B and C, Fig. 17) and 13 kilometers south of Windermere Basin at 50 Point Conservation Area (south of station D, Fig. 17). Fifty-point Conservation Area was the farthest foraging area from the colony that was consistently used by terns during this study. The area of Lake Ontario adjacent to the colony was also an active location during Late 1992, with one third of all presumed foraging bouts occurring there. These generalizations underestimate the importance of the foraging areas to the south, and in the vicinity of the colony, as a result of including the unique foraging pattern exhibited by male 2/10 (Table 23). A Kendall's Coefficient of Concordance test revealed that the foraging pattern exhibited by male 2/10 was significantly different from the pattern exhibited by all other males. There was no association ($W=0.43$,

Table 22. Number of five-minute sampling periods during which signals of radio-tagged common terns were detected from specific listening stations located around Hamilton Harbour and the western shores of Lake Ontario during Late 1992. Only one signal detection per individual per five-minute sampling period was included.

Bird ¹	Detection location ²														
	D ³	C	B	A	BB ⁴	J	K	E	F	G	H	I-T	L	M	N
<u>female</u>															
3/5b	2	1	1	4	58 (0)	2	0	0	0	0	0	0	0	0	0
<u>male</u>															
2/10	0	0	4	7	74 (9)	6	1	0	10	2	2	0	0	5	0
3/2	2	6	4	8	65 (3)	3	0	0	0	0	0	0	0	0	0
3/4	1	3	6	6	68 (7)	1	0	0	1	0	0	0	0	0	0
3/5a	3	6	14	15	46 (3)	4	1	0	1	0	0	0	0	0	0
3/6	1	1	0	17	89 (5)	1	3	0	1	1	1	0	0	0	0
total⁵	7	16	28	53	342 (27)	15	5	0	13	3	3	0	0	5	0
grand total = 490															

¹ Bird transmitter codes and number of transmitter hours are as in Table 21.

² Refer to Figure 17 for location of listening stations.

³ Includes signal detections from 50 Point Conservation Area.

⁴ Blind base: telemetry sampling station approximately 200 m east of colony. Numbers in column are total signal detections from this station, while numbers in brackets represent instances when an individual was detected from the colony base station but not placed at the colony.

⁵ Total for males only.

Table 23. Number of five-minute sampling periods during which radio-tagged common terns were detected at presumed foraging locations around Hamilton Harbour and the western shores of Lake Ontario during Late 1992. Only one signal detection per individual per five-minute sampling period was included.

Bird ¹	Designated locations ²														
	<u>South</u>		<u>Vicinity</u>				<u>North</u>					<u>Harbour</u>			
	1	2	3	4	5	6	7	9	10	11	12	8	13	14	15 ³
<u>female</u>															
3/5b	5	1	0	0	0	0	0	0	0	0	0	0	0	0	0
<u>male</u>															
2/10	0	0	10	0	2	0	10	2	1	7	0	0	1	5	0
3/2	3	6	4	0	0	0	0	0	0	0	0	0	0	0	0
3/4	10	8	3	0	0	0	0	0	0	0	0	0	0	0	0
3/5a	9	19	15	0	0	0	0	0	0	0	0	0	0	0	0
3/6	1	4	5	0	4	0	0	0	0	0	0	0	0	0	0
total⁴	<u>23</u>	<u>37</u>	<u>37</u>	<u>0</u>	<u>6</u>	<u>0</u>	<u>10</u>	<u>2</u>	<u>1</u>	<u>7</u>	<u>0</u>	<u>0</u>	<u>1</u>	<u>5</u>	<u>0</u>
	60		43				20					6			

¹ Bird transmitter codes and number of transmitter hours are as in Table 21.

² Refer to Figure 17 and Table 11 for designated locations. Locations are grouped into four general areas: south of the colony along the Lake Ontario shoreline, within a 2 km radius of the colony (vicinity), north of the colony along the Lake Ontario shoreline, and Hamilton Harbour.

³ Designated foraging areas 15 and 16 pooled.

⁴ Total for males only.

$N=4$, $k=5$, $p>0.05$) among the five transmitted males with respect to their relative use of various compass bearings while foraging. However, when male 2/10 was removed from the analysis, there was significant ($W=0.83$, $N=4$, $k=4$, $p\leq 0.01$) association among the remaining five males with respect to their foraging patterns. If male 2/10 is considered separately from the other transmitted birds, then the areas to the south of, and adjacent to the colony account for 66.7 and 33.3% of all presumed foraging activity. None of the other four males nor the female were ever detected foraging to the north of the colony or in Hamilton Harbour. In contrast, male 2/10 was never detected to the south of the colony and only 31.6 % of its presumed foraging activity occurred in the immediate vicinity (within a two kilometer radius) of the colony (Table 23). While away from the colony, tern 2/10 was very predictable in its movement patterns. A typical foraging trip consisted of male 2/10 traveling along the Lake Ontario shoreline from the colony to the lift bridge or "CP Bay" (locations 9 and 12, Fig. 17), and either crossing overland to forage along the north shore of Hamilton Harbour to location 14 (between stations L and M, Fig. 17), or foraging back along the shore of Lake Ontario towards the colony until it obtained a fish.

Female 3/5b was also somewhat of an anomaly. Not only was she infrequently detected at the colony (39.7% of total), but her signal was only detected in 10 five-minute telemetry samples collected from stations away from the colony (Table 23).

In summary, during Late 1992 all radio-tagged terns with the exception of male 2/10, foraged exclusively within a two kilometer radius, or south of the colony. Male 2/10 exhibited a foraging pattern unique from the other transmitted birds, never foraging to the south of the colony, but instead concentrating its foraging activities along the Lake Ontario shore north of the colony and the north shore of Hamilton Harbour.

3.10 Summary

The foraging data for the four nesting periods sampled during this study are summarized in Table 24. During the Peak nesting period of 1991, 88% of all foraging activity by the six radio-tagged males occurred either in the immediate vicinity of the colony (within a two kilometer radius) or to the north of the colony along the shoreline of Lake Ontario, distributed equally between the two locations. The maximum distance traveled to foraging areas by males during this period was approximately 14 kilometers from the colony. Study birds were rarely detected foraging to the south of the colony or within Hamilton Harbour.

In contrast, during the Late period of the same year the general trend was for transmittered males to forage closer to the colony. Greater than half (54.5%) of all foraging bouts occurred in the immediate vicinity of the colony. While males continued to forage north of the colony along the shore of Lake Ontario as they had during the Peak period, they were rarely detected north of the lift bridge. Foraging trips into Hamilton Harbour occurred more frequently during Late 1991 than any other telemetry period (23% in Late 1991 compared to about 6% in all other periods; Table 24).

The trend for males to forage in the vicinity of the colony during Late 1991, was even more pronounced during the Peak nesting period of 1992. During this period 75% of all presumed foraging activity occurred within a two kilometer radius of the colony. Radio-tagged males were rarely detected foraging to the south of the colony or in Hamilton Harbour, and never south of "CB Bay" (between stations B and C, Fig. 17) which is located approximately 3.5 kilometers from Windermere Basin. The presumed foraging bouts that occurred north of the colony (15.2% of total) were located predominantly between the colony and the lift bridge, approximately four kilometers away (location 7, Fig. 17). Therefore, virtually all of

Table 24. Distribution of five-minute sampling periods during which radio tagged male common terns were detected at presumed foraging locations around Hamilton Harbour and the western shores of Lake Ontario during Peak and Late nesting periods of 1991 and 1992 (percent of total is in parentheses). Only one signal detection per individual per five-minute sampling period was included.

Year	Period	Males (N)	General Foraging Area			
			South of Colony ¹	Colony Vicinity ²	North of Colony ³	Hamilton Harbour ⁴
1991	Peak	6	23 (6.0)	164 (43.0)	173 (45.0)	24 (6.0)
	Late	4	19 (3.0)	335 (54.5)	119 (19.5)	141 (23.0)
1992	Peak	6	6 (4.5)	99 (75.0)	20 (15.2)	7 (5.3)
	Late	5	60 (46.5)	43 (33.3)	20 (15.5)	6 (4.7)

¹ Includes designated foraging locations along the shore of Lake Ontario to the south of the colony (locations 1, 2, and 50 Point Conservation area; Fig. 17, Table 11).

² Includes designated foraging locations within a 1.5 km radius of the colony (locations 3, 4, 5, 6, and Van Wagner's Pond; Fig. 17, Table 11).

³ Includes designated foraging locations along the shore of Lake Ontario to the north of the colony (locations 7, 9, 10, 11, and 12; Fig. 17, Table 11).

⁴ Includes designated foraging locations within Hamilton Harbour (locations 8, 13, 14, 15, and 16; Fig. 17, Table 11).

the presumed foraging activity during Peak 1992 occurred within approximately four kilometers of the colony.

Transmitted male common terns foraged at much greater distances from the colony during Late 1992 compared to the earlier nesting period of that breeding season. All foraging activity to the north of the colony and in Hamilton Harbour (20.2% of total; Table 24) is the result of a single individual that exhibited a foraging pattern different from all other males during this period. The remaining four males foraged predominantly to the south of the colony, and to a lesser extent in the immediate vicinity of the colony. Away from the colony these radio-tagged terns foraged most intensively in "CB Bay" (between stations B and C, Fig. 17) and 50 Point Conservation Area (located 13 kilometers to the south of Windermere Basin). In many instances terns foraged first in "CB Bay", and if unsuccessful at obtaining a fish continued on to 50 Point Conservation Area.

DISCUSSION

4.1 Effects of radio transmitters

Presently, the only reliable method available for collecting information on foraging locations and activity patterns of individual seabirds away from the colony is through the use of devices such as radio transmitters or activity recorders. Although these techniques produce valuable data on foraging patterns of individuals, they can also cause animals to behave abnormally. Recent seabird-telemetry studies have reported both adverse (Massey *et al.* 1988, Wanless *et al.* 1988, 1989) and negligible (Hill and Talent 1990, Wanless *et al.* 1991, Klaassen *et al.* 1992, Wanless 1992) effects of transmitter packages on attendance and chick-provisioning behaviour of subjects. Even when transmitters have no demonstrated effect on behavioural patterns of subjects, there may be subtle energetic costs associated with attachment of units. Pennycuik *et al.* (1990) did not detect differences in chick feeding frequency or mass of food delivered to chicks between white-tailed tropicbirds carrying transmitters and those without. However, using a doubly-labeled water technique, the authors determined that transmittered birds achieved similar foraging performance to that of controls through higher energy expenditures. An increased energetic cost due to transmitter attachment may adversely effect an individual's foraging ability in conditions of poor food availability, or may reduce an individual's fitness through an expenditure of energy that could be potentially invested in future reproductive efforts (*sensu* Trivers 1972).

The transmitter packages and attachment procedures employed during this study are identical to the those used on common terns by Morris and Burness (1992). They found that these units did not affect brood attendance or chick-provisioning rates of radio-tagged males, or their female partners, when compared to non-transmittered controls. Data collected from 24 radio-tagged terns during two

breeding seasons at Windermere Basin further support that these transmitter units have no adverse effects on parental-care behaviours of common terns.

There were no obvious behavioural changes observed among transmitted individuals following attachment. Most birds returned quickly to their nests after capture, and radio-tagged terns were observed to peck at transmitters only during the first day after receiving units. No differences were detected between radio-tagged males and control males in either amount of time spent in brood attendance, or rate of fish delivery to chicks. During Peak 1992, transmitter and control males differed with respect to the species composition and sizes of fish delivered to chicks. However, the observed size differences were opposite to those expected for a "transmitter effect", namely, a decrease in payload mass to compensate for the mass of the transmitter package. Instead, radio-tagged males delivered a greater proportion of the larger size classes of fish than control males. No other differences were detected between transmitter and control males in either species or size distributions of prey items delivered to chicks.

If transmitters adversely affected the foraging efficiency of males, their female partners might be forced to increase their own foraging effort to compensate, and consequently reduce the amount of time spent in brood attendance compared to female partners of control males. This was not observed. Furthermore, the attachment of transmitters to males was found to have no effect on the survival of their chicks.

Klaassen *et al.* (1992) observed no significant differences in energy expenditure (determined using doubly-labeled water), body mass change, behaviour, or breeding success between common terns carrying 8 g transmitters and control birds. As these units are at least four times the mass of transmitters attached to terns at Windermere Basin (8 g compared to approximately 1.3 g), it is reasonable to assume that the transmitter packages used in this study did not result in increased energy expenditures or differential body mass changes in study birds.

Furthermore, in 1992, five common terns previously fitted with transmitters were observed at Windermere Basin, while none of the colour-banded control birds were resighted. Thus, transmitters do not appear to effect winter survival, migration, or site tenacity of these individuals.

In summary, the transmitter packages used during this study had no effect on brood attendance or chick-provisioning ability, do not appear to result in increased energy expenditure, or have any long term effects on common terns.

4.2 Relative contributions by the sexes to parental care

Among seabirds, biparental care is usually required for the successful rearing of young. Both parents participate actively in the various aspects of parental care, including territorial defence, incubation, brood attendance and chick feeding (Lack 1968). In cases where parental effort has been measured, the allocation of effort to parental care by males is approximately equal to (western gulls, *L. occidentalis*, Pierotti 1981; greater black-backed gulls, *L. marinus*, Butler and Janes-Butler 1983; red-throated loons, *Gavia stellata*, Reimchen and Douglas 1985; Atlantic puffins, *Fratercula artica*, Creelman and Storey 1991) or greater (black skimmers, *Rynchops niger*, Burger 1981, Quinn 1990; common terns, Wiggins and Morris 1987; Caspian Terns, *S. caspia*, Quinn 1990) than that of females. Although the sexes may provide similar investment, they often differ in the degree to which they engage in different activities.

Female common terns at Windermere Basin allocated significantly more time to brood attendance in comparison to their male partners, spending at least twice as much time at the nest during all periods of the study. Attendance time decreased gradually as the chicks grew older. After hatching, common tern chicks are dependent on adults as they cannot independently thermoregulate until between the fourth and seventh day post-hatching (LeCroy and Collins 1972; Ricklefs and White 1981). Therefore, female common terns are tied to the nest for

at least the first four days after the hatching of the last chick, equivalent to a brood age of five to six days depending on the hatching synchrony of the brood. As their chicks aged and were able to maintain a constant body temperature, females spent increasingly more time away from the brood, presumably foraging. In contrast, male attendance rates were lower than their female partners and generally remained constant over the observed brooding period.

The amount of time allocated to brood attendance by females was consistent between study periods, presumably because females are constrained by the developmental patterns of chicks, which are relatively invariable. However, males spent more time in attendance during Late 1991 than Peak 1991. Males foraged most intensively in the immediate vicinity of the colony during Late 1991, and foraging trip times were reduced. This allowed males to spend longer periods of time at the colony while still maintaining a high rate of fish delivery.

Males spent more time away from the colony and delivered fish to chicks at significantly higher rates than their female partners during all periods of the study. Of the total numbers of fish delivered to chicks during the periods of observation, males were responsible for between 65% and 77% of all deliveries. This trend is consistent with previous studies on the Great Lakes: females perform the bulk of brood attendance, while males are predominantly responsible for feeding chicks (Wiggins and Morris 1987, Burness 1992).

Similar studies of common terns on the Atlantic coast of North America have produced varying results. Nisbet (1973) found that males fed chicks more frequently than females. In contrast, Wagner and Safina (1989) reported no differences between males and females in the number of fish delivered to chicks over three breeding seasons. However, results may have been biased in favour of females that fed chicks at higher rates, as only pairs that successfully fledged one or more young were included in their analysis. Alternatively, the authors speculated that prey distributions are patchier and less predictable in marine

compared to freshwater systems, due to the interactions of tides and predatory fish. Thus, in marine systems, it may be necessary for both parents to actively forage in order to provide sufficient food to chicks. In support of this hypothesis, the relative contributions of the sexes to some aspects of parental care have been shown to vary in western gulls (Pierotti 1981) and fulmars (*Fulmarus glacialis*, Hatch 1990), presumably due to differences in food availability between years.

In addition to differing in chick-provisioning rates, male and female common terns also differed with respect to species and sizes of fish brought back to the colony. During Peak nesting periods, in both years, males and females differed in the relative frequency with which they delivered different fish species to chicks, with females consistently delivering a higher proportion of alewife. Similar sex differences in the species composition of prey delivered to chicks have been previously reported in common terns (Wagner and Safina 1989) and other waterbirds (California gulls, *L. californicus*, Jehl and Mahoney 1983; red-throated loons, Reimchen and Douglas 1985). The occurrence of inter-sexual differences in the species composition of prey delivered to chicks suggests that males and females might differ with respect to either 1) prey capture abilities resulting from morphological differences, 2) prey selectivity, or, 3) foraging location, such that sex differences in species composition delivered to chicks reflect differences in prey availability among locations. Common terns are essentially sexually monomorphic, differing only in bill morphology (Coulter 1986; Wagner and Safina 1989). Therefore, it is not likely that the sexes differ in their ability to capture prey. Jehl and Mahoney (1983) observed that in California gulls, females fed closer to the colony and brought back different types of prey than males. This explanation is also plausible for Common Terns, because radio-tagged females tended to forage in the vicinity of the colony, while males often ranged over greater distances. Males and females might be selected to differ in either foraging technique or foraging locations, as this would provide an evolutionary advantage by reducing

niche overlap and competition between pair members, thereby increasing the probability of finding enough food to provision chicks.

Sex differences were also observed with respect to size of fish delivered to chicks. During Late 1991 and Peak 1992, females delivered a significantly greater proportion of larger sized fish. This trend is unexpected, as there is only slight sexual dimorphism in common terns (Coulter 1986). In species where differences in size of prey delivered to chicks have been reported, the sex with the larger body size delivers longer fish or heavier loads to offspring (black skimmers, Quinn 1990; red-throated loons, Reimchen and Douglas 1985; white-tailed tropicbirds, Schaffner 1990). Therefore, in common terns, sex related differences in foraging ability are not predicted, as neither sex should be more proficient at capturing and carrying large prey items. In contrast to this study, Wagner and Safina (1989) found that male common terns delivered longer fish than females.

The observed differences in the size of prey delivered by males and females can also not be attributed to differences in prey availability resulting from differential use of foraging areas. Radio-tagged females tended to forage in the vicinity of the colony. In Late 1991 and Peak 1992, when the inter-sexual differences in size distributions of prey were observed, males also concentrated their foraging activity in areas within a two kilometer radius of the colony.

An alternative explanation is that differences in the size class distributions of prey between the sexes results from the high incidence of kleptoparasitism on adults and chicks by conspecific females. Inter-specific kleptoparasitism was used as a conditional foraging strategy by some females at Windermere Basin (DJM unpubl. data), and has also been reported at a colony on Lake Erie (Burness 1992). Females using kleptoparasitism as a foraging strategy would have greater success at stealing larger sized prey items for three reasons: 1) a higher probability of detecting males and chicks with large sized fish 2) large fish have a greater surface area, which increases the chances for a kleptoparasitic female to

successfully steal a fish, and 3) large fish require increased handling times by chicks, and thereby present a greater window of opportunity for a kleptoparasitic act. Furthermore, larger fish are more profitable to steal. If females were obtaining larger fish in this manner, it would be predicted that sex differences would be most pronounced during periods when males predominantly delivered small fish. Consistent with this hypothesis, the differences in size class distributions of fish between males and females occurred only during Peak 1991 and Late 1992, when the majority of fish delivered to chicks by males belonged to the smallest (0.5 and 1.0 bill length) size classes.

4.3 Temporal patterns of chick provisioning

Compared to their female partners, males delivered fish to chicks at a higher, but constant rate. Females exhibited relatively low feeding frequencies immediately after hatching, but prey delivery rates increased with increasing chick age. During the Peak nesting periods of 1991 and 1992, female feeding frequencies increased over the first six and four brood days respectively, and delivery remained constant afterwards. The time when females began delivering fish to chicks at a constant rate corresponds closely to the time when chicks reach thermal independence (4-7 days post hatch, LeCroy and Collins 1972; Ricklefs and White 1981). As the chicks were better able to regulate their own body temperature, females were free to allocate more time to foraging, and delivered food to chicks at a fairly constant rate. Through the hatching and chick brooding periods of Late 1992, the weather was uncharacteristically cold and it rained almost daily. As a result of the adverse weather conditions, females were required to brood chicks beyond the time when they usually attain thermal independence. Consequently, the feeding frequency of females was lower in Late 1992 than in any other nesting period, and chick-provisioning rates continued to increase over at least the first eight brood days rather than leveling off by a brood age of six days.

Late 1991 was an exception to these trends for both males and females. Males delivered predominantly small fish during the early stages of chick rearing, but compensated for the small size of prey by delivering fish at elevated rates. Male feeding frequencies decreased significantly until a brood age of eight days, and remained constant thereafter (at approximately 0.4 fish/chick/hr.). Female chick-provisioning rates did not increase during this period, but remained constant throughout chick rearing at a rate comparable to the delivery rates observed for females during other nesting periods.

The rates of prey delivery to chicks by males at Windermere Basin, during 1991 and 1992, were lower than those reported for a nearby ternery at Port Colborne, Lake Erie (Wiggins 1984; Burness 1992). However, females at Windermere provisioned chicks at a rate approximately in the median of the range of feeding rates reported for females at Port Colborne (0.10 to 0.65 fish/chick/hr.: Wiggins 1984; Burness 1992). The differences in feeding rates between Port Colborne and Windermere Basin suggest that prey are more accessible at Port Colborne, either because they are easier to find or concentrated closer to the colony. Alternatively, males at Port Colborne may have delivered smaller size classes of fish to chicks, but compensated by increasing their feeding frequency, as was observed during Late 1991 at Windermere Basin.

Among males at Windermere Basin, a relationship existed between chick feeding rates and the distance males had to travel away from the colony to obtain prey. During Late 1991 and Peak 1992, male feeding frequencies were the highest (approximately 0.4 fish/chick/hr.) recorded during this study. In both nesting periods, transmittered males concentrated their foraging activities in the immediate vicinity of the colony. Travel times between the colony and foraging locations were substantially reduced during these two periods, and therefore males were able to provision chicks at higher rates. Burness (1992) also reported relatively higher feeding rates by males during one of his nesting periods due to

the rapid delivery of larval fish captured within sight of the colony. In contrast, during both Peak 1991 and Late 1992, the rate of prey delivery by males was lower (approximately 0.3 fish/chick/hour), and during these periods radio-tagged males ranged over greater distances from the colony.

Although there is some variation in feeding rates during the initial period following hatching, for the most part, male and female common terns at Windermere Basin delivered fish to chicks at a constant rate over the periods observed. Several studies have reported constant delivery rates by adults under varying conditions. Wiggins (1989) found that although breeding common terns increased their foraging effort with increasing brood size, there was no difference in the overall amount of food received per chick for broods of different sizes. Ricklefs (1987) increased food demand upon Leach's storm-petrel (*Oceanodroma leuchoa*) parents by rotating into the nest unfed conspecific chicks of similar age and size. Adults did not increase either the size of fish fed to chicks or the overall rate of food delivery to the nest. In a similar experiment, Shea and Ricklefs (1985) increased food demand by cross-fostering larger sooty tern (*S. fuscata*) chicks into the nests of grey-backed terns (*S. lunata*). Foster parents responded to the larger chick by increasing both size of food items and overall rate of prey delivery. These results suggest that adults were apparently able to judge the overall size or numbers of chicks and alter their foraging behaviour accordingly, but are unable to judge or do not adjust foraging according to a chick's recent feeding history.

Selection may favour a constant prey delivery rate to chicks for two reasons. First, individuals are selected to optimize their reproductive fitness over a lifetime rather than investing in any single brood (Trivers 1972). Chick survival in common terns is dependent upon a number of stochastic factors independent of parental influence, such as weather (Becker and Specht 1991), food availability (Murphy *et al.* 1984; Safina *et al.* 1988), and predation (Nisbet and Welton 1984, Burness 1992). Therefore, an increased provisioning effort on the part of parents does not

necessarily ensure the survival of offspring. Second, individuals are selected to maximize energy transfer to chicks while minimizing their own energy expenditures. Seabirds that deliver fish whole to chicks can accomplish this by increasing the size of prey delivered to chicks as they grow, while maintaining a constant rate of fish delivery.

Consistent with this hypothesis, I found that male and female common terns delivered larger fish to chicks with increasing brood age. This pattern has previously been reported for common terns (Courtney and Blokpoel 1980; for males, not females, Wiggins and Morris 1987; pooled sexes, Safina *et al.* 1990), other tern species (black-naped tern, *S. sumatrana*, Hulsman and Smith 1988; crested terns, *S. bergii*, Smith 1989; black skimmers and caspian terns, Quinn 1990), and seabirds in general (gannets, *Sula bassana*, Montevecchi 1987; black guillemots, *Cephus grylle*, Cairns 1987; common murre, Hatchwell 1991; pigeon guillemots, *C. columba*, Emms and Verbeek 1991). Possible explanations for the observed increase in prey size over the brooding period is that adults either selectively capture, or preferentially deliver (select a subset of the fish they capture) larger sized prey to chicks as they grow older. Several independent studies provide support for this hypothesis. Hulsman and Smith (1988) found that the sizes of prey males fed to young chicks were smaller than the sizes of prey offered to mates, whereas the sizes of fish males fed to older chicks and their mates did not differ. They also found a difference between the size of prey that foraging adults ate themselves and those they delivered to their offspring. Therefore, male Black-naped Terns selectively fed smaller fish to chicks during early chick rearing, even though there was clearly a variety of different sized prey available to foraging males at this time. In addition, Quinn (1990) found that the length of prey delivered by Caspian Terns to chicks was positively correlated with brood age, but not calendar date. These findings suggest that the observed increase in fish size during the chick-provisioning period does not result from changes in availability of

different sized fish, and provide support for size-selective capture or delivery of prey by adults.

Another alternative hypothesis for the increase in the size of fish delivered to chicks with increasing brood age simply reflects the growth of fish over the period of chick rearing. Hatchwell (1991) provides contradictory evidence to this hypothesis. The length of sandeels (*Ammodytes tobianus*, the major prey species) delivered to common murre chicks increased by 5-6 mm per seven day period, whereas the mean growth rate of sandeels at that study location was 1.3 mm per week. Therefore, the observed change in the size of sandeels fed to chicks exceeded that expected if the change in prey size was entirely due to the growth of fish.

In light of findings of these studies, the most parsimonious explanation for the observed increase in size of fish delivered to chicks with increasing brood age at Windermere Basin is that adults selectively capture or deliver different sized prey depending on the age of chicks. Two selective forces are likely acting to produce the observed increase in prey size with chick age. First, small chicks are constrained by the size of their gape, and are only able to eat fish less than a certain size. Gape size increases with growth, allowing chicks to swallow a greater variety of prey sizes. Second, foraging adults are selected to minimize their own energy expenditures, while maximizing the amount of energy they deliver to chicks (Stephens and Krebs 1986). Foraging adults can increase the delivery of energy to chicks in two ways: increase payload mass or increase the rate of delivery. The increased energy expenditure that results from increasing payload mass is proportionately lower than the energy expenditure of a round trip from the colony to a foraging area. Therefore, by increasing the size of fish rather than the rate of delivery as chicks grew older, common terns breeding at Windermere Basin delivered increased amounts of energy at lower energetic costs to themselves.

4.4 Species composition of prey delivered to chicks: Seasonal and annual patterns.

In both years of the study, the relative proportions of different fish species fed to chicks by both males, and their female partners, changed over the course of the breeding season. There was also considerable variation between years with respect to the relative frequency adults delivered different fish types to chicks. Each sampling period was dominated by one (or two, Peak 1991) fish species comprising greater than 45% of total deliveries, while no other species delivered during that period individually consisted of more than 20% of the total. Smelt and emerald shiner were most numerous prey during Peak 1991, whereas 55% of fish brought to the colony during the late-nesting period were small, unidentified, larval fish (less than 1.0 bill length). The predominant species fed to chicks in 1992 changed from fathead minnows and smelt early in the breeding season, to alewife during the Late period. Among seabirds, similar variability in prey composition has been reported over the course of a breeding season (pigeon guillemots, Emms and Verbeek 1991), between or among years (black guillemots, Cairns 1987; common terns, Safina and Burger 1989), and simultaneously on both of these temporal scales (common murre, Hatchwell 1991; common and roseate, *S. dougallii*, terns, Safina *et al.* 1990).

Although the relative importance of each major prey species differed among nesting periods, delivery patterns for each prey species were consistent between years. Both the pattern and magnitude of smelt deliveries remained constant between 1991 and 1992. In both years, smelt comprised one quarter of fish delivered to chicks during the Peak period, whereas this proportion dropped to 10-15% of total fish delivered during the Late nesting period. Similar trends (although differing in magnitude between years) occurred with the other major prey species. Higher proportions of shiner and salmonid parr were delivered to chicks during the Peak periods of both years, whereas alewife and larval fish were delivered to

chicks more frequently during the later part of the breeding season. The abundance or accessibility of a prey species may change dramatically from one year to the next. However, certain life history parameters, such as the timing of spawning or migration, are relatively less variable. This might explain why all of the major prey species maintained a seasonal pattern of delivery (for example, larval fish were always detected with greatest frequency late in the breeding season), while apparently varying widely in either abundance or accessibility to study birds between years.

Overall, the most important prey species to breeding terns at Windermere Basin in 1991 and 1992, ranked in order of importance were; smelt, alewife, larval fish, shiner, salmonids and fathead minnows. These results are consistent with other studies of common tern foraging, conducted at Lake Ontario tern colonies. Gilbertson and Reynolds (1972) reported that the predominant prey species fed to chicks at Hamilton Harbour during May and June were alewife and smelt. Similarly, Courtney and Blokpoel (1980, Eastern Headland) reported that the principal fish eaten during May and June was alewife, followed in importance by smelt and emerald shiner. However, these data are at variance with patterns observed at a nearby tern colony at Port Colborne, Lake Erie, where the diet of chicks consisted mostly of smelt and emerald shiner (Courtney and Blokpoel 1980, Burness 1992). The differences between colonies with respect to the types of fish most frequently fed to chicks likely reflect differences in the abundance of fish between locations. Similar differences in prey composition have been reported among black guillemot colonies, and attributed to local differences in prey abundance (Cairns 1987).

The availability of prey to feeding terns is affected by both absolute abundance and accessibility of fish (Smith 1990). Prey abundance is particularly difficult to measure in aquatic systems because fish are usually highly mobile, patchily distributed, and difficult to observe (Safina *et al.*, 1988). Equally difficult to

quantify, prey accessibility is determined by both fish behaviour (ex. movement patterns, depth in water column) and factors that directly affect the foraging efficiency of plunge-diving seabirds, including wind speed (Dunn 1973, 1975; Becker and Specht 1991), rainfall (Dunn 1975; Becker *et al.* 1985; Becker and Specht 1991), fog (Hébert 1987), and tides (Smith 1990; Becker and Specht 1991). Age-specific foraging abilities are also well documented among seabirds (Dunn 1972; Buckley and Buckley 1974; Morrison *et al.* 1978; Searcy 1978; Burger and Gochfeld 1979, 1981; Greig *et al.* 1983; Maclean 1986; Burger 1987; Carl 1987). Therefore, determining the availability of prey at a given location during a particular period is a difficult task.

In instances when prey abundance has been measured, variability in chick growth, feeding patterns, and seasonal reproductive success of seabirds have reflected fluctuations in prey availability (Anderson *et al.* 1982; Schaffner, 1986; Safina *et al.* 1988). When abundance is not measured directly, prey availability is often inferred using corroborative evidence. For example, Bertram *et al.* (1991) observed considerable variation in mass of prey delivered to chicks among years. During this study, an oceanic disturbance (El Nino Southern Oscillation event) is known to have affected zooplankton productivity, salmon survival, and herring recruitment in the general region. There is likely a correlation between the ENSO event and variation in mass of prey delivered to chicks among years. However, it is impossible to determine whether prey availability was affected by a drop in fish abundance corresponding to lowered oceanic primary productivity, or whether shifts in fish distribution rendered fish unavailable. Seasonal differences in abundance of common tern prey have also been inferred from differences in feeding frequency between periods (courtship feeding, Morris 1986).

The observed variation in prey composition over the course of a breeding, and between years, likely reflects temporal variation in the availability of prey within foraging distance of Windermere Basin. Although I did not measure prey

abundance during this study, there is some evidence that suggests (for at least one prey species) the frequency with which a species was delivered to common tern chicks was relative to its abundance. Salmonid parr comprised approximately 15% and 10% of fish delivered to chicks during the Peak nesting periods in 1991 and 1992 respectively, but were virtually absent from Late samples. During Peak 1991 and 1992, chick-rearing took place during the time trout and salmon stocking programs were operating at the mouth of Hamilton Harbour and at 50 Point Conservation Area (13 km south of the colony; M. Whittle, pers. comm.). The greater proportion of salmonid parr delivered to chicks during Peak compared to Late periods may reflect opportunistic predation on this species by common terns during a time when salmonid parr were concentrated and relatively abundant.

Further evidence also suggests that the observed variation in prey composition during the study reflects temporal variation in the availability of prey in the vicinity of the colony. There was considerable variation over the course of the breeding season, and between years, in the size distributions of fish delivered to chicks. During 1991, the modal prey size delivered to chicks changed from 1.5 bill lengths during the peak-nesting period, to 1.0 bill length or less by the late-nesting period. The prey size distribution of fish delivered to chicks by Peak males was skewed in favour of small fish (1.0 bill length or less), while the modal prey size delivered to chicks by males during the Late period was 1.5 bill lengths. Not only did males deliver different size classes of fish during different nesting periods, but they also concentrated foraging activity in different locations. During Late 1991 and Peak 1992, when predominantly small fish were delivered to chicks, radio-tagged males foraged most intensively in the immediate vicinity of the colony (within a 2 km radius). Conversely, periods in which the modal prey size was large (Peak 1991, Late 1992) corresponded to periods when transmittered males foraged at greater distances from the colony. The most likely explanation for the

observed seasonal variation in prey sizes and foraging locations is that the availability of different prey species changed over the course of the study.

4.5 Movement patterns of male Common Terns: general trends and comparisons between two Great Lakes colonies.

Within each nesting period, transmittered males either foraged predominantly in the same directional bearing, or concentrated their foraging activity in the immediate vicinity of the colony. However, males often favoured specific foraging locations falling within these general areas, and differed in their secondary foraging patterns. Therefore, the foraging patterns of radio-tagged, male common terns were highly individualistic, and birds were predictable in their choice of foraging areas during the time they were provisioning chicks.

Most seabird telemetry studies have reported a similar clumping of departure bearings within a particular nesting period, indicating that colony members tend to forage in the same general areas (Harrison and Stoneburner 1981; Anderson and Ricklefs 1987; Pennycuik *et al.* 1990; Schaffner 1990; Wanless *et al.* 1990, 1991; Burness 1992). However, when the movement patterns of individual birds have been monitored, high intra-individual variability in foraging patterns has been revealed. Several studies have reported that different individuals foraged in widely separated areas on a particular day, and that some individuals foraged in different places on consecutive days, or even on consecutive excursions on the same day (masked and blue-footed boobies, *Sula nebouxii* and *S. dactylatra*, Anderson and Ricklefs 1987; common murre, razorbills, a puffin, Wanless *et al.* 1990). Although uncommon in the literature, predictable individual foraging patterns have been reported for herring gulls (Morris and Black 1980) and common terns (Burness 1992; this study). As these latter studies were conducted at colonies located on the Great Lakes whereas the others were conducted in marine areas, the use of predictable foraging locations by seabirds breeding in

freshwater habitats may reflect differences in prey availability between marine and aquatic systems.

The Lake Ontario shoreline between "CB Bay" (3-3.5 km south of colony) and the lift bridge canal (4 km north of colony) was the foraging area used most frequently by males during the chick-rearing periods of this study. Hamilton Harbour was used much less frequently, and use was variable among individuals and breeding seasons. The maximum foraging range of common terns at Windermere Basin appears to be approximately 14 km: terns were never detected north of Bronte Creek (14 km north of colony) or south of 50 Point Conservation Area (13 km south of colony). The median and maximum foraging ranges exhibited by terns breeding at Windermere Basin are similar to those previously reported for common terns (Atlantic coast, Duffy 1986; Mediterranean, Fasola and Bogliani 1990). Breeding terns are tied to a central place and constrained in the distance they can travel to forage by the energetic requirements of their offspring. The similarities in median and maximum foraging ranges among common terns nesting in these different systems suggests that there is some maximum foraging radius where an individual's energy budget is balanced: shorter foraging distances result in an energy surplus, while longer distances produce a deficit. Similar maximum foraging radii have been shown to exist for black-headed gulls (*L. ridibundus*, Brandl and Gorke 1988) and sooty terns (Flint 1991).

Although the Lake Ontario shoreline was the predominant foraging area used during the study, the extent that birds used this shoreline, and secondary foraging areas, varied among nesting periods. Males foraged farther to the north in Peak 1991, the colony vicinity was favoured in Late 1991 and Peak 1992, and terns concentrated foraging activity to the south of the colony during the late-nesting period of 1992. Similar trends were reported by Wanless *et al.* (1991), who found that locations of feeding areas of shags (*Phalacrocorax aristotelis*) remained more or less constant among years, but their relative importance

changed. The authors inferred that switches among foraging locations resulted from changes in availability of prey among years. The results from Windermere Basin are also similar to patterns exhibited by peak-nesting, radio-tagged, male common terns at a colony in Port Colborne, Lake Erie (Burness, 1992).

At Port Colborne, peak-nesting males showed almost identical patterns between years, exhibiting low inter- and intra-individual variability in departure bearings from the colony. As a group, males showed directional specificity, with the majority (>65%) of foraging trips occurring to the west in both periods. However, the foraging patterns of male common terns at Windermere Basin differed from those of late-nesters at the Port Colborne colony. Late-nesting males at Port Colborne showed increased intra-individual variability compared to Peak males, and as a group, did not show directional specificity in departure bearings from the colony, and often foraged to the east. Conversely, at Windermere Basin, late-nesting males showed identical patterns to their peak-nesting counterparts: namely, little inter-individual variability in departure bearings from the colony, and low intra-individual variability in foraging locations used.

Burness (1992) viewed the differences in foraging patterns between Peak and Late males at Port Colborne as representing either changing prey availability over the course of the breeding season, or that late-nesting terns were a behaviourally distinct group of birds. The literature suggests that late-nesting birds are often less experienced individuals, or failed breeders attempting to renest, implying qualitative differences between Peak and Late nesting groups (Hays 1978; Haymes and Blokpoel 1980; Massey and Atwood 1981). At Windermere Basin, fish species and size distributions, chick-provisioning frequencies, and foraging locations differed between years, as well as over the course of a breeding season. However, radio-tagged males showed directional specificity, as a group, within a particular nesting period, and low intra-individual variability in foraging location was maintained during all study periods. Furthermore, the highest feeding

frequencies were reported during Late 1991, resulting from the close proximity of foraging locations to the colony. Therefore, data from Hamilton Harbour suggest that at this location the distribution or availability of prey is the most important factor determining the foraging patterns of individuals within a breeding period. Late nesters at Port Colborne, might have simply been faced with low prey availability and changed their foraging tactics accordingly, rather than being "inferior" foragers *per se*.

One of the major findings of this study is that, similar to peak-nesting terns nesting at Port Colborne, males exhibited individual foraging patterns, and were consistent and predictable in their choice of foraging locations. The different patterns exhibited by late-nesting males at these colonies, likely reflects differences in the seasonal availability of prey. At Windermere Basin, individual prey species appear to fluctuate annually in their abundance and/or accessibility. However, overall distributions or availability of potential prey remain relatively constant, at least over the chick-brooding period, because males foraged in predictable locations during this time. Individuals may forage using the "strategy" to return to patches based on recent history of success. Conversely, fish availability at Port Colborne appears to be stable from year to year during the Peak nesting periods, but prey availability may deteriorate as the breeding season progresses. During both years of Burness's (1992) study, Morgan's Point was used extensively during the Peak periods, and both smelt and shiner were consistently the predominant species delivered to chicks. Individual males followed over consecutive breeding seasons, returned to Morgan's Point during both years.

4.6 Patterns of breeding success at Windermere Basin

Morris and Black (1980) speculated that parents successful in raising and fledging chicks might be expected to exhibit a foraging strategy different from those

that are unsuccessful. They found a clear relationship between the movement patterns and eventual brood success of four radio-tagged herring gulls: two pairs that foraged at greater distances from the colony and took flights of long duration lost chicks early in the brooding period, while two foraged locally and raised chicks successfully. However, patterns of chick loss at Windermere Basin during this study suggest that stochastic factors, such as predation or weather, may influence survival of common tern chicks to a greater extent than prey availability or the foraging efficiency of adults.

At Windermere Basin in 1991, there was no difference between Peak and Late nesting pairs in the mean number of chicks per brood surviving to a brood age of 15 days, even though feeding frequencies were significantly higher during the Late period. Furthermore, there was no correlation between an individual male's mean feeding frequency over the first five brood days, and the number of chicks still surviving by brood age 15, for either the Peak or Late nesting periods of 1991. A possible explanation for this result is that prey availability may not have been limiting during these periods, and even males provisioning chicks at relatively low rates provided sufficient food to sustain chicks. Alternatively, sampling periods during this study may not have been long enough for the observed differences in feeding frequency to translate into differential fledging success among males.

During the 1992 breeding season, stochastic events clearly outweighed any advantage that 'quality' individuals may have conveyed to their offspring. In the Peak period of 1992, black-crowned night-herons were responsible for predating 8 of 11 study broods during a single night. During this period, all individuals realized the same breeding success, regardless of the quality of parental care given to chicks. This predation event occurred at a time when radio-tagged males were foraging most intensively in the immediate vicinity of the colony and feeding frequencies were relatively high, indicating that foraging opportunities were favorable. Furthermore, during the same nesting period, another sub-colony in

Windermere Basin suffered no predation and many breeding pairs in this area successfully fledged chicks (D. Barbour, pers. comm.). Therefore, during Peak 1992, seasonal breeding success was determined by stochastic factors, extrinsic to the terns. Similar catastrophic effects of predation on common tern colonies have previously been reported (Nisbet and Welton 1984; Burness 1992).

A similar situation occurred during Late 1992, when 9 of 13 study broods failed by brood age of five days. The poor breeding success of common terns nesting during Late 1992 compared to terns nesting in Peak or Late 1991, can probably be attributed to environmental factors. In general, the summer of 1992 was colder and had greater amounts of precipitation than the summer of 1991. In particular, it rained every day during the hatching period of Late 1992. The majority of chicks were found dead in or near the nest scrape, and many had been wet or cold to the touch on the day preceding their death. The dependence of chick mortality on rain and minimum temperatures has been reported previously for common terns nesting on the German Wadden Sea (Becker and Specht 1991). As it was during the Peak nesting period of 1992, breeding success of terns during Late 1992 was determined by factors extrinsic to an individual's parental care abilities.

The failure to relate components of parental care to fledging success during this study, however, does not infer that this relationship does not exist. Natural selection acts to maximize an individual's lifetime, rather than seasonal, production of offspring (Trivers 1972). Therefore, over the period of a lifetime, terns that allocate 'quality' parental care to chicks are likely to realize differential reproductive success.

4.7 Future directions of study

There was considerable variability among sampling periods with respect to both the size and species of prey delivered to chicks, and the locations where radio-tagged males concentrated foraging activity. This suggests that different prey species may vary widely in availability, even over relatively short temporal scales. In order to conclusively link foraging patterns with prey availability, fish sampling needs to be incorporated into the design of future studies (Keeping in mind the inherent difficulties this presents).

During this study, prey size was quantified using bill lengths as an index of the amount of food delivered to chicks. Conversion of different size classes of the major fish species to caloric equivalents (using a technique such as bomb calorimetry) might provide a better currency for determining the relationships between chick-provisioning and offspring survival.

Finally, observed differences in the sizes and species of prey delivered to chicks by males and females, raise the possibility that the sexes differ in either their foraging techniques or foraging locations. Radio-tagging a larger sample of females would help to clarify whether sex-related differences in foraging behaviour exist in common terns.

SUMMARY AND CONCLUSIONS

The Lake Ontario shoreline between "CB Bay" and the lift bridge canal (within a four kilometer foraging radius of the colony) was the foraging area used most frequently by radio-tagged males during chick-rearing periods. The use of Hamilton Harbour as a foraging area was infrequent and variable among individuals. Within each nesting period, transmitted males foraged predominantly in the same directional bearing, or concentrated foraging activity in the immediate vicinity of the colony. However, individual radio-tagged males often favoured specific locations within these areas and differed in their secondary foraging patterns. The consistent and predictable foraging patterns exhibited by transmitted males at Windermere Basin are similar to patterns exhibited by peak-nesting males at a nearby colony (Port Colborne, Lake Ontario), despite differences in geography and colony age structure between the two locations. Similarities in foraging patterns between peak-nesting terns (and differences between late-nesters) at Windermere Basin and Port Colborne likely reflect differences in annual patterns of fish availability between locations.

There was a clear separation of parental roles among pairs nesting at Windermere Basin: males were primarily responsible for feeding chicks while females allocated more time to brood attendance. The prey species most commonly delivered to chicks by adults were rainbow smelt and alewife, larval fish, emerald shiner, salmonids, and fathead minnows. Males delivered fish to chicks at constant rates, while females increased their feeding frequency over the first six to ten brood days. The length of fish delivered to chicks by adults increased significantly as chick age increased.

The relative proportions of various fish species delivered to chicks by males differed over the course of each breeding season, and there was also much variability in species composition of prey between years. The size distributions of

prey delivered to chicks also differed among sampling periods. During periods when predominantly small fish were delivered to chicks, the foraging activity of radio-tagged males was concentrated within a two kilometer radius of the colony. The observed variation in prey composition and foraging locations during the study likely reflects temporal variation in prey availability in the vicinity of the colony.

No relationship was found between foraging proficiency of adults and survival of their offspring. Data from Hamilton Harbour during the 1991 and 1992 breeding seasons suggest that stochastic factors, such as predation and adverse weather conditions during early chick rearing, may be more important determinants of breeding success than parental quality or fish availability.

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Appendix 1 Statistical comparisons of fish size distributions between Transmitter and Control males, and the female partners of Transmitter and Control males, during the Peak and Late nesting periods of 1991 and 1992 at Windermere Basin.

Year	Nesting Period	Time	Sex	χ^2	d.f.	p
1991	Peak	A.M.	Males	3.41	4	0.49
			Females	5.33	4	0.26
		P.M.	Males	0.22	4	0.99
			Females	3.20	4	0.52
	Late	A.M.	Males	2.47	4	0.65
			Females	9.33	4	0.053
		P.M.	Males	6.47	4	0.17
			Females	5.03	4	0.28
1992	Peak	A.M.	Males	26.58	4	0.0001 **
			Females	7.29	4	0.12
		P.M.	Males	21.64	3	0.0001 **
			Females	2.04	2	0.36
	Late	A.M.	Males	5.18	4	0.27
			Females	---	--	0.28 ¹
		P.M.	Males	2.15	2	0.34
			Females	---	--	0.28 ¹

** Significant at alpha = 0.05

¹ Analysis = Fisher exact test.

Appendix 2 Statistical comparisons of chick-provisioning rates between Transmitter and Control males, and the female partners of Transmitter and Control males, during the Peak and Late nesting periods of 1991 and 1992 at Windermere Basin.

Nesting Period	Time	Sex	Days Analyzed¹	F	d.f.	p
Peak 1991	A.M.	Males	1- 8	4.05	1, 6	0.09
		Females	1- 8	0.19	1, 6	0.68
	P.M.	Males	1- 6	0.06	1, 7	0.82
		Females	1- 6	2.75	1, 7	0.14
Late 1991	A.M.	Males	1- 6	1.13	1, 6	0.33
		Females	1- 6	1.88	1, 6	0.22
	P.M.	Males	1- 10	4.56	1, 9	0.06
		Females	1- 10	0.15	1, 9	0.71
Peak 1992	A.M.	Males	1- 6	0.04	1, 5	0.86
		Females	1- 6	0.04	1, 5	0.86
	P.M.	Males	1- 4	0.47	1, 6	0.52
		Females	1- 4	0.64	1, 6	0.46
Late 1992	A.M.	Males	1- 6	0.21	1, 5	0.67
		Females	1- 6	5.55	1, 5	0.07
	P.M.	Males	1- 6	0.002	1, 4	0.97
		Females	1- 6	0.16	1, 4	0.71

¹ Brood ages on which analyses were performed. The rate of loss of study broods differed between sampling periods. As repeated measures ANOVAs do not tolerate missing data, it was necessary to truncate data at a point that maximized both the number of days and the number of broods included in each analysis.

Appendix 3. The number of five-minute sampling periods collected from each of the 22 telemetry sampling stations located around Hamilton Harbour and the western shores of Lake Ontario during the Peak and Late nesting periods of 1991 and 1992.

Period	Telemetry sampling station ¹														
	D ²	C	B	A	BB ³	J	K	E	F	G	H	O-T ⁴	L	M	N
<u>1991</u>															
Peak	10	13	56	63	130	7	34	3	177	21	19	22	22	13	6
Late	0	8	21	41	317	23	87	58	184	19	4	0	91	32	3
<u>1992</u>															
Peak	10	11	22	57	192	8	9	42	29	8	3	1	2	17	2
Late	57	23	25	74	168	24	5	8	15	5	6	0	1	17	2
total	77	55	124	235	807	62	135	111	405	53	33	23	116	79	13
grand total = 2328															

¹ Refer to Figure 17 for location of listening stations.

² Also includes signal detections from 50 Point Conservation Area.

³ Telemetry sampling station approximately 200 m east of colony.

⁴ Also includes sampling station, I (this column includes all telemetry stations along the Lake Ontario shoreline north of 'CP Bay').