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Effects of California Gulls on nesting Forster's Tern behavior

Aidona Outsiau Kakouros
San Jose State University

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EFFECTS OF CALIFORNIA GULLS ON NESTING FORSTER'S TERN BEHAVIOR

A Thesis

Presented to

The Faculty of the Department of Environmental Studies

San Jose State University

In Partial Fulfillment

of the Requirements for the Degree

Master of Science

by

Aidona Outsiau Kakouros

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APPROVED FOR THE DEPARTMENT OF
ENVIRONMENTAL STUDIES

Dr. Lynne Trulio, Professor of Environmental Studies
Committee Chairperson

Dr. Rachel O'Malley, Associate Professor of
Environmental Studies

Cheryl Strong, Biologist, San Francisco Bay Bird
Observatory

APPROVED FOR THE UNIVERSITY

12/05/06

ABSTRACT

EFFECTS OF CALIFORNIA GULLS ON NESTING FORSTER'S TERN BEHAVIOR

by Aidona Outsiou Kakouros

This thesis examined patterns of nest defense in Forster's tern (*Sterna forsteri*) colonies with respect to California gull (*Larus californicus*) intrusions at three different salt pond sites with Forster's tern colonies in the South San Francisco Bay area. In addition, a spatial analysis of the dispersion of California gull colonies, Forster's tern colonies, and landfills was performed to investigate factors contributing to variability in gull activity.

Forster's terns responded more aggressively to attacking California gulls as compared to gulls that exhibited less aggressive flight behavior, in which gulls were zigzagging or scanning above the tern colonies. California gull activity rates and time spent in defense by terns differed significantly between the three salt pond sites. The spatial analysis suggested that flight paths potentially used by California gulls to travel to landfills for foraging may explain the differences in the California gull activity at the three salt pond sites.

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INTRODUCTION

Nest predation is a major factor limiting breeding success in birds (Martin 1992, 1993). Gulls predate frequently on the eggs and young of other seabird species, which can be a serious threat to the breeding success of entire colonies (Hatch 1970, O'Connell and Beck 2003). Under the pressure of nest predation, birds employ several defense techniques to increase the probability of offspring survival, which in turn involve costs in time, energy, and risk (Montgomerie and Weatherhead 1988). Since the choice of anti-predator behavior associated with nest defense is a function of costs and benefits (Montgomerie and Weatherhead 1988), behavioral studies may be used to evaluate the risk the breeding birds face (Shordal 1990). Particularly for terns (*Sterna* spp.), several studies linked aggressive behavior during nest defense with the magnitude of predator activity on a site-specific basis (Erwin 1988, McNicholl 1973).

The negative effect of gulls as nest predators is further amplified by significant increases in their populations worldwide during the last decades (Kadlec and Drury 1968, Conover 1983, Shuford and Ryan 2000). Rapid increases in gull populations have often been associated with gulls using landfills as dependable sources of food (Hunt 1972, Belant 1997, Belant et al. 1998). Landfill use by gulls may be especially intensive during the breeding season (Pierotti and Anett 2001) and may positively affect their reproductive success (Spaans 1971). Thus, in urban areas where human refuse is ample and a shortage of nesting habitats may exist, fierce competition for nesting space could occur between the outsized population of gulls and other bird species sharing the same nesting habitats.

In South San Francisco Bay, large historic tidal marsh areas were diked for salt production from the 1850's to 1950s (Goals Project 1999). While historically there were some natural salt ponds along the eastern edge of South Bay, the high demand for salt in the early years of the 20th century resulted in the conversion of almost half of the tidal marshes into salt ponds (Goals Project 1999). The conversion of tidal marshes to salt ponds was detrimental for many native species; however, for other species, the creation of salt ponds and particularly dredge spoil islands and levees offered additional nesting habitats and enabled increased populations; shorebirds and colonial seabirds were particularly favored (Gill 1972, Gill and Mewaldt 1979).

California gulls (*Larus californicus*) and Forster's terns (*Sterna forsterii*) were species that benefited from the created salt ponds in South San Francisco Bay. Prior to 1981, California gulls were considered migrants or visitors during winter months. The first breeding colony of California gulls in the South Bay was recorded in 1981 at a salt pond in Alviso (Jones 1986). Since then, their population has increased exponentially (Strong et al. 2004) establishing the second largest breeding aggregation in the state (Shuford and Ryan 2000) at more than 30,000 individuals in 2005 (San Francisco Bay Bird Observatory unpublished census data). Since 1948, Forster's terns have formed breeding colonies on South Bay salt ponds (Sibley 1953). Terns are attracted to dredge spoil islands, which are placed at the corners and edges of the levees that surround salt ponds to delay levee erosion from wind and wave action. In San Francisco Bay, American avocets (*Recurvirostra americana*), black-necked stilts (*Himantopus mexicanus*), and black skimmers (*Rynchops niger*) often co-nest in Forster's terns

colonies (San Francisco Bay Bird Observatory unpublished data, personal observation). The Forster's tern population has decreased from 3,766 breeding birds in 1984 to 2,442 breeding birds in 2003 (Strong et al. 2004). The dramatic decrease of the Forster's tern population in the last two decades has been attributed, in part, to the nest predation and nesting habitat loss to California gulls.

Studies have shown the great importance of human refuse to breeding California gulls in the South San Francisco Bay. Jones (1986) found that anthropogenic food was the primary type of food in California gull diets, accounting for up to 40% of the total volume. He also reported that gulls were actively foraging in landfills located within a 15 km radius of his study site in Alviso. Dierks (1990) also found that 40% of California gull diets in Alviso was garbage. Furthermore, Cogswell (1974) reported intense use of landfills by California gulls and increased gull activity on sites close to landfills in the South San Francisco Bay. All of the above support the contention that landfill locations are significant factors in California gull movements.

Information about the effect of California gulls on the welfare of other species in the South San Francisco Bay is lacking. This information can assist managers in evaluating the danger posed to nesting species by the dramatic expansion of California gull populations and may support certain management measures. The South San Francisco Salt Pond Restoration Project plans to convert 15,100 acres former salt production ponds to tidal marsh and managed pond habitat. This project may reduce habitats currently used by terns and gulls, which could result in fierce competition for nesting space (Strong et al. 2004). Moreover, the project plans to create a large number

of new nesting islands. Creating specially designed islands for breeding terns may help alleviate this problem, but, if improperly located and managed, may attract California gulls (Strong et al. 2004).

The goal of this thesis is threefold: 1) describe the behavioral response of breeding Forster's terns during California gull intrusions, 2) compare the California gull activity, the time spent by nesting birds in defense, and the degree of breeding bird defensive response at several different sites in the South Bay with Forster's tern colonies, and 3) explore how the location of landfills may contribute to California gull activity in areas with Forster's tern colonies.

Related Research

Nest defense behavior. Nest predation is one of the proximate factors that can considerably limit reproductive success in many species of ground-nesting birds (Ricklefs 1969) and particularly colonial waterbirds (Burger 1982, Parnell et al. 1988). Predation pressures have influenced the evolution of nesting patterns of many bird species (Burger 1982). Nest defense behavior is considered one adaptation that reduces the vulnerability of the nests to predators (Montgomerie and Weatherhead 1988).

In the mid-1950s, many studies of bird behavior attempted to categorize observed nest defense behaviors according to the parental drive involved (Tinbergen 1952, Altman 1956). Nest defense behavior patterns were believed to be innate and relatively stereotyped in a way that could reveal the origins of this behavior for each species (Tinbergen 1952, Armstrong 1949). The focus of these studies on the innate nature of

nest defense behavior overlooked the influence of factors such as environmental conditions, experience and age of the defender, or time in the breeding season that could shape nest defense behavior (Lehrman 1952). However, even at that time it was recognizable that nest defense behavior would vary according to the intensity of the stimulus that provoked it (Tinbergen 1952) and the species of predator (Altman 1956). Moreover, the fact that some species would react with different intensity to various predator species and threatening situations according to their experience (Lehrman 1952, Altman 1956) supported the alternative hypothesis that defense behavior could be learned by experience; one test of the validity of this hypothesis in natural environments is by using the geographic distribution of the birds of a species that mob and those that do not (Altman 1956).

In later years, there was a shift from interspecific comparisons of the nest defense behavior (Siglin and Weller 1963) to studies on the benefit of this behavior to the performing individual. For example, Barash (1975) tested the prediction that defense would increase throughout incubation because of the increased value of the offspring and the decreased ability to re-nest, a prediction supported by the parental investment theory (Trivers 1972). Other avian behavioral studies questioned whether and how parents could recognize different predators (Curio 1975) and offered evidence of a variation in the parental defense according to the proximity and hunting behavior of the predator (Altman 1956, Hatch 1970). In a review of the nest defense studies, Montgomerie and Wheatherhead (1988) presented another hypothesis, proposing that the intensity of nest defense behavior can be treated as an optimization problem where the risk parent birds

are willing to take defending their nest and young is defined by the difference between fitness costs and benefits gained by defense. Within this optimality framework, they also predicted that the intensity of nest defense increases with parental experience, and nest accessibility and conspicuousness.

There is much research focusing on nest predation and nest defense behavior of colonial species as their breeding success is particularly affected by avian predators (Burger 1982, Parnell et al. 1988). Specifically for terns, studies have shown that the intensity of nest defense behavior varies with predator hunting behavior (Hatch 1970, Cavanagh and Griffin 1993, Whittam and Leonard 2000) and the breeding stage of terns (Whittam and Leonard 2000, Palestis 2005). Hatch (1970) found that terns responded aggressively to gulls flying at a height less than 20 meters and exhibiting hunting behavior as characterized by direct attacks or zigzagging flights over the tern colony. Cavanagh and Griffin (1993) found, also, that terns responded selectively to gulls that exhibited behaviors associated with predation, such as landing on the tern island. Whittam and Leonard (2003) additionally found a higher response of terns during the chick stage than during the egg stage.

Some studies reported that variation in defense response by terns may also be site-specific (Erwin 1988, Cavanagh and Griffin 1993). Although predatory pressure may be higher on tern colonies located closer to gull colonies (O'Connel and Beck 2003) and nest defense more intensive at tern colonies experiencing more intrusions (Jackson et al. 1982), under some circumstances the tern response may be weaker at sites that gulls visit

frequently (Cavanagh and Griffin 1993) or where gulls breed in close proximity (McNicholl 1973), due to habituation.

Parameters used to measure costs associated with nest defense vary among studies. For example, some researchers used the number of defenders as a representative measure of defense response (Erwin 1988, Shealer and Burger 1992, Cavanagh and Griffin 1993, Palestis 2005). Time spent defending is also used to quantify the cost of antipredator behavior (Altmann 1956), although it may be a poor approximation of risk when it does not consider the specific defense behavior (Sordahl 1990). Moreover, the distance from the predator at which defenders react may represent the risk the defenders face (Sordahl 1990).

Distribution and ecology of Forster's terns in San Francisco Bay. Prior to 1948 in San Francisco Bay, the Forster's tern was considered only a visitor or migrant during winter (Grinnell and Miller 1944). The first colony of Forster's tern was reported in 1948 and included roughly 100 pairs (Sibley 1953). In the following years more colonies were established and, by 1979 they totaled 3000 pairs in 13 colonies in San Francisco Bay (Gill and Mewaldt 1979). In 1988, 1,775 pairs were breeding at 21 San Francisco Bay colonies (Carter et al. 1990). In the area of South San Francisco Bay, Forster's tern population peak was in 1981 when they reached approximately 5000 breeding birds (Harvey et al. 1992). In 2003, a total of approximately 2,712 breeding birds were nesting in 17 colonies (Strong et al. 2004).

The Forster's tern is a widespread tern species, which can be found along the California Coast, around beaches, marshes, and salt ponds (Small 1994). They feed

mainly on small fish in saltwater and freshwater habitats by hovering over prey and then diving from a height of 3-10 m (10-33 ft). They also may scoop small prey from shallow water (Cogswell 1977). Forster's terns are colonial nesters. In South San Francisco Bay, most of the Forster's tern colonies are located in salt evaporator ponds. Terns are attracted to dredge spoil islands and levees (Gill 1972) which are placed at the corners and edges of the levees that surround salt ponds to delay levee erosion from air and wave action. Tern nests can be scrapes in the substrate lined with dead material, built on mounds of vegetation, or nesting depressions in areas with short, dense vegetation (Dakin 2000). Dakin (2000) found a strong preference for Forster's tern to nest in areas with some vegetation. She also attributed her finding of a negative correlation between reproductive success and the number of neighbors within 2m to the increased visibility to predators (Dakin 2000). In the San Francisco Bay area Forster's terns' nesting period typically begins in early to late May. Forster's terns lay their eggs in clutches of 2 to 4 and both parents incubate them in shifts for a period of about 25 days (Harrison 1978). Young hatch in semiprecocial state (Baicich and Harrison 1997). They leave the nest on the fourth day (Hall 1988). Fledging occurs after 28 days (Baicich and Harrison 1997).

Distribution and ecology of California gull in San Francisco Bay. The California gull is a colonially-nesting species that typically breeds on shores and islands of saline and freshwater lakes in western North America. The historical breeding distribution of California gulls ranged from Mono Lake, California, north to the Great Slave Lake, Canada, and from Central Oregon and Washington, east to Stump Lake, North Dakota

(American Ornithologist's Union 1983). In California, major California gull colonies existed at Mono Lake since the beginning of the 19th century (Shuford and Ryan 2000).

In the San Francisco Bay area, the first California gull colony was established in 1981 and represented a unique and radical departure from this species' typical nesting habitat at inland sites to sites in the estuarine habitats along the Pacific Coast (Jones 1986). The first colony in San Francisco Bay area was located in salt ponds adjacent to the town of Alviso and accounted for 12 nests. In the following years, the gull population exhibited an exponential growth pattern and, by 1985, a total of 1,576 nests were counted in the San Francisco Bay at three locations (Jones 1986). Since 1983, breeding California gulls have expanded to eight additional colonies in San Francisco Bay area, the species' second largest breeding aggregation in the state next to Mono Lake (Shuford and Ryan 2000). In 2003, the approximate count in San Francisco Bay was 21,106 breeding California gulls (Strong et al. 2004).

California gull nests are simple scrapes in the substrate. They prefer to nest on sandy, rocky places with some grasses. The clutch size ranges from 1 to 3 eggs. The incubation period is about 25 days. Chicks remain at the colony until they can fly, at about 40 days (Jones 1986, Ehrlich et al. 1988). In San Francisco Bay, California gulls nest at sea level primarily on earthen islands and levees in salt ponds (Shuford and Ryan 2000). They start laying eggs in late April to early May (Shuford and Ryan 2000). At Alviso, some fledged chicks return to the colony to be fed until they are at least 65 days old (Dierks 1990).

California gulls are highly opportunistic feeders. Their main diet consists of insects, carrion, aquatic invertebrates, earthworms, young birds, fish and rodents (Ehrlich et al. 1988). At San Francisco Bay colonies, Jones (1986) found that garbage comprised 40% of the pellet volumes and 60% was from natural sources. In 1990, another study of a San Francisco Bay California gull colony showed that 40% of the gulls' diets consisted of garbage (Dierks 1990).

Gulls in Landfills. Many studies have documented that gulls forage extensively in landfills (Pierotti and Annett 2001, Belant et al. 1998, Drury and Kadlec 1974, Hunt 1972). Most of these studies found a positive relationship between gulls and landfill presence. For example, Hunt (1972) found that herring gull (*Larus argentatus*) chick survival was inversely correlated with the distance from waste sources. Belant et al. (1998) found that anthropogenic food from landfills was the major component of ring-billed gulls (*Larus delawarensis*) diets in Ohio. Spaans (1971) found that herring gull chicks grew faster on a diet of garbage and natural food than chicks raised on a diet with only natural prey items. Gulls may use human refuse more heavily during the early part of the breeding season, less when the chicks hatch, and again heavily after the chicks are well grown (Pierotti and Annett 2001). The degree to which gulls use landfills may also depend on the type of waste received and the management techniques followed at the facilities (Belant 1997).

In San Francisco Bay, Jones (1986) notes that gulls were actively foraging in landfills located within 15 km radius of his study site. Dierks' (1990) study also shows the importance of human refuse dumps in the gull diet in the South San Francisco Bay.

California gulls may also forage heavily in landfills during fall and early spring in San Francisco Bay (Johnston 1956). Cogswell (1974) suggested that the gull flight movements in the South San Francisco Bay area were largely determined by the location of dumps.

Objectives and Hypothesis

This study was designed to: 1) characterize the nest defense behavior of breeding Forster's terns and co-nesting species in the South San Francisco Bay with respect to the magnitude of California gull intrusions, 2) compare the frequency of California gull intrusions and time spent in defense by Forster's terns in response to California gull intrusions at three different South Bay salt pond sites with tern colonies, 3) examine whether the frequency of California gull intrusions at Forster's tern colonies change over time within the tern breeding season, 4) investigate spatial attributes potentially related to California gull activity in areas with Forster's tern colonies based on the location of landfills. To meet these objectives I tested the following null hypotheses and research question:

Ho1. a) The type of nest defense (moderate or dynamic) and the strongest defense response exhibited by breeding Forster's terns did not depend on the magnitude of California gull intrusion.

b) The amount of time spent in defense by nesting birds was not affected by the type of California gull intrusions.

Ho2. a) The rate of non-attack intrusions and the rate of attacks by California gulls did not differ between the tern colonies at three salt pond sites.

b) Defense time and intensity of nest defense response in response to each type of California gull attacks did not differ between colonies at three salt pond sites.

Ho3. The frequency of California gull intrusions did not significantly change over time during the 2005 tern breeding season.

Research question 1: What spatial relationships occur among California gull colonies, Forster's terns colonies, and landfills and how these are related to the California gull activity in Forster's tern nesting sites?

METHODS

Site Description

This study took place in four different salt pond sites with Forster's tern breeding colonies, south of the San Mateo Bridge in the San Francisco Bay. Two sites were in salt ponds A1 and B1 located in ponds adjacent to Shoreline Park, in Mountain View, Santa Clara County. The other two sites were located adjacent to the town of Alviso in San Jose, Santa Clara County (Figure 1). The names of the colonies follow the names of the salt ponds used by U.S. Fish and Wildlife Service, the agency that owns the ponds. Each pond had one nesting island, except for pond A16, which had four.

Observations occurred weekly at randomly selected times during daylight. Nest visibility at each island differed, due to vegetation and the distance of observation points from the nesting islands. However, the study was not designed to observe all nests on each island, only enough nests to characterize interactions between terns and gulls.

Table 1 shows the number of observed nests.

Table 1. Number of observed nests at Forster's tern colonies. Data come from seven islands with Forster's terns colonies in 2005.

Site	Island	Number of nests				Total nests
		Forster's tern	American Avocet	Black-necked stilt	Black skimmer	
A1		120	8	0	0	128
A16	1	18	16	0	0	34
	2	63	16	0	0	79
	3	52	21	6	0	79
	4	35	7	0	0	42
A8		100	67	0	2	169
B1		80	10	8	3	103

Figure 1. Map with the location of Forster's tern colony study sites located in the South San Francisco Bay.

The Forster's tern colony in A1 was located on a dredge material island, close to the south end of the salt pond in the Mountain View area. The island had a round to oval shape and was sparsely vegetated. This Forster's tern colony was well established and had been occupied from 1989 to 2005 (Strong et al. 2004, personal observation).

American avocets were also co-nesting with these terns. There were 21 American avocet nests during 2004, but only seven pairs exhibiting nesting behavior in 2005, and only at the beginning of the tern breeding season; by June 10 there were no avocet nests. A California gull colony was also established at the opposite side of pond A1, approximately 500 meters away. The first three observation sessions at this pond took place from a point at the foot of the levee closest to the colony, approximately 80 meters from the tern colony. Later, I used another observation point at a higher elevation on the levee, which allowed a less obscured view of the tern colony. The levee was a recreation trail relatively heavily used by joggers and bikers.

The other Forster's tern colony in the Mountain View area, on an island in salt pond B1, was close to the northwestern levee of the pond. This colony was first established in 2005. The island in B1 was heavily vegetated and the tern's nests were barely visible. Only approximately 1.5 m² in the middle of the island was bare ground and this was occupied by three Black skimmer nests. Additionally, a narrow band along the edge of the island lacked vegetation. The shape of the island was approximately round. Observations at this site were made from a spot on the levee closest to the colony and at approximately 50 meters distance. The nesting island was located close to the end

of the recreational trail but a locked gate limited public access on the levee, resulting in light recreational use.

The third study colony was in the A16 salt pond, in Alviso. In 2005 Forster's terns, American avocets, and black-necked stilts nested on four elongated oval islands in the salt pond. I considered the four islands as a single colony. A managed tidal marsh area lay on the other side of the levee. At the beginning of the tern breeding period, I was able to see six Forster's terns nests located in this semi-tidal area, near the levee. These nests were abandoned later in the breeding season. Forster's terns nested on the islands of the A16 pond each year from 1984 to 2005 (Strong et al. 2004, personal observation), although not on all four islands. For example, in 2004, the terns initiated nesting activities on one of the islands, but they abandoned the island in less than two weeks. Later in the breeding season, some of the islands were abandoned, possibly due to flooding (personal observation). In 2005, tern breeding activities occurred on all four islands. The A16 pond is located in a recreational area of the Don Edwards National Wildlife Refuge, next to the Environmental Education Center in Alviso. Recreation traffic was moderate during weekdays and high on weekends next to this pond.

The fourth study site was in salt pond A8, in Alviso. Forster's terns, American avocets, and several pairs of black skimmers nested on a T-shaped island with two distinct types of ground cover. The part of the island closest to the levee was heavily vegetated in the center. Most of the tern and avocet nests were positioned along the edge of this part of the island. On the other part of the island, the ground was bare and fewer nests were present. This site was not open to the public. Birds in pond A8 abandoned the

island suddenly in the middle of the 2005 breeding season possibly due to predation; thus, only a limited number of surveys were completed at this site.

Observation Protocols

In 2004, surveys were conducted at five Forster's tern colonies to collect pilot data. These pilot data were used to determine the duration of surveys and number of observers, evaluate methods of observation, tabulate nest defense behavior, and identify the types of California gull intrusions. These data were not used further in my thesis. The data for this thesis were collected during the 2005 Forster's tern breeding season.

Field surveys took place from June 6 to August 3, 2005. The time and day of each survey in each week period were randomly selected, starting approximately ten days after terns had laid nests and the colony was well established. The reproductive period of the terns in the South San Francisco Bay typically starts in early May and ends in early August (San Francisco Bay Bird Observatory Unpublished data). However, in 2005, terns started nesting at the end of May and early June at the A1, A8, A16, and B1 sites.

All observations took place between 6:30 and 19:00. Observations of each colony were made from a levee at more than 30 meters from the tern island. I sat quietly and restricted my movements to avoid agitating the birds. A pair of 8-22x binoculars was used to scan for California gulls attacks on terns and other co-nesting species nests, a compass to identify the direction of predator approaches, a watch to record time of attack, a stop watch to estimate the duration of each event and the duration of each type of defensive behavior, and a tape recorder to record details or notes during an attack event. Upon my arrival at the observation spot some of the terns, avocets and stilts often left

their nest to mob me. Data collection started as soon the birds had settled back on their nests, usually about three minutes after arrival. The time of visit or attack by California gulls or other predators on the tern colony, the number of predators, the direction from which the predator was coming, and predator behavior were documented at each survey. The defensive response for each of the defending species, the number of defenders, duration of each type of defense behavior, and the outcome of the attack were all recorded for every predator intrusion. Additionally, interactions among the nesting species and the response of the terns to other types of disturbance were recorded. Finally, all visible nests on each island were counted from my vantage point on every survey.

Variables and Estimates

Type of gull intrusion. A predator intrusion was counted every time a potential predator approached the nesting island closer than approximately 30 meters. The five classes of California gull intrusions based on the gull behavior were:

- i. Overflight: when the gull flew high, directly over the colony island or near the edge of the island.
- ii. Zigzag: when the gull flew high above the colony in a zigzag pattern.
- iii. Active scan: when the gull flew directly through and/or in a zigzag pattern above the colony at a low height but it did not attempt to land on the island.
- iv. Attack: when a gull flew low above the colony and attempted landing on the island.

- v. Fierce attack: when the gull attempted a landing on the island, dropped rapidly on a nest or chick, and/or persistently harassed the nesters.

Whittam and Leonard (2000), Cavanagh and Griffin (1993), and Hatch (1970) used similar classification in their gull predation studies. I divided these five intrusion classes into “attack intrusion” consisting of the attack and fierce attack types which were associated with a high degree of bird harassment (including predation), and “non-attack intrusions,” which encompassed the overflight, zigzag, and active scan intrusions. “Passing flights” consisted of the overflights and zigzag intrusions; by definition, passing flights were associated with a vague, and perhaps non-existent, predation risk for the breeding birds. The active scanning behavior was the most ambiguous type of gull intrusion regarding the gull’s intention to attack.

Nest defense behavior. During a California gull intrusion event at a Forster’s tern nesting island, breeding birds would employ a combination of defensive techniques. Listed from the least to the most active, the four types of defensive techniques were:

- i. Alarm call: Bird gave an alarm call and/or flew within 1m above its nest, but did not approach or flee from the predator.
- ii. Flying up: Bird flew up, higher than 2m from the island but did not pursue the predator.
- iii. Mobbing: One or more birds pursued and/or swooped at the predator but within 20 m of the subcolony.
- iv. Chasing: Birds pursued and swooped at the predator and/or hit the predator with their bill or feet. Birds chased the predator above the nesting

island and until reaching a distance more than 20 m from the edge of the island.

Whittam and Leonard (2000) and Shealer and Burger (1992) used similar behavior classes in their studies for terns, while Sordahl (2004) used similar description of American avocets' and Black-necked stilts' defense behavior. I divided these four behaviors into "dynamic defense" and "moderated defense," distinguished by bird's level of potential physical risk when defending. Dynamic defense included mobbing and chasing, two risky techniques for the defenders, as they involved pursuing the predator. Moderate defense included the less energetic alarm call and flying up behaviors. Finally, I called "active defense" the techniques of flying up, mobbing, and chasing because they involved birds leaving their nest.

Defense time measures. Three different measures that reflected time spent in defense were used to evaluate disturbance caused by California gulls: 1) time spent in defense during a gull intrusion event, 2) time spent in defense per hour, and 3) intensity of defensive response. The number of defenders, the amount of time they spent defending, and the type of defense were considered in all three estimates. All three measures reflect defense time that involved birds leaving their nests, i.e., the active defense techniques. The following formulas were used to calculate the three defense time measures:

$$\text{Time spent in defense during an intrusion event } (d_e) = \sum \frac{x_i \times t_i}{n}$$

$$\text{Time spent in defense per hour } (D_s) = \frac{\sum_1^a d_e}{h_s} = \frac{\sum_1^a \sum \frac{x_i \times t_i}{n}}{h_s}$$

$$\text{Intensity of defensive response } (R_s) = \frac{D_s}{\alpha_s}$$

In each formula, i was the type of employed defense technique (flying up, mobbing, or chasing), x_i was the number of birds exhibiting i type of defense, t_i was the time in seconds spent by defenders, n was the number of observed nests, α_s was the number of events during the survey (s), and h_s was the duration of the survey in hours.

All defense time measures expressed the time birds defended per nest. However, each measure addresses a separate aspect of parental nest defense. For example, the time spent in defense during an intrusion event describes defense response on a case by case basis, while the time spent in defense per hour shows the total defense time per nest for each tern colony. Lastly, the intensity of defensive response measured the average time birds defended every time a California gull intruded into the colony area during a one hour survey. Additionally, since both the D_s and R_s measures are calculated for each survey, their use allows for a balanced experimental design in natural settings and a more robust data analysis. In contrast, the d_e measure is associated with an unpredictable number of events in a certain time period. Depending on the research hypothesis, I calculated all of the three measures for each type of gull intrusion.

Statistical Analysis

Nest defense versus magnitude of California gull intrusions. I used a 2x2x4 stepwise backward hierarchical log linear analysis (SPSS 12.0™) to test whether there was relationship between the presence of moderate defense (present or absent), the presence of dynamic defense (present or absent), and/or the type of California gull intrusion (over flight, zigzag, active scan, and attack). Log linear is a type of multi-way frequency analysis used with discrete variables (Tabachnick and Fidell 2001). California gull intrusions from all seven breeding islands were clumped for the analysis, resulting in 327 intrusions.

I used a 4x4 stepwise backward hierarchical log linear analysis to test whether the strongest defense response exhibited by terns (no reaction, alarm call, flying up, and pursuing the predator) depended on the type of California gull intrusions (overflight, zigzag, active scan, and attack). The strongest defense response displayed by breeding birds during an attack was identified for each gull intrusion, using the 327 intrusions pooled from all seven breeding islands.

One-way ANOVA with unequal sample size (SPSS 12.0™ GLM) was used to test whether the time spent in defense during a gull intrusion event (d_e) was the same for all types of gull intrusions (attack, active scan, and passing flights). The defense time data were log transformed after I multiplied the raw data with 100 and added one ($\ln(100x+1)$) to improve normality (Sokal and Rohlf 1995). The Levene's test of equality of error of variances showed that variances across the groups were not significantly different for the transformed defense time variable ($F(2,324)=2.647, p=0.072$). Data

from all the sites were pooled. There were 115 gull attacks, 100 active scan intrusions, and 112 gull passing events. I used *a priori* comparisons ($\alpha=0.05$) to test for differences in the time spent in defense between: 1) attacks and all other types of intrusions, 2) passing flights and active scan intrusions. I also tested *a posteriori* the difference in defense time between the active scan and attack intrusions ($\alpha=0.017$), and between passing flights and active scan intrusions ($\alpha=0.0127$) using a Dunn-Sidak correction of the significance level (Zar 1999).

Difference in gull intrusion rates between sites. I tested the effect of salt pond site (A1, A16, B1) on a) the rate of gull attack intrusions (events/hour), and b) the rate of non-attack intrusions (events/hour) using a one-way ANOVA (SYSTAT 10.0™) on weekly survey data. For A16, data from the four islands were compiled. Data for the dependent variables were log transformed after I added a unit to the data to avoid having zero values ($\ln(x+1)$) (Tabachnick and Fidell 2001). For tests with a significant ANOVA result, I performed pair-wise comparisons to test for differences in the intrusion rate between sites following the same order of comparisons for both intrusion rate variables (Table 2).

Table 2. Summary of pair-wise comparisons for the California gull attack and non-attack intrusion rate in South San Francisco Bay salt pond sites.

Dependent variable	Type of Comparison	Description	Criterion of significance (α)
Gull attack rate	<i>A priori</i>	A1 vs. A16	0.050
Non-attack gull intrusions rate		A1 vs. A16	0.050
Gull attack rate	<i>A posteriori</i>	A1 vs. B1 B1 vs. A16	0.025 0.017
Non-attack gull intrusions rate	<i>A posteriori</i>	A1 vs. B1 B1 vs. A16	0.025 0.017

Site effect on the time spent in defense. To test whether defense time spent per hour (D_s) differed between the three sites (A1, A16, B1), I performed a one-way between-subjects MANOVA (SPSS 12.0™) on three dependent variables: defense time spent hourly in response to California gull attacks (D_{sa}), defense time spent hourly in response to gull active scan intrusions (D_{ss}), defense time spent hourly in response to gull passing flights (D_{sp}). The A16 data from the four islands were compiled. To eliminate skewness in all three dependent variables, the data were log transformed ($\ln(100x+1)$) (Sokal and Rohlf 1995). Results of the evaluation of assumptions of the equality of error variances, homogeneity of variance-covariance matrices, normality, linearity and multicollinearity were satisfactory.

Pooled within-cell correlation was not zero between each pair of variables; thus, I performed a Roy-Bargmann step-down analysis on the prioritized dependent variables to investigate the impact of the salt pond nesting site on each individual defense time variable (Tabachnick and Fidell 2001). Following Quinn and Keough (2002), I entered the variables in the step-down analysis in order of their univariate F-ratios. Defense time spent hourly in response to gull attacks entered first; next I tested the defense time spent hourly in response to active scan gull intrusions with the defense time spent hourly in response to gull attacks as a covariate. Finally, I tested defense time spent hourly in response to passing gulls with the other two variables as covariates. I performed pair-wise multivariate comparisons to test for differences between sites. I performed univariate pair-wise comparisons to interpret significant differences (Tabachnick and

Fidell 2001). A summary of all the types of comparisons and the criterion of significance used is presented in Table 3.

To establish whether significant differences existed in the intensity of defensive response (R_s), which reflected the average time spent in defense per intrusion during each survey between the three study sites, I compared intensity of defensive response for each type of intrusion (overflights, zigzagging, active scanning, and attack intrusions) using a Kruskal-Wallis ANOVA. Some types of intrusions were absent during some of the surveys; only the surveys with existing events of the corresponding type of gull intrusion were used. For every variable that was significantly affected by the site, Mann-Whitney U-test was used to make pair-wise comparisons between A1 and B1, A1 and A16, and B1 and A16.

Frequency of gull intrusions over time. I performed a one-way repeated measures ANOVA (SYSTAT 10.0 TM) to test whether there was a change in the frequency of gull intrusions during the four two-week periods of the breeding season. Each level was a two week period starting 10 days after Forster's terns laid eggs on each island. I tested mean California gull non-attack intrusion rate and attack rate. The mean non-attack intrusion rate was calculated as the average of the California gull non-intrusion rate of all the surveys in each two week period at each of the six islands.

Table 3. Summary of pair-wise comparisons for the time spent in defense per hour in response to California gull intrusions in South San Francisco Bay salt pond sites.

Comparison	Dependent variable	Type of Comparison	Criterion of significance (α)	Planned
A16 vs. A1	Combined variables of defense time spent per hour (D_{sa} , D_{ss} , D_{sp})	Multivariate	0.050	<i>A priori</i>
	Defense time spent per hour in response to attacks (D_{sa})	Univariate	0.020	
	Defense time spent per hour in response to active scan (D_{ss})			
A1 vs. B1 B1 vs. A16	Combined variables of defense time spent per hour (D_{sa} , D_{ss} , D_{sp})	Multivariate	0.025 0.017	<i>A posteriori</i>
A1 vs. B1 B1 vs. A16	Defense time spent per hour in response to attacks (D_{sa})	Univariate	0.010 0.007	
	Defense time spent per hour in response to active scan (D_{ss})			

Distribution of gull colonies, tern colonies and landfills. To explore how the spatial distribution of California gull colonies, Forster's tern colonies, and landfills is potentially related to the gull activity at each Forester's tern colony, I calculated three different estimates considering spatial and population parameters. Specifically, the three estimates were defined as follows:

1. Potential gull abundance at a site measured by the inversely weighted by distance California gull nests. There were six California gull colonies in the study area. Each of these gull colonies was located at a certain distance from each tern

colony. The number of nests in a gull colony divided by the distance from a tern colony represented the weight of this particular gull colony for the corresponding tern colony. In this way, I calculated six weights for each Forster's tern colony. The sum of these six weights would represent the total inversely weighted by distance California gull nests for a tern colony. This measure should be indicative of the potential occurrence of California gulls at a particular Forster's tern colony site because it is analogous to the number of gull nests and inversely related to the proximity to the gull colony.

2. Density of potential California gull foraging routes in the area of each tern colony.

The foraging gull routes were defined as the shortest linear path from each gull colony to landfills within 15 km. The density of these paths was calculated in a 500 meter buffer zone around each tern colony as total length path (m) per area unit (m^2). Two types of foraging gull paths were distinguished: 1) paths connecting a gull colony with an active landfill within 10 km, and 2) those within 15 km.

3. Potential gull use of the area at each tern nesting site measured by the density of potential gull routes in the area and the number of breeding gulls that would potentially use these paths to forage in landfills. In each 500 m buffer zone of a tern colony, the length of each potential gull path was multiplied with the number of breeding California gulls that would potentially use the path. The sum of these products for each tern colony divided by the buffer's zone area should give a

measure of potential California gull movements in each study site if gulls use the shortest paths.

The position of the tern colonies was based on my observation points and defined by GPS readings and aerial photos. The location of the California gull colonies was based on San Francisco Bay Bird Observatory (SFBBO) data (Strong et al. 2004). Breeding gull data came from SFBBO California gull nest census for 2005 (C. Strong, pers. comm.). The locations and types of landfills were retrieved from the Solid Waste Information System (SWIS) data base (California Integrated Waste Management Board 2005). I considered only the landfill facilities that included or was characterized as disposal, composting, and transferring stations because only these types of stations can potentially include food resources for gulls. The choice of the 15 kilometer buffer zone was based on Belant et al. (1998), who found that gulls forage extensively in landfills within this distance.

ESRI ArcGIS 9.2 software was used to create maps with all these data layers. Using the ArcGIS inventory on the created maps, the distance between Forster's tern colonies and California gull colonies, the length of each potential gull route in each 500 meter buffer zone, and the type of each potential gull route were determined.

RESULTS

Predator Activity

More than 90 percent of the intrusions recorded at all study sites were California gull intrusions (Table 4). Because of their small number, further statistical analysis was not possible for intrusions due to non-California gull predators. Additionally, the California gull was the only species observed preying on tern eggs and young, although these cases were very rare. I observed a gull taking a chick only three times (twice at B1, once at A8) and only once taking an egg at A8.

Table 4. Species that caused a disturbance at Forster's tern breeding colonies in 2005. For A16 data from the four nesting islands were compiled.

Species	Predator intrusion rates (intrusions/hour)				% of total intrusions
	A1	A16	A8	B1	
California gull <i>Larus californicus</i>	3.45	5.36	8.05	9.56	91.34
Snowy Egret <i>Egretta thula</i>	0.34	0.13	0.00	0.11	2.23
Great Egret <i>Ardea alba</i>	0.11	0.06	0.00	0.33	1.68
Turkey Vulture <i>Cathartes aura</i>	0.00	0.06	0.00	0.33	1.40
American Crow <i>Corvus branchyrhynchos</i>	0.00	0.06	0.40	0.00	1.12
Double-crested Cormorant <i>Phalacrocorax auritus</i>	0.00	0.03	0.00	0.11	0.56
Northern Harrier <i>Circus cyaneus</i>	0.11	0.00	0.00	0.11	0.56
American White pelican <i>Pelecanus erythrorhynchos</i>	0.23	0.00	0.00	0.00	0.56
Black-crowned Night Heron <i>Nycticorax nycticorax</i>	0.00	0.03	0.00	0.00	0.28
Great blue heron <i>Ardea herodias</i>	0.00	0.03	0.00	0.00	0.28

Descriptive Statistics for the A8 Forster's Tern Colony

While I planned to conduct eight surveys on each island, this was not possible at the A8 pond. The colony at A8 was deserted after the 5th week of observations. On the 6th visit to this colony I saw that terns, avocets, and skimmers had abandoned their nesting sites; these birds seemed to be gathered on an island at more than 100 meters from the nesting island. After three days I visited again the colony but there was no sign of the terns, avocets, or skimmers in the vicinity. Descriptive statistics for the A8 study site and the other three sites are presented in Table 5 for the data collected in the period between June 6 to July 5, 2005. Terns and other shorebirds abandoned the A8 site early; the limited number of observational surveys did not allow statistical comparisons between A8 and the rest of the study sites. However, as the data in Table 5 show, in the first five weeks, the A8 terns experienced a greater rate of gull attacks than those at the other islands and terns at A8 spent more than twice as much time defending compared to birds at A1, A16 or B1.

Nest Defense Behavior versus Magnitude of Gull Intrusions

Type of nest defense in response to the type of gull intrusion. There was a significant interaction between dynamic and moderate defense, an interaction between type of gull intrusion and dynamic defense, and an interaction between type of gull intrusion and moderate defense (Table 6). Specifically, the proportions of events with birds defending in a dynamic way by pursuing the gull increases as gull intrusions become fiercer (Figure 2a). From more to less often, nesting birds defended in a

moderate manner through flying up and alarm calls during zigzag gull flights, active scans, gull attacks, and overflights (Figure 2b). Finally, the proportion of the events with moderate defense present was higher when the dynamic defense was absent (Figure 2c).

Table 5. Means of the time spent in defense by terns and frequency of gull attacks at A8 and the other salt pond study sites for the first five weeks of observations. Standard deviations are reported in parenthesis.

Parameter		Site			
		A8	A1	A16	B1
Mean time spent hourly in defense (defense seconds per nest/hour)	During gull attacks	9.935 (14.3981)	0 (0)	4.283 (1.9990)	4.946 (6.173)
	During gull scanning flight	0.726 (1.310)	0.043 (0.0956)	1.535 (3.265)	3.796 (4.667)
	During gull passing flights	0 (0)	0.014 (0.0190)	0.320 (0.9870)	1.946 (3.089)
Mean frequency of gull intrusions (intrusion/hour)	Rate of gull attacks	4.416 (4.9550)	0 (0)	1.798 (3.0285)	3.5 (1.2910)
	Rate of non-attack gull intrusions	3.561 (2.9861)	1.994 (1.2314)	4.067 (3.0485)	7.75 (2.9861)

Table 6. Summary of the hierarchical log linear analysis for the type of waterbird defense during California gull intrusions at three study sites.

If deleted Simple Effect is	Df	L.R. χ^2 Change	Prob
Dynamic defense*Moderate defense*Gull Intrusion	3	4.162	0.2445
Dynamic defense * Moderate defense	1	58.166	<0.001
Moderate defense * Gull Intrusion	3	75.191	<0.001
Dynamic defense * Gull Intrusion	3	217.111	<0.001
Dynamic defense		Not applicable	
Moderate defense		Not applicable	
Gull Intrusion		Not applicable

Figure 2. The hierarchical log linear analysis showed that there was a significant interaction between: a) dynamic nest defense and magnitude of gull behavior, b) dynamic nest defense and magnitude of gull behavior, and c) dynamic and moderate defense of breeding birds at Forster's tern colonies.

The strongest defensive response of a tern colony to a gull intrusion and the type of California gull intrusion were significantly related (likelihood ratio $\chi^2(9) = 270.481$, $p < 0.001$). The proportion of events in which at least one tern pursued the predator increased as gull intrusions became more aggressive, and it was most commonly employed when the gulls attacked (Figure 3). Additionally, the proportion of events with birds not responding was highest during gull overflights and lowest when gulls attacked. Flying up was the predominant defense response when gulls were actively scanning, while alarm calling from or near the nest was the most common defense response when gulls were zigzagging above the colony.

Time spent on nest defense in response to gull intrusion types. The amount of time nesting birds spent in response to gull intrusions differed significantly with intrusion type ($F(2, 324) = 137.684$, $p < 0.001$). The *a priori* comparisons showed that the time birds spent in defense was significantly higher ($F(1, 324) = 189.374$, $p < 0.001$) during California gull attacks versus non-attack intrusions (Figure 4), and significantly greater ($F(1, 324) = 77.526$, $p < 0.001$) when the gulls were actively scanning versus when gulls were passing (Figure 5). The *a posteriori* comparisons showed that birds spent significantly more time defending in response to gull attacks than to active scan gull flights ($F(1, 324) = 52.315$, $p < 0.001$), and than to passing gulls ($F(1, 324) = 274.699$, $p < 0.001$) (Figure 5).

Figure 3. Relationship between the type of strongest defense response exhibited by nesting birds and the type of California gull intrusion. Percent of events in which birds exhibited different defense responses based on the type of California gull predatory behavior.

Figure 4. Difference in the term defense time per nest spent between gull attacks and all other types of intrusion.

Figure 5. Amount of defense time spent per nest in response to three different types of gull intrusion.

Site Level Effects

Frequency of gull intrusions. There was a significant difference in the gull attack rate between the three sites ($F(2,21)=6.230$, $p=0.008$). The frequency of gull attacks was significantly lower at A1 than at A16 salt pond site ($F(1,21)=5.698$, $p=0.026$). The rate of gull attacks was also significantly lower at A1 site than at B1 site ($F(1,21)=11.872$, $p=0.002$) (Figure 6). However, there was no significant difference in the gull attack rate between the A16 and B1 sites ($F(1,21)=1.121$, $p=0.302$). For the non-attack intrusion rate, the ANOVA showed that there was no significant difference among the three sites ($F(2,21)=3.327$, $p=0.056$).

Time spent in nest defense in response to gull intrusions. The combined dependent variables of time spent hourly in defense due to gull attacks, active scan intrusions, and passing gulls were significantly affected by salt pond site ($F(6, 38) = 4.481$, ($p=0.002$)). The significant result reflected a substantial association between tern colony nest site and the combined dependent variables, $\eta^2=0.66$. The only variable that made a unique contribution to predicting differences among the three salt pond sites was the time spent in defense due to California gull attacks (stepdown $F(2, 21)=12.805$, $p<0.001$, $\eta^2 = 0.55$). Results of tests to determine which variables were affected are summarized in Table 7. Although the stepdown tests showed that time birds spent in defense in response to gull scanning intrusions did not significantly contribute in predicting differences (stepdown $F(1/20)=2.221$, $p=0.135$) among sites, a univariate comparison ($F(2, 21)= 9.537$) showed that there was a significant difference somewhere between the three sites in this variable.

Figure 6. California gull attack rate on Forster's tern colonies at the three salt pond sites.

Table 7. Test of the salt pond site effect for the defense time spent in response to California gull intrusions into Forster's tern colonies. Asterisks denote significant results.

Effect	Dependent Variable	Univariate F	df	Step-down F	df	Significance of Stepdown F	α
Salt Pond Site	Defense time per nest spent hourly due to gull attacks	12.805	2/21	12.805	2/21	<0.001*	0.020
	Defense time per nest spent hourly due to gull active scans	9.537	2/21	2.221	2/20	0.135	0.020
	Defense time per nest spent hourly due to passing gulls	1.619	2/21	0.712	2/19	0.503	0.010

The amount of time spent per nest in defense due to both gull attacks and active scans was significantly greater at A16 than at A1 (Figure 7), and significantly higher at B1 than at A1 (Figure 8) but not significantly different between A16 and B1 (Table 8).

The Kruskal-Wallis ANOVA by ranks showed that the intensity of defensive response, which was measured by the average time spent in nest defense per intrusion at each survey, was significantly different between the three ponds during gull attacks ($H(3,7,8)=6.881, p=0.032$). The intensity of defensive response during gull attacks was lower at A1 site than the A16 and the B1 sites (Table 8). However, there were no significant differences for the three pond sites regarding the intensity of defensive response during gull overflights ($H(6,7,6)=0.428, p=0.807$), during zigzag gull flights ($H(3,6,6)=2.21, p=0.331$), and during active scans ($H(5,8,8)=3.866, p=0.145$) (Table 9).

Table 8. Paired comparisons results for the defense time variables. Asterisks denote significant results.

Dependent Variable	Comparison description	DF	F value	p value
Combined variables of defense time per nest spent hourly in defense due to gull attacks, active scans, and passing gulls	A1 vs. A16	(1, 20)	10.630	0.001*
	A1 vs. B1	(1, 20)	14.454	<0.001*
	B1 vs. A16	(1,20)	0.639	0.538
Defense time per nest spent hourly due to gull attacks	A1 vs. A16	(1,21)	17.145	<0.001*
	A1 vs. B1	(1, 21)	21.069	<0.001*
Defense time per nest spent hourly due to active scan intrusions	A1 vs. A16	(1,21)	9.443	0.006*
	A1 vs. B1	(1,21)	17.844	<0.001*

Table 9. Results of the paired comparisons between the salt pond sites for the intensity of defensive response variable.

Comparison	Df	U statistic	p value	Median of the intensity of defensive response (defense sec/nest per attack)		
				A1	A16	B1
A1 vs. A16	(3,7)	1	0.03	0.359	2.361	
A1 vs. B1	(3,8)	<0.001	0.014	0.359		1.617
A16 vs. B1	(7,8)	21	0.463		2.361	1.617

Figure 7. Significant differences in the means of the two defense time variables between the A1 and A16 salt pond sites.

Figure 8. Significant differences in the means of the two defense time variables between the B1 and A1 salt pond sites.

Change of the Frequency of California Gull Intrusions over Time

The repeated measures analysis of variance showed no significant change in the California gull non-attack intrusion rate ($F(3, 15)=1.419$, $p=0.276$) or for the gull attack rate ($F(3, 15)=3.003$, $p=0.098$) throughout the tern nesting season.

Geographic Relationships between Colonies and Landfills

The estimate of the potential gull abundance measured by the weighted by inverse distance California gull nests for each Forster's tern colony was highest for the B1 tern nesting site and lowest for the A16 tern nesting site (Table 10). The tern colony in pond B1 was located very close to other gull colonies while the tern colony in A16 pond was the most remote tern colony from gull colonies (Figure 9). However the tern nesting site at A16 was very closely located to two landfills (Figure 9), which were within 15 kilometers from five gull colonies (Figure 10).

The density of potential gull routes in a 500 meter buffer zone around each tern nesting island was highest for the B1 site and lowest for the A1 site (Table 11). The vectors of the shortest path from gull colonies to landfills appear to pass right through or within 100 meters particularly from the Forster's tern colony islands at sites B1 and A16 (Figure 11, Figure 12). On the other hand, there is no path within 400 m from the A1 Forster's tern colony and only one vector passes right over the A8 tern colony island (Figure 12).

The value of potential gull use of the 500 meter buffer zone area around each tern nesting island, which was analogous to the length of potential gull paths and the number

of gulls that would potentially use each path, was the highest for the A8 site and the lowest for the A16 site (Table 11). However, when considering only the gull paths with a total length less than 10 kilometers, the values of the potential gull use of the area at the B1 and A16 tern nesting site were higher than at the other tern nesting sites (Table 11).

Table 10. Potential gull abundance measured by the inversely weighted by distance California gull nests for each Forster's tern colony study site in 2005. The asterisk indicates the closest California gull colony to each tern colony.

<i>Forster's tern colony site</i>	<i>California gull colony</i>						<i>Potential gull abundance</i>
	<i>Knapp (A6)</i>	<i>Mowry (M1/2)</i>	<i>Alviso (A9/10)</i>	<i>Mountain View (A1)</i>	<i>Moffet Field (B2)</i>	<i>Coyote Hills (2/3A)</i>	
A1	3.144	0.475	0.056	1.236*	0.109	0.386	5.407
B1	7.449	0.614	0.081	0.360*	0.299	0.388	9.191
A16	3.343	0.348	0.129*	0.079	0.053	0.287	4.239
A8	5.095	0.378	0.156*	0.101	0.078	0.295	6.103

Table 11. Density of potential California gull foraging routes and potential gull use of the area values for each study site. The values refer to the 500 m buffer zone area around each colony island. All routes refer to the shortest path connecting California gull colonies with active landfills.

<i>Forster's tern colony site</i>	<i>Gull route to landfills density (meters /m²)</i>			<i>Potential gull use of the area (# of gulls*meters/ m²)</i>		
	<i>For paths shorter than 10 km</i>	<i>For paths longer than 10 km</i>	<i>Total</i>	<i>Only with paths shorter than 10 km</i>	<i>Only with paths longer than 10 km</i>	<i>Total</i>
A1	0.000	0.017	0.017	0.000	298.218	298.218
A16	0.031	0.015	0.046	169.062	12.314	181.376
B1	0.024	0.051	0.075	171.738	42.088	213.826
A8	0.000	0.018	0.018	0.000	303.735	303.735

Figure 9. Active landfills, California gull colonies, and Forster's tern colonies in the South San Francisco Bay during the 2005 breeding season.

Figure 10. California gull shortest path to landfills in the South San Francisco Bay. Only landfills within 15 meters from a California gull colony are included.

Figure 12. California gull shortest path to landfills segments in a 500 meters buffer zone around each island with breeding Forster's terns.

DISCUSSION

This study showed that over 90% of the predatory intrusions to the tern colonies studied were due to California gulls. The type of defense and the time Forster's terns spent defending nests were associated with the magnitude of California gull intrusions. More energetic and risky defense techniques were employed for a longer time span by the terns in response to attacking gulls than to passing gulls. These findings support the hypothesis that the response of the parent should increase as the predator gets closer to the nest as the risk a breeding bird parent is willing to be exposed is associated with the expected benefits (Montgomerie and Weatherhead 1988). More specifically, terns pursued gulls most often during gull attacks compared to other potential tern responses. Flying up was the most common response during California gull active scanning, alarm calling was used predominately during gull zigzagging events, while usually there was no defense reaction during overflights. Classifications of gull intrusions based on flight height and direction allow these results to be compared with the findings of other studies. Hatch (1970) reported that breeding terns pursued gulls only when the latter were flying at heights less than 20 meters. Whittam and Leonard (2000) found that terns responded more strongly during gull hunting flights than overflights. Cavanagh and Griffin (1993) found that terns mobbed only gulls that either attempted landing within the colony or noticeably changed direction while flying over. The thesis work presented here support the literature.

The amount of time nesting birds spent defending during an intrusion event depended on the type of the California gull behavior. Time spent in defense per nest was

almost five times longer during gull attacks when compared to gull active scanning events, and 65 times longer when compared to events with passing gulls. Additionally, time spent in defense during active scanning was ten times higher due to actively scanning gulls than gull passing flights. These findings show that nesting birds spent more energy in response to more aggressive gull intrusions compared to less threatening gull flights over the colony. Time spent in defense is very often used to quantify the cost of antipredator behavior, even though it may be a poor approximation of risk when used alone (Sordahl 1990). On the other hand, distance from the predator may better represent the risk the defenders face (Sordahl 1990). In this study, the type of defense behavior performed by the parents, by definition, encompasses proximity to the predator, and it may be a good estimate of the risk the defenders face. However, since I found that the amount of time spent in defense was greater during gull attacks and during gull attacks birds used the most energetic and risky defenses, time spent in defense appears to be a good measure of risk and energy costs when considered with the type of gull intrusion. Overall, terns took the highest risk during gull attacks. The risk defenders faced during gull active scanning events was less than during attacks, but, since mobbing and chasing was used very often as defense practices, active scanning gull intrusions may have exposed parents to considerable risk over time.

Results showed that the amount of time spent in defense hourly was different between the three study sites and this was because breeding colonies were more heavily disturbed at B1 and A16 than at A1. Defense time spent in response to California gull attacks accounted for most of the difference in defense time. These results show clearly

that the colonies in A16 and B1 ponds were more susceptible to harassment and predation by California gulls than the colony in the A1 pond.

During the study period, the frequency of California gull intrusions was not the same for all the sites with Forster's terns' colonies in the South San Francisco Bay. More specifically, the hourly rate of California gulls attacks and the rate of non-attack gull intrusions were lower at A1 site when compared with either A16 or B1 sites. The difference was even stronger between the A1 and B1 sites, with the mean non-attack intrusion rate two times greater and the attack rate more than four times higher at the B1 site compared to A1. These results suggest that the strong difference in the amount of time spent in defense hourly between A1 and the other two sites was primarily due to the lower frequency of attacks at A1 site.

A number of researchers have suggested that gull activity may be more intense in tern colonies closer to gull colonies (O'Connell and Beck 2003, Lauro and Tanagredi 2002). However, this study did not find this effect as the A1 colony, which was closest to a gull colony, had the lowest disturbance of the three sites. A possible explanation for the higher gull activity in the A16 and B1 sites could be the dispersion patterns of gull colonies and abundance of California gulls in the broader area. For example, when the size of all gull colonies and their proximity to each tern colony were considered, the newly established Forster's tern colony in B1 had almost double the potential California gull abundance than the A1 site (Table 10). However, the potential gull abundance score was lower for A16 than A1. This means that the higher frequency of gull intrusions at A16 may not be explained by the potential gull abundance measure.

Another possible explanation of the higher frequency of California gull intrusions in A16 and B1 than in A1 may be the relative location of landfills to gull and tern colony sites. In the South Bay, California gulls forage extensively in landfills surrounding salt ponds (Johnston 1956, Cogswell 1974, Jones 1986). Thus, gull foraging routes to landfills may be related to their presence at a tern nesting site. According to the maps showing the shortest path vectors from each gull colony to landfills, the A1 tern breeding island is the only site not crossed by any vector within 400 meters (Figure 12) and A1 is the site with the lowest density of short gull paths to landfills in a 500 meters radius (Table 11). In contrast, the gull short path vector density within a 500 meter buffer zone of B1 or A16 sites was higher. This scenario, which is based on the assumption that gulls use the shortest linear routes to access landfills, may help explain the results of this study. The California gull diet in the South San Francisco Bay consists of a large portion of anthropogenic food (Jones 1986, Dierks 1990) and sources of this type of food are easily accessible (Johnston 1956, Cogswell 1974) in the area (Figure 10). Gulls did not pass over the tern colony at pond A1 to approach landfills (Figure 12), and therefore did not encounter the nests at A1 as a food source. It also seems that gulls did not seek out A1 as a food source destination, separate from landfills.

Intensity of defensive response, which expressed the average time spent in defense at each intrusion, was significantly higher at A16 and B1 than at A1 for gull attacks. In contrast, intensity of defensive response was the same for all colonies when the terns defended other types of gull intrusions. There were no significant differences in the intensity of defensive response between the B1 and A16 colonies. McNicholl (1973)

suggested that when potential predators nest near the periphery of a tern colony, terns may habituate to those predators, while little habituation occurs when terns nest far away from the predator. Since the A1 tern colony is located approximately 600 meters from a California gull colony, habituation may be a possible explanation of the low intensity of defensive response in this colony. On the other hand, the closest California gull colony is out of sight for both A16 and B1 Forster's terns colonies, a situation that may result in little, if any, habituation.

However, Cavanagh and Griffin (1993) suggested that it was the frequent flights of large gulls over a Common tern (*Sterna hirundo*) colony and not the proximity of the gull breeding colony that caused habituation. In this study, the rate of California gull intrusions within 30 meters from the edge of the island was very limited at the A1 site compared to the B1 and A16 sites. Cavanagh and Griffin (1993) reported an intrusion rate of three gulls per minute average. In B1, the site with the more frequent gull intrusions, the frequency of gull intrusion barely reached 0.15 gull intrusions per minute. Secondly, California gull flights were very common at a distance further than 30 meters from the edge of the A1 tern colony, but these events were not associated with predation. Furthermore, the A1 Forster's tern colony was established more than ten years ago (Strong et al 2004) and it is very possible that parental experience associated with the evaluation of threat posed by California gulls was high. These conditions may suggest that the terns of A1 colony have perceived little threat from California gulls and, consequently, they responded less vigorously to gull attacks (Montgomerie and Weatherhead 1988). The tern colony in A16 was established nine years ago; however,

this tern colony may have encountered more gull predation over the years and therefore responded intensely to gull intrusions. In this study, a limitation of using the average time spent in defense to measure intensity of defensive response is that this measure depended on the number of nests in the colony. Even if the same number of birds were defending for the same amount of time during a gull attack at two different colonies, the intensity of defensive response would be lower for the colony with the larger number of nests. Nevertheless, as used in this study, the intensity of defensive response measure should be indicative of the assertiveness of the nesting birds and should make possible comparisons between different size colonies. Another study, with a different design, is necessary to access the relationship between parental age and experience with habituation.

Early desertion of the tern colony in A8 site provided only a limited number of surveys and did not allow further statistical analysis. During the first five weeks of the season when A8 was occupied, the frequency of gull intrusions and the amount of defense time spent in response to California gull intrusions were higher in A8 compared to A1, A16, and B1. It is not possible to know whether terns abandoned their nests due to California gull activities, but an investigation of the spatial analysis results could indicate potential explanations. First, the A8 colony had the highest potential gull abundance score (Table 10) from all the other colonies, which means that the distribution of California gulls around the A8 tern colony was very dense. The California gull colony that particularly influenced this gull weight value was the Knapp colony (Table 10) which is the oldest and largest California gull colony in the San Francisco Bay area

(Jones 1986, Strong et al 2004). Currently, approximately 25,000 gulls nest at the Knapp site. In contrast, the density of gull aerial paths to landfills was very low within 500 meters from the colony (Table 11). However, when the number of gulls that would potentially use this path was considered, the measure of the potential use by gulls of this area at A8 was the highest of the study sites (Table 11). Additionally, during the field surveys I often saw California gulls roosting on nearby small dredge spoil islands. Perhaps gull presence in an area could be predicted by both trespassing aerial gull paths to landfills and availability of roosting space. Finally, at my last visit to the A8 colony, terns and the other shorebirds had already abandoned their nests but they were sitting on an island more than 100 meters away and exhibiting alert flights, while California gulls were sitting on the sites previously occupied by terns. These observations suggest that disturbance by California gulls is a very likely explanation of the desertion of A8 tern colony.

While this study assesses disturbance caused by California gulls on Forster's tern colonies using time spent in defense and frequency of gull intrusions, it does not offer direct evidence that this disturbance reduces the breeding success in the tern colonies. Conversely, breeding success is also affected by a plethora of factors such as predator abundance, predator species (Montgomerie and Weatherhead 1988), physiographic characteristics (Dakin 2000, Amat and Masero 2004), weather (Weimerskirch 2002), size of the colony (Hernandez-Matias, Jover and Ruiz 2003), human disturbance, and many others (Weimerskirch 2002). Such factors could mask the effect of California gulls on the studied colonies. The limited number of tern colonies in the area inhibits the analysis

of all these variables simultaneously. Studies focusing on disturbance and predation at the same time could show more clearly the effect of California gulls. Observational studies, unless conducted on an everyday basis and for many hours a day, fail to record a large number of real predation events (Palestis 2005, Whittam and Leonard 200, Shealer and Burger 1992), and subsequently they do not succeed in giving proof of lethal gull effects. In more than 60 observation hours, I saw only three events in which a gull took a tern chick, and only once taking an egg. All of these cases happened at the B1 and A8 sites where the amount of time spent in defense by nesting birds was also high. However, it is not clear whether predation pressure can be predicted by time spent in defense. Research that would combine both an observational study measuring disturbance and a study assessing avian predation with counts of chicks and eggs on the island could elucidate this point.

While observational studies for nest predation have several disadvantages, they also have some considerable advantages over studies that include visits on the island. The latter can be weak in two ways. First, it is possible that a connection of an observed loss of chicks or eggs with the rate of predation by a specific predator can be unjustified or supported poorly (Oro 1996). Secondly, the disturbance caused during the visits of researchers may be of a great magnitude (Jackson et al. 1982). Many studies show that research can significantly disrupt colonial bird nesting and even cause colony abandonment (Carney and Sydeman 1999). During my fieldwork, four of my observation days were concurrent with the visit of a research team on the A16 islands with breeding Forster's terns. This other team was banding chicks for a mercury study

and was inspecting nests for a predation study. I was able to observe California gulls attacking the exposed tern nests while all parents were flying high above the island during the research work. Twice a California gull almost captured a tern chick. Additionally, the research work on each island would last approximately an hour, and during this hour all or the majority of the parents would fly high above the colony. Every time the researchers visited the nesting islands, I would observe an unusual amount of California gull activity. I did not use these surveys in my analysis to avoid bias and I could not analyze these data further due to the small number of surveys. However, because disturbance associated by human presence on the breeding grounds during the early nesting stages may affect the breeding performance of terns (Hatch 1970), and the disruption of nesting activities is associated with parental costs (Montgomerie and Weatherhead 1988, Ellis 1984), there is the need of an evaluation of the field methods that are currently used to assess predation pressures.

The investigation of the spatial relationship between California gull colonies and Forster's tern colonies indicates possible patterns and generates new research questions. I used three different measures derived from spatial attributes to investigate the potential intensity of California gull activity at each Forster's tern colony. First, the potential gull abundance measure could summarize the presence of gulls at each tern colony while taking in to account their relative spatial distribution. The potential gull abundance score was the highest at B1 and this colony had highest disturbance levels. However, the same measure had a higher value for A1 than A16, but there was a higher disturbance level at the A16 site. In fact, the measure of potential gull abundance is highly affected by the

proximity to gull colonies. Strong et al. (2004) found that in the South San Francisco Bay, Forster's terns had the highest colony site fidelity at sites closest to California gulls, which implies that the role of proximity to a gull colony is neutral for Forster's terns in the area.

The measure of potential gull abundance is based on the assumption of gulls stochastically moving around their colony and ignores the distribution of food resources in the area. Ultimately, this measure does not seem to be as good a predictor of tern colony disturbance as measures that include gull foraging trips. The investigation of potential California gull foraging trips reveals a different pattern. According to the maps showing the potential paths used by gulls to forage in landfills in relation to the terns' colonies, tern colony sites that are below or adjacent to potential gull aerial paths are the ones that experienced higher disturbance by gulls. Moreover, I used the density of these paths and their potential use by gulls in a 500 meters buffer zone around each tern colony to evaluate potential gull activity at the tern colony sites. The values of both these measures (Table 11) can be better interpreted when used along with the maps showing the paths' relative position to the tern colonies (Figure 12). Potential gull path density seems to be analogous with gull activity at each site; the exception was the A8 site case, which is better explained by the potential gull use of the area measure. Because of the fact that both measures are affected by scale, a change in the radius of the buffer zone would alter their value for each site. For example, since the vector of a gull path passes directly through the A8 colony island (Figure 12), in a buffer zone less than 500 meters the potential gull use would still be high and the path density higher. In contrast, the very

high value of the potential gull use of 500 meters buffer zone at A1 would be reduced to zero for a buffer zone of 300 meters. Although this study cannot statistically show the contribution of the potential gull foraging routes dispersion in predicting gull activity, there are strong indications that the distribution of aerial paths used by gulls to visit landfills could predict part of the magnitude of gull disturbance on Forster's tern colonies. Another study that uses banded gulls and on-site observations along with telemetry is necessary to address gull foraging decisions, gull movements, and their effect on other species' welfare. This study considered only the type of landfill and not the received volume of refuse, or the methods of processing refuse. Including the type and volume of landfill resources available to the gulls might be useful in developing a predictive model of gull movements.

Overall, this thesis offers evidence of the negative effect of California gulls on breeding Forster's tern colonies in the South San Francisco Bay and proposes that this effect may be site dependent. The basic limitation of this study is that the conclusions could not be generalized given the lack of spatial replication and the limited duration of the study. However, the results of the statistical analysis and the qualitative investigation of California gull distribution and their potential use of the area suggest that disturbance on islands with Forster's tern colonies may be affected by the relative position of the islands to the landfills and the gull colonies, and further stress the need for more extensive studies. If nesting habitats are reduced for Forster's terns, American avocets, and black-necked stilts in the future in the South San Francisco Bay due to the salt pond restoration, increased competition for nesting sites will most likely occur; the creation of

replacement sites for the affected species is critical (Strong et al 2004). The location of the new nesting sites may be affected by the relative proximity of gull nesting colonies and local landfills.

This thesis offers information on the California gull activity on a site-specific basis, which should help inform decision-making with respect to the creation of new islands with optimal habitat location for terns and shorebirds. The ongoing South San Francisco Salt Pond Restoration Project is an excellent opportunity to design and execute experimental studies to explore the role of potential factors in disturbance caused by gulls, and the development of a model that would predict the size of this disturbance. For example, if the creation of new islands for Forster's Terns and shorebirds in the A16 salt pond is desirable (Trulio pers. com) for several socioeconomic reasons, then it could also be possible to test the disturbance on each island relative to location and distribution of potential aerial paths of gulls. Such research would offer practical solutions in reducing conflict with California gulls in addition of increasing the odds of successful establishment of tern colonies.

RECOMMENDATIONS

The results of this thesis research as well as findings in the literature suggest the following management recommendations as ways to protect tern and related species nesting on islands from gull attacks:

1. *Whenever possible, construct new tern and avocet nesting islands in areas that are not on a direct path between gull colonies and landfills.* Other researchers have found that 40% of gull's diets in the South Bay come from landfills. In addition, this study found that nesting islands with the highest gull attack and intrusion rates were located on the trajectory between gull nesting islands and landfills. It seems that gulls did not seek out tern nesting islands, but attacked opportunistically on their way to and from the landfills. These findings argue for placing new islands, such as those that may be constructed as part of restoration in the South Bay, away from these trajectories. While landfill locations do not change, new nesting island placement is complicated by the fact that gulls may be move or be forced from current nesting locations. New island design and location should be developed with advice from South Bay gull and tern experts.

2. *Whenever reasonable, restrict prolonged human access on the terns' nesting sites and when these visits are necessary, take measures to protect vulnerable terns' nests and young from attacking gulls.* Many studies have reported that human visits to the nesting islands, even from experienced researchers, may cause a considerable amount of disturbance to the nesting terns, even colony abandonment. Furthermore, gulls, as

opportunistic feeders, may attack unattended nests. During this study intense gull activity and gull attacks on young terns were observed during visits of a research team on the tern nesting islands. Especially when all members of the research team were standing at one end of the island, gulls attacked unattended nests on the opposite side of the island. On-site visits at tern colonies where gull presence is common should be brief and protection measures for unattended nests should be taken to minimize the risk of chick depredation.

Considering the results and limitations of this thesis study, further research is recommended as follows:

1. *Conduct studies that assess California gull foraging movements in the San Francisco Bay area relative to nesting colonies of other species.* The results of this thesis study support the existence of a relationship between the rate of gull attacks to nesting terns and the location of the tern colony with respect to potential gull foraging paths. Moreover, the definition of potential gull foraging paths is based on the assumptions of gulls using the shortest linear path to access landfills. However, it is necessary to have more information about the actual flight movements of foraging gulls to test the existence of such a relationship. Specifically, information on the type of trajectory, frequency, and direction of foraging gull flights, as well as how these parameters are related to the availability of other resources such as roosting sites for gulls in an area is necessary to develop an accurate model predicting gull activity at tern and other species nesting sites.

2. *Study the fitness costs (energetics and reproductive success) to nesting terns, avocets, and stilts to evaluate the impact of gulls and other predators.* While many studies recognize the importance of energy expenditure for parental defense purposes,

there is lack of information on the energy costs in terms of caloric values associated with specific types of defensive response and ultimate effects on fitness of gull intrusions.

3. *Conduct long term studies and/or studies with more spatial replicates to address the parameters associated with California gull activity at tern and shorebird nesting sites.* Gull activity at a given site may vary annually depending on environmental and human-induced conditions. For this reason, studies that synthesize data collected during long time span are essential for improving our knowledge of the California gull effect on other breeding species. Studies with many spatial replicates allow the evaluation of many parameters and increase the robustness of the analysis.

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