

AN ABSTRACT OF THE THESIS OF

Mark A. Stern for the degree of Master of Science
in Fisheries & Wildlife presented on October 14, 1987
Title: Site Tenacity, Mate Retention and Sexual Dimorphism
in Black Terns

Abstract approved: Redacted for privacy
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Between 1982-1984 I studied site tenacity and mate retention in Black Terns at Sycan Marsh, Lake County, Oregon. I banded 778 adult Black Terns and used this marked population to test the hypotheses that site tenacity and mate retention would be less for Black Terns which nest in variable marsh habitats than for other larids that nest in stable habitats. Based on 76 recaptures of previously banded terns, I estimated that only 40% of the banded Black Terns survived and returned to Sycan Marsh. Seventy-one percent of the recaptured individuals nested in the same Primary Nesting Area, but only 38% of the terns nested in the same colony site in consecutive years. Overall, I estimated that approximately one half of the surviving Black Terns returned to Sycan Marsh, indicating low site tenacity. Of 89 pairs of banded terns, only 5 pairs maintained their pairbonds during consecutive seasons. In 21 instances, terns were nesting with a new mate. There were no instances of terns nesting with a new mate when the old mate was also known to be present. These results indicate that if both members of a pair returned to the same breeding area,

pairbonds were likely to be maintained. However, site tenacity in Black Terns was low, and consequently relatively few pairbonds were maintained for consecutive breeding seasons.

In 1984, I examined sexual dimorphic size traits and trap bias in Black Terns. Based on two traits, culmen length and total head length, males were significantly larger ($p < 0.05$) than females, though not all males were larger than all females. Within pairs, however, the male was always larger than its mate. I also found that males were more likely than females to be the first individual of a pair captured in a nest trap. I used three variables (culmen length, total head length and trap order) in a discriminant function to correctly predict the sex of individuals approximately 80% of the time.

SITE TENACITY, MATE RETENTION AND SEXUAL DIMORPHISM
IN BLACK TERNS

by

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A THESIS

submitted to

Oregon State University

in partial fulfillment of
the requirements for the
degree of

Master of Science

Completed October 14, 1987

Commencement June 1988

ACKNOWLEDGEMENTS

This project was funded by the Oregon Field Office of The Nature Conservancy, the Frank Chapman Fund of the American Museum of Natural History, a Paul A. Stewart Award from the Wilson Ornithological Society, and the Northwest Scientific Association.

I thank Dr. Robert L. Jarvis for serving as my major professor, and providing guidance and counsel with both patience and good humor throughout my tenure as a graduate student. I also thank Drs. Robert Anthony and Robert Frenkel for their support and assistance. Geoff Pampush was instrumental in securing funding for this project, and provided both assistance and camaraderie throughout all phases of this project. And I thank my parents and Ginny Rosenberg for their support and patience. To all these people, I express my sincere gratitude.

I was assisted in the field by Richard Del Carlo (1982-1984), Kurt Kristensen (1983), Eric Horvath (1983), Karen Theodore (1984) and Julie Goodnight (1984). Their dedication and hard work were paramount to the completion of this project, and I thank them for their interest and assistance.

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SITE TENACITY, MATE RETENTION AND SEXUAL DIMORPHISM
IN BLACK TERNS

I. GENERAL INTRODUCTION

Black Terns (Chlidonias niger) belong to family Laridae (gulls and terns) and build nests in emergent vegetation associated with freshwater marshes and lakes throughout the interior portions of the northern United States and southern Canada (Harrison 1983). Despite the abundance of published literature on other species of Laridae, relatively few articles have been published on Black Terns (Baggerman et al. 1956, Cuthbert 1954, Bergman et al. 1970, and Dunn 1979). This thesis addressed two aspects of the breeding biology of Black Terns: 1) site tenacity and mate retention, and 2) sexual dimorphic size and behavioral traits.

II. STUDY AREA

I conducted this study at Sycan Marsh, in Lake County, Oregon. Sycan Marsh is a 25,000 acres wetland system, lying at 1540 m, surrounded by a lodgepole (Pinus contorta) and ponderosa pine (P. ponderosa) forest (Figure 1). The marsh lies in a basin, bounded on the east by the gentle west-sloping Winter Rim fault block, and on the West by the Yamsey Mountain shield volcano. Water flow to the marsh comes principally in the form of snowmelt from adjacent peaks and rims. During this study (1982-1984) water flow to the marsh was higher than the long term mean, and nesting habitat for Black Terns was readily available. Nesting habitat for Black Terns is described in more detail in the first section of the text.

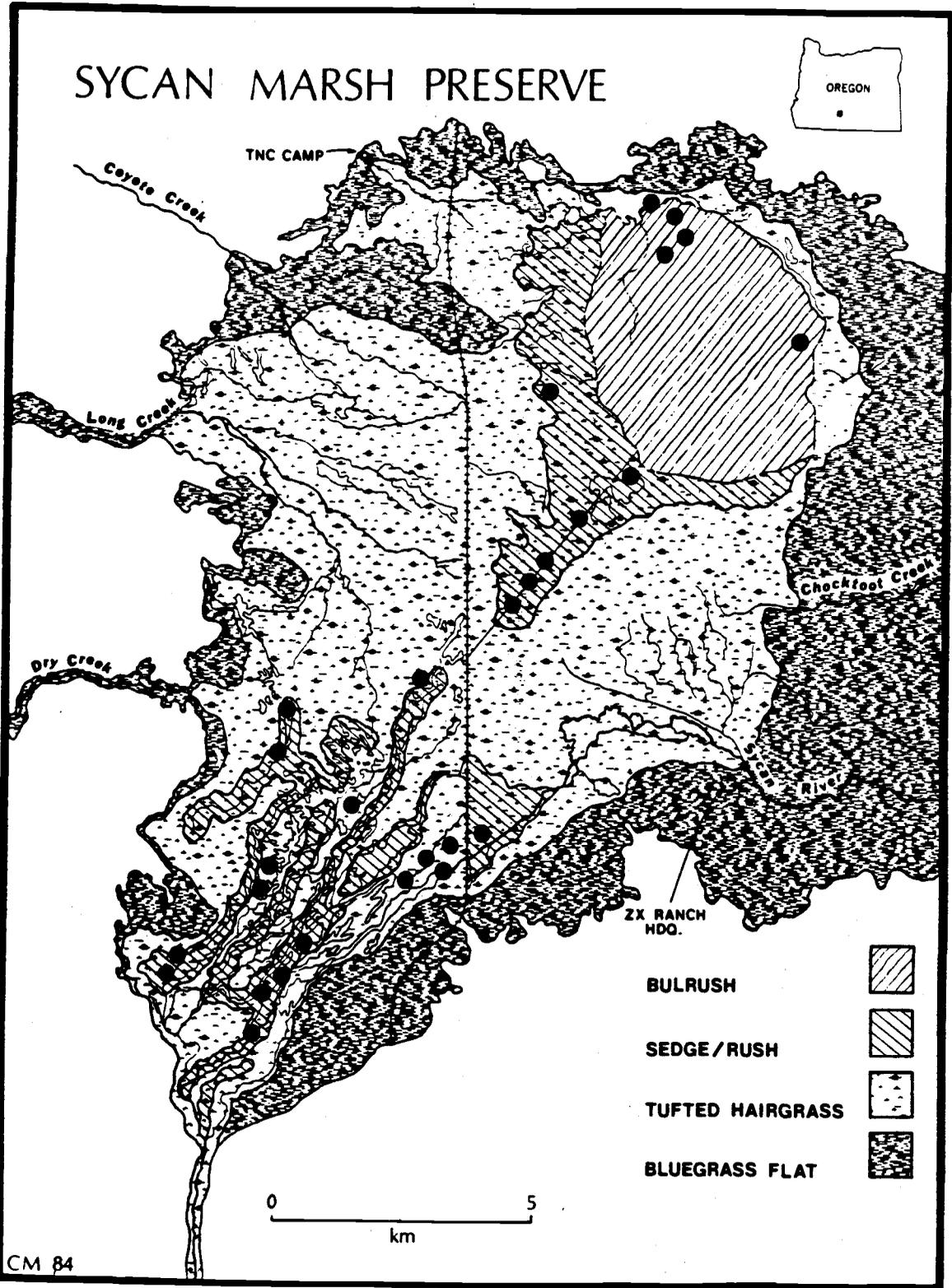


Figure 1. Distribution of Black Tern Colonies at Sycan Marsh, Oregon, 1982-1984. (● = location of tern colonies)

III. METHODS

Black Terns arrived at Sycan Marsh in early May each year and nesting began on approximately 25 May. Peak nest initiation occurred during the first 10 days of June and most incubation was completed by the end of June. Colonies of nesting terns were located by thrice weekly searches through all appropriate nesting habitats. Nests were found by watching individual terns. Once clutches were completed (usually 3 eggs) adult Black Terns were captured in a nest trap, and then banded. In total, I banded 779 adult terns; this marked population formed the basis for my analysis of site tenacity and mate retention.

In 1984, I captured 37 terns and determined the sex of each by laparotomy. I also measured culmen length and total head length and recorded whether each tern was the first or second of a given pair to be caught in the nest trap. I used these data and discriminant function analysis to describe sexual dimorphic size and behavioral traits in Black Terns.

IV. SITE TENACITY AND MATE RETENTION IN BLACK TERNS

INTRODUCTION

Colonial nesting Larids (gulls and terns) often return each year to the same colony and/or nest site and breed with the same mate. The degree to which site tenacity and mate retention occur in Laridae is variable. Within a species, age (Austin 1940, Blokpoel and Courtney 1980) and experience (Coulson and White 1958, Hunt 1980), especially successful reproductive experience (Coulson 1966, Mills 1973), positively affect site tenacity and mate retention. Among species, site tenacity and mate retention may be related to habitat stability (McNicholl 1975, Cuthbert 1985). Larids nesting in stable habitats have high rates of site tenacity (Austin 1940, Coulson and White 1958, Southern 1977, Haymes and Blokpoel 1978, Southern and Southern 1979, Blokpoel and Courtney 1980) and mate retention (Austin 1947, Coulson 1966, Southern and Southern 1982) or both (Vermeer 1963, Mills 1973). Limited observation of Forster's Terns (*Sterna forsteri*; McNicholl 1971), Franklin's Gulls (*Larus pipixcan*; Burger 1974) and Black Terns (*Chlidonias niger*; Dunn 1979), which nest in variable habitats (marshes), indicated that these species have low site tenacity. A pattern of low mate retention was recently observed in Caspian Terns (*Sterna caspia*) nesting in variable habitats (Cuthbert 1985). However, both site tenacity and mate retention have not been thoroughly examined for species

nesting in variable habitats, specifically in marsh environments.

I set out to test the hypotheses set forth by McNicholl (1973) and Cuthbert (1985) which predict that larids nesting in variable marsh habitats will have lower rates of site tenacity and mate retention than larids nesting in stable habitats. Specifically, my objectives were (1) to examine patterns of site tenacity and mate retention in Black Terns nesting in a variable habitat (marsh), and (2) to compare these results with investigations of larids nesting in stable habitats.

STUDY AREA

This study occurred during May, June and July of 1982-1984 at Sycan Marsh, Lake Co., Oregon. The marsh lies at 1540 m elevation, is 9306 ha in size, and encompasses a mosaic of wetland vegetation types. Tern nesting habitat included deep water sites (40.0-60.0 cm) in hard-stemmed bulrush (Scirpus acutus), sites of intermediate water depths (15.0-30.0 cm) associated with broad leafed sedges and rushes (Carex vesicaria, C. nebraskensis, Juncus nevadensis, and J. balticus) and shallow water sites (<15.0 cm) in tufted hairgrass (Deschampsia caespitosa) (Figure 1).

Spring and summer water levels on Sycan Marsh are dependent upon runoff from winter snowpack on surrounding mountains. The volume of water from winter snowpacks varies annually, hence marsh water levels vary annually, resulting

in variable amounts and quality of habitat for marsh nesting birds. During the past 30 years, the snowpack in the head waters of the Sycan River, which drains into Sycan Marsh, averaged 17.4 ± 6.5 (S.E.) inches of water (US Soil Conservation Service Snowpack Records, Portland, OR). During the same 30 years, discharge from the Sprague River, which drains Sycan Marsh, averaged $120,501 \pm 44,665$ (S.E) cubic feet/second (US Geological Survey Stream Discharge Data, Portland, OR). Sycan Marsh had high water levels during 1982-84; snowpack and stream discharge varied from 124 to 146 percent of the 30 year averages. Thus, while quantity and quality of marsh habitat vary considerably at Sycan Marsh, both were consistent during the three years of this study.

METHODS

Adult Black Terns were captured and banded at nest sites with a cylindrical cage of hardware cloth (modified after Burger 1971, Dunn 1979). The number of terns banded each year varied: 141 individuals in 1982 (including 13 pairs), 365 individuals in 1983 (including 76 pairs), and 273 terns in 1984 (including 124 pairs).

Colonies of Black Terns often lacked distinct boundaries, and I defined a colony as 2 or more pairs nesting close enough that social interactions among individuals occurred daily. Colony sites sufficiently distant to minimize daily social interactions, but located

adjacent to each other along or within a localized unit of the marsh were defined as an aggregation of colony sites within a Primary Nesting Area (PNA). There were 11 primary nesting areas on the marsh, which contained several colonies consisting of 2 to 85 pairs. A few PNAs consisted of a single large colony, while isolated colonies with less than 4-6 pairs were considered as disjunct colonies, and not PNAs.

I calculated annual survivorship of banded adult Black Terns using the Jolly-Seber method for open populations (Seber 1973).

RESULTS

Overall, the rate of recapture of Black Terns at Sycan Marsh was 15% (Table 1). Annual survival of banded adult Black Terns was $40\% \pm 13$. This survival rate applies only to those banded terns that returned to Sycan Marsh and were at risk of being recaptured. Thus, 60% of the banded terns either died or emigrated to another nesting location.

In total, I recaptured 76 Black Terns at Sycan Marsh; 54 (71%) exhibited some degree of site tenacity nesting at either the same colony site as the previous year, or at an adjacent colony site within the same PNA (Table 2). The remaining 22 (29%) exhibited little site tenacity within the marsh and nested in a different PNA.

Although 24% (9/38) of the Black Terns selected new colonies when their previous colony site was active, most shifts (81%, 38/47) to different colony sites occurred when

the former colony site was inactive (Table 3). Of the terns that shifted colony sites, approximately half (25/47) remained within the same PNA and half (22/47) dispersed to other PNAs. The tendency of terns to relocate in the same or different PNA was similar for terns whose previous colony site was active (5 of 9 in same PNA) as for terns whose previous colony site was inactive (20 of 38 in same PNA). Thus, when colony sites were active in successive years, terns (if they returned to the marsh) tended to nest at the same colony site. If terns selected a new colony site, however, they were just as likely to nest in a different PNA as to remain in the original PNA.

Few Black Terns maintained pair bonds between consecutive breeding seasons (Table 4). Based on pairs of known fate, only 22% (5/23) of the pairs remained intact for consecutive breeding seasons. There were no instances of mate swapping, and the failure to retain mates was apparently not a function of infidelity but rather that the previous mate was not known to be present (18 of 18). Among 63 of 89 pairs (71%), neither member was recaptured at Sycan Marsh, and the fate of these pairs is unknown.

DISCUSSION

Other investigators have used the proportion of marked individuals resighted at the study area as a measure of site tenacity. By this standard, site tenacity in Black Terns was only 15% (76/506), three to five times less

than larids nesting in stable habitats (Table 5). That procedure does not adjust the rate of site tenacity for survival, which may vary considerably by species and population.

The estimate of 40% annual survival of adult Black Terns (as derived by the Jolly-Seber method) is another means of assessing site tenacity. Simply, approximately 40% of the banded adult Black Terns survived and returned to Sycan Marsh, while (60%) either died or nested elsewhere. If all these unaccounted for terns died, then site tenacity to the marsh for Black Terns was 100% because all surviving terns returned to the marsh. In contrast, if all unaccounted for terns nested at other marshes, then site tenacity in Black Terns is low (40%). In the following discussion I argue that the low rate of return of banded Black Terns to Sycan Marsh was a function of low site tenacity, and not low annual survival.

If a majority of the surviving banded terns returned to Sycan Marsh (which I doubt), then the estimate of annual survival of banded adult terns that returned to Sycan Marsh (40%) should also approximate annual survival for all banded terns (White et al. 1982). Henny et al. (1970) developed a model of population stability that estimates the allowable rates of mortality, survival, and productivity necessary for a stable population. Using the model for species that produce young at the end of their second year,

$$m = \frac{1-s}{(S_0 S_1 (1-S+S_2))}$$

where $2m$ = the number of young produced annually by each adult female, S = annual survival of adults, and S_0 , S_1 , and S_2 are age specific survival rates for young, and subadults, and adults. Given a 40% annual survival, then, in order to maintain a stable population, each female adult Black Tern must produce 7.5 young per year. I did not have an estimate of survival for first and second year terns, and instead used the survival rate of adult terns. Survival is generally lower during the juvenile and subadult period of life for most species, and hence by using this higher value of survival for young and subadult birds, I conservatively estimated the level of productivity necessary to maintain a stable population.

Maximum reproductive capability of Black Terns is 3 young per year (3 egg clutch, one nesting/year). Clearly, Black Terns are not capable of producing 7.5 young per year per adult female. Indeed, Black Terns rarely raised a brood of 3, but more often raised, at most, one chick to flight stage per adult female (Stern and Jarvis, unpublished data). If each adult female Black Tern raised one young each year, then average annual survival rate for Black Terns must be 0.70-0.75 to maintain a stable population. An annual survival rate of this magnitude for adult Black Terns is comparable to known survival rates for other larids

(Chabrzyk and Coulson 1976, Coulson and Horrobin 1976, Coulson and Wooller 1976) and is consistent with the K-selected life history traits of this species.

Although I do not know annual survival of adult Black Terns, it is clearly higher than .40 that I estimated from the survival rates. Thus, I tentatively conclude that a substantial number of Black Terns survived but emigrated from Sycan Marsh to other breeding locales. Hence, the low rate of return of banded adult Black Terns at Sycan Marsh occurred because site tenacity was weak in adult Black Terns and not because annual survival was low.

I speculate that the low rates of site tenacity in Black Terns occurred because terns employ what I have called a "first good" strategy in selecting nesting locales each year. Simply, terns that migrate northward during spring "home" towards the marsh used the previous year. However, if a marsh with suitable habitat is encountered during migration, the choice becomes one of remaining to nest where conditions are known to be suitable versus continuing on to the "home" marsh where conditions are unknown. The risks involved in nesting in a new area entail unfamiliarity with the distribution of resources. The risks of continuing migration to the "home" marsh entail the unpredictability of marsh environments. The balance of risks then is determined by the variability of nesting habitats; stable habitats favor high site tenacity, and variable habitats favor using new areas with favorable habitat encountered during

migration.

In the intermountain west, quality and quantity of marsh habitat is highly variable, and marshes are somewhat independent of each other as they are annually dependent on local snowmelt. Thus, low site fidelity ("first good") would be expected of Black Terns at Sycan Marsh. Perhaps previous successful experience provides sufficient advantage for some birds to risk passing over suitable habitat during migration in favor of uncertain conditions at the "home" marsh.

This scenario does not require that birds first return to the home marsh and then choose to remain or go elsewhere based on habitat conditions on the home marsh, as hypothesized by Burger and Shisler (1980). The "first good" scenario explains the low rate of site tenacity of Black Terns during a period of above average habitat conditions at Sycan Marsh. Marshes throughout the intermountain generally experienced high water levels in 1982-84, providing many suitable nesting areas for migrating Black Terns.

Larids which nest in stable environments are often strongly site specific, with individuals often nesting not only at the same colony site, but also at the same nest site as in the previous year (Table 5). In Black Terns, site tenacity was not nearly so site specific: 71% of the recaptured terns returned to the same PNA and only 38% returned to the same colony site. Thus, in comparison with larids nesting in stable environments, Black Terns nesting

in a variable marsh habitat were not only less likely to return to the same marsh in the following season, but of those individuals that did return to the same marsh, tenacity to specific nesting sites occurred at a more generalized level (PNA).

The "first good" strategy also explains the patterns of mate retention we observed. Members of a pair are unlikely to be reunited in subsequent years because they are unlikely to utilize the same marsh. However, when both terns returned to the marsh used previously, then they are likely to remate again (5 of 5 pairs). Thus, mate fidelity was high for pairs where both individuals returned to the same breeding area, but because site tenacity was low, overall patterns of mate retention were also low.

Overall, site tenacity and mate retention for Black Terns nesting in the variable marsh habitat at Sycan Marsh were low compared to larids nesting in stable habitats (Table 5, Table 6). These results generally support hypotheses concerning habitat stability and the development of site tenacity and mate retention in larids as proposed by McNicholl (1975) and Cuthbert (1985). I suggest that a "first good" strategy is an adaptive trait well suited to avian species nesting in marsh habitats, and that this mechanism more than others explains low rates of site tenacity and mate retention observed in Black Terns, even when habitat conditions are excellent.

ACKNOWLEDGEMENTS

I thank R. Del Carlo, J. Goodnight, E. Horvath, K. Kristensen and K. Theodore for assistance in the field; and Geoff Pampush and John Hoffnagle for essential logistical support. Funding was provided by Frank Chapman Fund, the American Museum of Natural History; the Paul A. Stewart Award, the Wilson Ornithological Society; the Northwest Scientific Association and the Oregon Field Office of The Nature Conservancy.

Table 1. Banding and return data for adult Black Terns banded at Sycan Marsh, Oregon.

Year Banded	# Banded	Number Recaptured		
		1983	1984	Total
1982	141	12	7	19
1983	365		57	57
Total	506	12	64	76

Table 2. Site tenacity in Black Terns recaptured at Sycan Marsh, Oregon.

Location of Recaptured Black Tern	N	%
Same Colony Site	29	38
Different Colony Site		
Same Primary Nesting Area	25	33
Different Primary Nesting Area	22	29
Total	76	100

Table 3. Site tenacity and status of previous colony site of Black Terns banded and recaptured at Sycan Marsh, Oregon.

	Old Colony Site Active	Old Colony Site Inactive	Total
Same Colony Site	29	-	29
Different Colony Site (Same PNA)	9 (5)	38 (20)	47 (25)
(Different PNA)	(4)	(18)	(22)
Total	38	38	76

Table 4. Mate retention in Black Terns at Sycan Marsh, Oregon.

Fate of Pairs	Number of Pairs
Pair Bond Intact	5
Pair Bond Broken Individual with New Mate (old mate not observed)	18
Individual with New Mate (old mate observed)	0
Status Unknown (Neither Individual Observed)	63
Individual Observed (status of mate unknown)	3
Total	89

Table 5. Comparison of site tenacity in Laridae.

Species of Laridae	Nesting Habitat	Proportion of marked birds resighted at area		Proportion of resighted birds observed at original colony &/or nest site	
		%	(N)	%	(N)
Black Tern (this study)	marsh	15	(506)	38	(76)
Black Tern (this study) ¹	marsh	40	(506)		
Ring-billed Gull ² (<i>Larus delawarensis</i>)	peninsula	60	(930)	-	
Ring-billed Gull ³	peninsula	49	(311)	97	(152)
Ring-billed Gull ⁴	spit/spoils	54	(151)	86	(83)
Ring-billed Gull ⁵	island	-		70	(154)
Common Tern ⁶ (<i>Sterna hirundo</i>)	island	53	(1000)	98	(532)
Common Tern ⁷	island	84	(93)	-	
Glaucous-winged Gull ⁸ (<i>Larus glaucescens</i>)	island	87	(68)	81	(58)
Red-billed Gull ⁹ (<i>Larus novaehollandiae</i>)	island	82	(153)	-	
Herring Gull ¹⁰ (<i>Larus argentatus</i>)	island	-	-	84	(55)
Black-legged Kittiwakes ¹¹ (<i>Rissa tridactyla</i>)	ledge	86	(77)	-	--

¹Based on annual survival rate derived from Jolly-Seber analysis; ²Southern 1977; ³Southern and Southern 1979; ⁴Blokpoel and Courtney 1980; ⁵Ludwig 1974; ⁶Austin 1949; ⁷Haymes and Blokpoel 1978; ⁸Vermeer 1963; ⁹Mills 1978; ¹⁰Chabrzyk and Coulson 1976; ¹¹Coulson and White 1958.

Table 6. Comparison of mate retention in Laridae.

Species	Nesting Habitat	Pair Bond Maintained % (N)	Evidence of mate swapping
Black Tern (this study) ¹	marsh	22 (23)	No
Caspian Tern ²	island	25 (25)	Yes
Ring-billed Gull ³	peninsula	59 (65)	Yes
Common Tern ⁴	island	80 -	?
Red-billed Gull ⁵	island	82 (153)	Yes
Black-legged Kittiwake ⁶	ledge	64 (458)	Yes
Glaucous-winged Gull ⁷	island	54 (13)	No
Western Gull ⁸ (<i>Larus occidentalis</i>)	island	87 (30)	?

¹Based on pairs of known fate only; ²Cuthbert 1985; ³Southern and Southern 1982; ⁴Austin 1947; ⁵Mills 1973; ⁶Coulson 1966; ⁷Vermeer 1963; ⁸Pierotti 1981.

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V. SEXUAL DIMORPHISM IN BLACK TERNS

INTRODUCTION

Black Terns (Chlidonias niger), like other Laridae, exhibit monomorphic plumages, and the sex of individuals is difficult to determine by observation in the field. In gulls, however, males are generally larger than females, and within mated pairs, males are almost always larger than their female mate (Harris 1964, Harris and Jones 1969, Mills 1971, Shugart 1977, Ryder 1978, Hunt et al. 1980, Fox et al. 1981, Pierotti 1981, Hanners and Patton 1985). In terns, size dimorphism has been documented only for Common Terns (Sterna hirundo; Coulter 1986). Coulter (1986) demonstrated that various morphometric measurements, in particular measurements of the culmen (length, depth, width), were useful in distinguishing between sexes. My objectives were to determine if Black Terns were sexually dimorphic in size, and whether males or females tended to be the first member from a given pair captured in nest traps. This latter attribute becomes important in situations where only one member of a pair is nest trapped. Sex-related trap bias may result in biased samples of trapped birds and could lead to erroneous conclusions about various population parameters (Burger 1983).

METHODS

In 1984, at Sycan Marsh, Lake Co., Oregon, individual Black Terns were captured in cylindrical traps placed on active nests containing two or more eggs. Traps were constructed of 2.25 cm mesh (1/2 inch) hardware cloth, 0.5 m h x 0.4 m dia, with a rectangular opening (9.0 cm x 27.0 cm (4 inches by 12 inches)) in the roof (Burger 1971, Dunn 1979). Terns were trapped one at a time. After banding and releasing the first individual, the trap was restationed to trap the second member of the pair. Thirty-seven terns, including 16 pairs, were trapped and sexed by laparotomy. The culmen length (CL) and total head length (THL-back of the head to the tip of the beak) were measured with vernier calipers to the nearest 0.1 mm. I employed discriminant function analysis (Klecka 1975), first using Wilks stepwise analysis to identify the relative importance of the two variables, and then Direct analysis forcing the inclusion of both variables to maximize the predictability of the discriminant functions. Subsequently, I added a third variable, trap order (TRPORD-first caught or second caught of a given pair), and used Direct analysis to derive a third discriminant function. An additional 88 pairs of terns were trapped and measured, but sex was not determined. I used these 88 pairs as an independent sample and employed V1 validation procedures (Frank et al. 1965, Fox et al. 1981) to test the accuracy of the discriminant functions. For the

test sample we assumed the larger of the two terns within the pair to be the male and the smaller the female; this dimorphic trait was consistent with the individuals of known sex in this study. T-tests and binomial probability were used to assess differences between means and frequencies (Snedecor and Cochran 1980).

RESULTS

Males had significantly ($p < 0.001$) larger total head length and culmen length than females (Table 1). Within each of the 16 pairs sexed by laporatomy, males were always larger than their mates. In addition to these sexual dimorphic size traits, sex-related trap bias was also evident: males were more likely than females (15 of 21) to be trapped first ($p < 0.05$) (Table 2).

I used these three sexual dimorphic traits to derive three different discriminant functions from various combinations of variables and types of analyses (Table 3). In all three analyses, total head length had the highest standardized discriminant coefficient (0.59-1.00) and was the most discriminating variable, followed by culmen length (standardized discriminant coefficient=0.21-0.73) and trap order (standardized discriminant coefficient=0.36). The use of all three variables, under the Direct method of analysis, resulted in the function with the greatest accuracy (92%) of correctly classifying terns according to sex. This function ($n=37$) was:

$$35.49 = .46\text{THL} + .33\text{CL} + .39\text{TRPORD}$$

Terns with discriminant scores greater than 35.49 were classified as male, and terns with lesser scores as female. Using this function, 18 of 20 males (90%) and 16 of 17 (94%) females were correctly classified. Eighty percent (135/168) of the terns from the validation sample were correctly classified according to sex; 91% (76/84) of the females and 70% (59/84) of the males.

DISCUSSION

Male Black Terns were significantly larger than females in both total head length and culmen length, but ranges overlapped, and it was not possible to sex individuals on the basis of a single trait with 100% accuracy. Within mated pairs, however, males were always larger than their female mate. These sex-dimorphic traits also occur in Common Terns (Coulter 1986) and many gulls (as cited in first paragraph of the introduction), and may be characteristic of all Laridae.

Differences between sexes in incubation schedules and nest site defense may contribute to the male biased trap response in Black Terns. Both mates of Black Terns share incubation duties, although incubation schedules are unknown. In Western Gulls (Larus occidentalis) incubation duties are shared by both sexes, with females incubating primarily at night (Pierotti 1981). If Black Terns have incubation schedules similar to Western Gulls, then males would be most likely to be captured in the nest traps. In

Western Gulls, Ring-billed Gulls (L. delawarensis) and Herring Gulls (L. argentatus), males are more aggressive than their mates in defending nest sites and chicks (Pierotti 1981, Southern 1981, Morris and Bidochka 1982). Aggressive nest defense would likely result in higher capture probabilities for males than females. I was unable to assess the relative contribution of incubation schedules and aggression to the male biased trap response I observed.

Discriminant function analysis has been used to successfully classify individuals according to sex for Herring Gulls, Ring-billed Gulls, and Laughing Gulls (L. atricilla) (Shugart 1977, Ryder 1978, Fox et al. 1981, Hanners and Patton 1985). Generally, total head length and bill depth at the gonys, were the most discriminating criteria, and when combined with other variables generated discriminant functions (and V1 validation tests) with predictive accuracies of 94-99%. In Common Terns, bill depth, bill length, bill width and body weight (but not total head length) were used to generate a discriminant function with a predictive accuracy of 80% (Coulter 1986).

The predictive accuracy of the discriminant functions derived in this study for Black Terns were lower than those for gulls, but higher than the values derived for Common Terns. I did not use bill depth at the gonys, and Coulter (1986) did not use total head length in his study on Common Terns. The omission of either of these two variables may have contributed to functions of lower predictive accuracies

for terns than those derived for gulls. The gonys, the prominent ridge formed by the fusion of the two halves of the lower mandible toward the tip of the bill, are well-developed in the species of gulls mentioned here. The weakly developed gonys in terns may partially explain why techniques discussed here were more successful in separating the sexes of gulls than terns. Also, terns are smaller than gulls, and thus sex-dimorphic size traits may be proportionately less pronounced, which would diminish their value as predictors of sex.

V1 validation scores of the discriminant functions derived for Herring and Laughing Gulls generally verified the accuracy of the discriminant functions (Fox et al. 1981, Hanners and Patton 1985). In Black Terns, however, there was a difference between the classification accuracies of the original sample group and the validation group (92% vs. 81%). Also, females were more accurately classified than males in the validation sample. These differences indicate the possible occurrence of sampling bias and/or error in assigning the sex of birds in the validation sample.

The small number (37) of terns (all from a single colony) used to generate the discriminant function may have influenced the results. Males in the validation group were significantly smaller ($p < 0.001$) for both morphological traits than males in the known sex group. Females in the two groups were not significantly different ($p > 0.45$) in size. For males in the validation sample, the smaller

values for the two morphometric measurements decreased the likelihood of achieving a discriminant score greater than 35.49, and increased the likelihood of incorrect classification. Thus, agreement between the predictive accuracy of the discriminant function and the VI validation scores was high for females (92%), but low for males (70%).

I evaluated the limitations of small sample size by generating a second set of discriminant functions from the larger sized validation sample (Table 4). These functions performed equally well for males and females but their predictive accuracies were less than (80-82%) the original discriminant functions (87-92%). The validation sample included terns from 20 different nesting colonies throughout the marsh, while the original sample was from a single nesting colony. Apparently the small sample of terns from the single colony was not representative of the variation inherent in the population. Intrapopulation differences in sizes has been observed in Ring-billed Gulls (Larus delawarensis) (Threlfall and Jewer 1978), and it is possible that inter-colony size differences occur for terns nesting in the same localized breeding area.

The application of discriminant function analysis provided a method for sexing individual terns trapped out of pairbond, but the predictive accuracy of the functions were lower than similar functions derived for gulls. Although Black Terns were clearly sexually dimorphic, the use of discriminant functions to classify the sex of individuals

was not 100% accurate. Use of more discriminating variables including total head length and bill depth, and large sample sizes of terns may generate functions with acceptable levels (>.90) of accuracy. However, Black Terns lack well-developed gonys and are relatively small compared to most other larids. I suggest that the measurements and techniques used for analysing such differences between the sexes of larger sized larids, particularly those with well-developed gonys, may not be sensitive enough to make similar distinctions between the sexes in smaller sized species of larids without well-developed gonys. Investigation of sex dimorphic size traits in a small species of gull with poorly developed gonys (Bonaparte's Gull (Larus philadelphia)) and a large species of tern (Caspian Tern (Sterna caspia)) would assist in further describing important sexual dimorphic size traits in larids.

ACKNOWLEDGEMENTS

We acknowledge R. Del Carlo, J. Goodnight and K. Theodore for assistance in the field; Geoff Pampush and Eve Prior for essential logistical support. Funds for this investigation were provided by the Oregon Field Office of The Nature Conservancy, the Frank Chapman Fund of the American Museum of Natural History, the Northwest Scientific Association, and the Paul A. Stewart Award of the Wilson Ornithological Society.

Table 7. Morphometric measurements of Black Terns of known sex (laparotomy) and sex presumed from relative size of mates (males largest) at Sycan Marsh, Oregon, 1984.

	Males		Females		P-value
	N	$\bar{x} \pm \text{S.D.}$ (mm)	N	$\bar{x} \pm \text{S.D.}$ (mm)	
Known Sex:					
Total Head Length	20	59.60 \pm 1.18	17	57.05 \pm 1.44	p<0.001
Culmen Length	20	27.30 \pm 1.14	17	25.37 \pm 1.18	p<0.001
Presumed Sex:					
Total Head Length	88	58.83 \pm 1.14	88	56.82 \pm 1.25	p<0.001
Culmen Length	88	26.59 \pm 1.12	88	25.24 \pm 1.11	p<0.001

Table 8. Capture order of nest-trapped Black Terns from sample groups of known sex (laparotomy) and sex presumed from relative size of mates (males largest), Sycan Marsh, Oregon.

	Males Caught First		Females Caught First		Binomial Probability
	N	%	N	%	
Known Sex	15	71.43	6	28.57	p<0.05
Presumed Sex	54	66.67	27	33.33	p<0.05
Total	69	67.25	33	32.35	p<.025

Table 9. Discriminant function analysis (DFA) for classifying Black Terns according to sex, Sycan Marsh, 1984.

Method of DFA	Variables Avail. for analysis	Variables Used for analysis	Classification Accuracy			
			Original sample		Validation sample	
			N	%	N	%
Wilks	THL, CL,	THL	37	87	176	79
Direct	THL, CL	THL,CL	37	90	176	79
Direct	THL, CL,TRPORD	THL, CL,TRPORD	37	92	168	80

THL=total head length; CL=culmen length; TRPORD=trap order.

Table 10. Discriminant function analysis (DFA) generated from the validation sample of Black Terns where sex was presumed from relative size of mates (males largest), Sycan Marsh, Oregon, 1984.

Method of DFA	Variables Avail. for analysis	Variables Used in analysis	Classification Accuracy			
			N	Overall	Male	Female
Wilks	THL	THL	176	81%	84%	77%
Direct	THL,CL	THL,CL	176	80%	84%	75%
Direct	THL,CL,TRPORD	THL,CL,TRPORD	168	82%	81%	83%

THL=total head length; CL=culmen length; TRPORD=trap order.

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VI. SUMMARY DISCUSSION

Patterns of site tenacity, mate retention and sexual dimorphic size traits were not as well developed in Black Terns as compared to other species of larids.

The results concerning site tenacity and mate retention generally support hypotheses suggested by McNicholl (1975) and Cuthbert (1985), specifically that larids nesting in variable marsh habitats are less likely to exhibit site tenacity and mate retention than larids nesting in less variable environments, such as cliffs, headlands and islands. Further, these results support the hypothesis presented by Morse and Kress (1984) that mate retention is dependent on the tendency of individual birds to return to the same site in subsequent years. Thus, in species like Black Terns, where site tenacity is only moderately developed, it follows that mate retention between successive breeding seasons would likewise be at best moderately developed.

I speculate that low rates of site tenacity in Black Terns occur because terns employ what I have called a "first good" strategy in selecting nesting locales each year. Simply, terns that migrate northward during spring "home" towards the marsh used the previous year. However, if a marsh with suitable habitat is encountered during migration, the choice becomes one of remaining to nest where conditions

are known to be suitable versus continuing on to the "home" marsh where conditions are unknown. The risks involved in nesting in a new area entail unfamiliarity with the distribution of resources. The risks of continuing migration to the "home" marsh entail the unpredictability of marsh environments. The balance of risks then is determined by the variability of nesting habitats; stable habitats favor high site tenacity, and variable habitats favor using new areas with favorable habitat encountered during migration.

Sex dimorphic size traits were evident in Black Terns, but differences were not nearly as pronounced as has been documented in other species of larids. This is partially explained by the relatively small size of Black Terns compared to most other larids, and I suggest that measurements and techniques for analysing such differences between the sexes, though satisfactory for larger sized larids with well-developed gonys, may not be sensitive enough to make distinctions between the sexes in smaller sized species of larids without well-developed gonys.

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