Effects of Nest Density, Location, and Timing on Breeding Success of Caspian Terns

MICHELLE ANTOLOS[1,3], DANIEL D. ROBY[1], DONALD E. LYONS[1],
SCOTT K. ANDERSON[1] AND KEN COLLIS[2]

[1]USGS-Oregon Cooperative Fish and Wildlife Research Unit, Department of Fisheries and Wildlife
104 Nash Hall, Oregon State University, Corvallis, OR 97331, USA

[2]Real Time Research, Inc., 61434 Linton Loop, Bend, OR 97702, USA

[3]Current name and address: Michelle Kappes, Department of Ecology and Evolutionary Biology
University of California Santa Cruz, Long Marine Lab-Center for Ocean Health
100 Shaffer Road, Santa Cruz, CA 95060, USA
Internet: kappes@biology.ucsc.edu

Abstract.—One of the proposed benefits of colonial nesting in birds is the protection afforded against avian predators. This advantage may be counter-balanced by the negative effects of intraspecific aggression on breeding success. Effects of nest density, nest location within the colony, and timing of nest initiation on productivity of Caspian Terns (*Sterna caspia*) were investigated on Crescent Island in the mid-Columbia River, Washington, USA. In the absence of intense nest predation at the Crescent Island tern colony, it was hypothesized that nest density would be negatively associated with productivity. A rangefinder was used to determine spatial distribution of Caspian Tern nests, and these data used to calculate nest characteristics (nest density, nearest neighbor distance, and distance to colony edge) for a randomly-selected subset of nests monitored for nest chronology and productivity. Productivity did not differ between nests in high- and low-density areas of the colony, and was positively associated with earlier nest initiation. Early nests were more productive, were located in areas of higher nest density, and were further from the colony edge than late nests. The strong effect of timing may have been attributable to seasonal declines in prey resources for terns at this site. Our results suggest that Caspian Terns nesting at the highest densities observed in this study did not incur immediate reproductive costs, despite increased potential for encounters between chicks and aggressive conspecific adults. *Received 13 April 2006, accepted 6 August 2006.*

Key words.—Caspian Tern, *Sterna caspia*, breeding ecology, coloniality, nest density, timing.

The adaptive significance of colonial nesting in birds is a topic that has received considerable attention in the study of avian life history strategies (see reviews by Wittenberger and Hunt 1985; Siegel-Causey and Kharitonov 1990; Danchin and Wagner 1997). A major hypothesis developed to explain coloniality in birds suggests that nesting densely should afford protection against predators, particularly avian predators (Kruuk 1964; Götmark and Andersson 1984; Anderson and Hodum 1993). However, studies investigating the effects of nest density on breeding success in colonial birds have produced mixed results. Birkhead (1977) found significant positive correlations between nest density and breeding success in Common Murres (*Uria aalge*), while Butler and Trivelpiece (1981) found that fledging success was significantly lower in high-density nesting areas for Great Black-backed Gulls (*Larus mari-*

nus). In the Common Tern (*Sterna hirundo*), Becker (1995) found breeding success was positively correlated with nest density and negatively correlated with nearest-neighbor distance, while Houde (1983) found no relationship between density and survival of chicks after accounting for habitat type. Breeding success was highest for intermediate nest densities in Herring Gulls (*L. argentatus*, Parsons 1976), but was not related to nest density in Ring-billed Gulls (*L. delawarensis*, Dexheimer and Southern 1974).

Hunt and Hunt (1976) suggested that with colonial nesting comes conflicting needs for protection against nest predation and the avoidance of intraspecific aggression, perhaps explaining some of the variation described above. Because these factors are likely to influence breeding success of colonial birds in opposing ways, it may be useful to examine cases where only one of these

factors is relevant (i.e., in colonial species where intraspecific aggression is minimal or in colonies with virtually no nest predation). In this study, the relationship between nest density and breeding success was examined at a colony where nest predation rarely occurred. In the absence of avian nest predation, it is expected that high nesting density will negatively affect breeding success if interference by conspecifics is an important source of mortality for eggs and young (Hunt and Hunt 1976).

Caspian Terns (*Sterna caspia*) are facultatively colonial waterbirds that typically nest in association with gulls and other terns (Cuthbert and Wires 1999). Gulls can opportunistically prey on tern eggs and chicks, especially after disturbance events (Penland 1981; Roby *et al.* 1998). This study was conducted at a colony where Caspian Terns experience low levels of disturbance and therefore nest predation by gulls rarely occurs (see Results). The low disturbance rates reflect low frequency of visits by avian or mammalian predators (Roby *et al.* 1998). Intraspecific aggression, however, may be an important source of mortality for Caspian Tern chicks, which are semi-nidifugous and can be attacked and/or killed by neighboring adults (Bent 1921; Cuthbert and Wires 1999).

Because a number of other factors likely influence the relationship between nest density and breeding success, data were also collected on nest centrality and breeding chronology to examine their effects in the analysis of Caspian Tern reproductive success. In colonial birds, centrality may be either positively (Coulson 1968; Becker 1995) or negatively (Brunton 1997) correlated with productivity, and this relationship may be affected by the type of nest predator present (Brunton 1997). Breeding chronology can also be an important factor, and it has been generally found that early (Davis and Dunn 1976; Becker 1995; Massoni and Reboreda 2001) or peak (Patterson 1965; Parsons 1975) breeders are more successful in raising a brood, although this relationship does not always hold (Birkhead 1977; Hunt and Hunt 1975). In addition, because distance to nearest neighbors may significantly affect aggression rates of conspecifics (Hill *et al.* 1997) and breeding success (Becker 1995), we included this factor in the analysis to determine if its effect differed from local nest density. Thus this study assessed the effect of nest density on reproductive success in the near absence of nest predation, after accounting for position within the colony and timing of breeding.

METHODS

Study Area

This study was conducted during April-July 2001 on Crescent Island (46.094°N, 118.929°W) in the reservoir created by McNary Dam on the Columbia River, Washington, USA. Crescent Island was created from dredged deposits in 1985 as waterfowl nesting habitat, and was colonized soon afterward by Caspian Terns (Ackerman 1994). In 2001, an estimated 688 pairs of Caspian Terns nested in a single colony on the northeastern side of the island. The area of Crescent Island is 3.2 ha, and the area of the Caspian Tern colony measured 676 m² (0.07 ha) in 2001. Overall nesting density in 2001 was 1.02 nests per m², and fledging success averaged 1.02 fledglings per breeding pair (Antolos 2003; Antolos *et al.* 2004). A large colony of California Gulls (*L. californicus*) was established on Crescent Island shortly after the Caspian Tern colony formed (Ackerman 1994), and consisted of approximately 2,700 breeding pairs in 2001 (M. Antolos, unpubl. data); small numbers of Ring-billed Gulls also nested on the island.

Disturbance Rates

Data on disturbance rates were collected in 2000 and 2001 by dividing the number of disturbances recorded in a day by the number of observation hours for that day, and then averaging these rates across the season. A disturbance was defined as an episode where Caspian Terns flushed from their nests, creating the potential for nest predation by opportunistic gulls. Three Caspian Tern colonies located in the lower Columbia River were used for comparison to assess the relative level of disturbance at Crescent Island in 2000 and to help test hypotheses developed for the present study. These three tern colonies on East Sand Island (46.263°N, 123.968°W), Rice Island (46.249°N, 123.716°W), and Three Mile Canyon Island (45.817°N, 119.963°W) also were under study by the authors during the 2000 breeding season. Average disturbance rate also was calculated at Crescent Island in 2001 to assess the conditions under which our study occurred. Disturbance rates were used instead of predation rates in this comparison because it was often difficult to determine if a predation event occurred during a disturbance, especially at large colonies. Additional observations of nest predation events are reported in this analysis to validate the assumption that disturbance rates reflect predation intensity at Caspian Tern colonies.

Nest Monitoring

Productivity plots were delineated by placing a large grid on the Caspian Tern colony before initiation of egg-laying, so that most of the colony was within the grid. The grid consisted of 5 m × 5 m plots that were created by placing brightly painted wooden stakes at each corner and connecting them with high-visibility nylon cord. The cord was then marked at one-meter intervals with brightly colored tags. These landmarks provided references so that each initiated Caspian Tern nest (whether it fell inside or outside a plot) could be mapped from an observation blind approximately 16 m from the edge of the tern colony. Nests were randomly selected for monitoring as they were initiated until early in the hatching period, so that monitored nests encompassed the range of breeding times at this asynchronous colony. These selected nests were then monitored from the blind a minimum of every third day throughout the course of the breeding season, so that productivity and chronology could be determined for each nest. In order to avoid encompassing re-nesting attempts, monitored nests were only included in the analysis if hatch date occurred within 30 days of when the nest was first initiated, the maximum incubation period in this species (Cuthbert and Wires 1999; Shuford and Craig 2002).

Productivity of a nest was defined as the number of surviving chicks at 20 days post-hatch, and the chronology of a nest was measured as the date on which the first chick hatched. Caspian Tern chicks do not fledge until they are approximately 37 days old (Cuthbert and Wires 1999); however, it was not possible to continue monitoring survival of young from a particular nest after about 20 days post-hatch, due to increased movements by the chicks and abandonment of the nest scrape by adults and their young. It was assumed that this measure of chick survival was highly correlated with fledging success and succeeded in capturing variation in productivity among nests.

Hatch date was determined by observing monitored nests for the presence of chicks; when nests were not examined on successive days, the midpoint of the dates when the colony was visited was recorded as the hatch date, following Mayfield (1975). Hatch date was a more accurate measure of nest chronology than lay date, because adults often sat on nest scrapes in incubation posture for several days before laying, but changed their posture and behavior at hatch.

Nest Site Characteristics

Spatial data were obtained on all initiated Caspian Tern nests (N = 676) early in the hatching period (15-17 May) using a rangefinder (Leica TCRA 1105) with an integrated reflectorless electronic distance meter accurate to ± 5 mm. Slope distance, horizontal angle, and vertical angle measurements for individual Caspian Tern nests were recorded, and later downloaded and converted to (x,y) coordinates using general trigonometric formulae. Coordinates were used to calculate nearest neighbor distance (m), distance to colony edge (m), and density of nests within a 5-m diameter circle (nests per m²) for each monitored nest. The colony edge was determined by importing nest coordinates into ArcView® software (Environmental Systems Research Institute, Inc.), and defining a polygon connecting the outermost Caspian Tern nests. Those nests situated on this polygon were defined as "edge point nests" and then used as a reference for calculating distance to colony edge. Coordinate data were then used to generate distances from each monitored nest to every other nest on the colony. From these data, the minimum distance between a monitored nest and any other nest was defined as the distance to its nearest neighbor, and the minimum distance to an "edge point nest" was defined as the distance to the colony edge. The number of nests with distances less than or equal to 2.5 m were summed and used to calculate nest density within a 5 m diameter circle of each monitored nest.

Grouping of Variables

Because data were not normally distributed, in order to examine relationships among variables, data were divided into discrete intervals, and data groups were compared nonparametrically. Nests were distinguished by density as either LOW (<1.0 nests per m²) or HIGH (≥1.0 nests per m²) density groups. Nests also were grouped by nearest-neighbor distance as either nests with NEAR (<0.75 m) or FAR (≥0.75 m) nearest neighbors. These groupings roughly bisected the range of densities and nearest-neighbor distances, as well as the number of data points. Distance to edge was used to group nests as either EDGE or CENTER nests. EDGE nests were defined as those < 2.5 m from the colony edge, or an average of three nests in from the colony edge, and all others as CENTER nests, following Brunton (1997). Timing of nest initiation was either assigned to one-week intervals, or grouped as EARLY or LATE nests. EARLY nests were defined as those with hatch dates within the first two and a half weeks of hatching (11-27 May), and LATE nests as those with hatch dates within the last two and a half weeks of hatching (28 May-14 June).

All observations in this study were made from a blind to minimize researcher disturbance and potential for nest failure. By mapping and monitoring nests from a blind and using a rangefinder to determine nest site characteristics, the data set was obtained without entering the colony, a necessary requirement in order to test density effects on productivity in an undisturbed colony. The colony was also never entered for any other research activities until the completion of this analysis.

Statistical Analyses

The nonparametric Kruskal-Wallis test was used to test for colony differences in disturbance rates and Wilcoxon rank-sum tests to examine effects of individual explanatory variables on productivity (nest density, nearest-neighbor distance, distance to colony edge, and hatch date) and to examine relationships between explanatory variables. Productivity was analyzed using Poisson log-linear regression for counts to assess relative effects of all explanatory variables. A main effects regression model including only nest density, nearest neighbor distance, distance to colony edge, and numerical hatch date was compared to a full model that included interaction, quadratic, and cubic terms to assess goodness-of-fit of the main effects model using a drop-in-deviance test. Because the full model did not significantly improve fit to the data ($\chi^2_{12} = 2.8$, n.s.), the main effects model was used as the inferential model for remaining analyses. Drop-in-deviance tests were used to assess significance of each main effect included in this analysis. All P-values are two-tailed, and the significance level was P = 0.05.

RESULTS

Disturbance Rates

Average disturbance rates differed among the four Columbia River Caspian Tern colonies during the 2000 breeding season (Kruskal-Wallis test, $\chi^2_3 = 70.9$, P < 0.001), and Crescent Island had the lowest average rate of disturbance (0.06 disturbances per hour, as compared to 3.3, 0.4, and 0.2 disturbances per hour at Three Mile Canyon, Rice, and East Sand islands, respectively). In 2001, the average disturbance rate at Crescent Island (0.1 disturbances per hour) did not differ from that observed on Crescent Island in 2000 (Z = 1.1, n.s.).

On Crescent Island in 2001, only one nest predation event was witnessed in > 250 hours of observation (0.004 nest predations per hour of observation): a California Gull preyed on a single tern egg during a disturbance event (unknown cause). At Rice Island in 2000, where disturbance rates were higher, 129 separate nest predation events were witnessed during approximately 470 observation hours (0.27 nest predations per hour of observation). Direct comparisons of the numbers of nest predation events between Crescent Island and Three Mile Canyon Island or East Sand Island were inappropriate because (1) high disturbance rates at Three Mile Canyon Island were related to nocturnal predation events by mink (*Mustela vison*; Antolos *et al.* 2004), and thus predation events were not witnessed directly; and (2) active gull control at East Sand Island in 2000 kept nest predation levels artificially low despite higher disturbance rates than at Crescent Island.

Productivity

At the Crescent Island tern colony, mean number of chicks at the nest on day 20 post-hatch was 1.54 and ranged from 0 to 3 (Table 1). Because some mortality occurred to Caspian Tern chicks between 20 days of age and fledging, this measure of productivity was higher than overall fledging success at Crescent Island in 2001 (1.02 fledglings per pair; Antolos 2003; Antolos *et al.* 2004). Productivity of Caspian Tern nests did not differ between LOW (N = 84) and HIGH (N = 108) density groups (Z = -1.3, n.s.; Table 2), contrary to our hypothesis. There was also no difference in productivity of nests with NEAR (N = 92) neighbors compared to those with FAR (N = 100) neighbors (Z = -0.4, n.s.). CENTER (N = 109) nests were more productive than EDGE (N = 83) nests at this colony (Z = 2.9, P < 0.01), and LATE (N = 70) nests were significantly closer to the edge than EARLY (N = 122) nests (Z = 6.3, P < 0.001), reflecting the overall pattern of nest initiation on the colony at Crescent Island (Fig. 1). There was a strong negative relationship between productivity and hatch date. EARLY nests were more productive than LATE nests (Z = 5.6, P < 0.001), and the negative trend was evident throughout the hatching period (Fig. 2). EARLY nests also had higher nest densities than LATE nests (Z = 4.7, P < 0.001), but there was no difference in nearest-neighbor distance between EARLY and LATE nests (Z = 1.3, n.s.). Nest density was not significantly associated with productivity after accounting for the main effects of nearest-neighbor distance, distance to colony edge, and numerical hatch date ($\chi^2_1 = 0.009$, n.s., drop-in-deviance test;

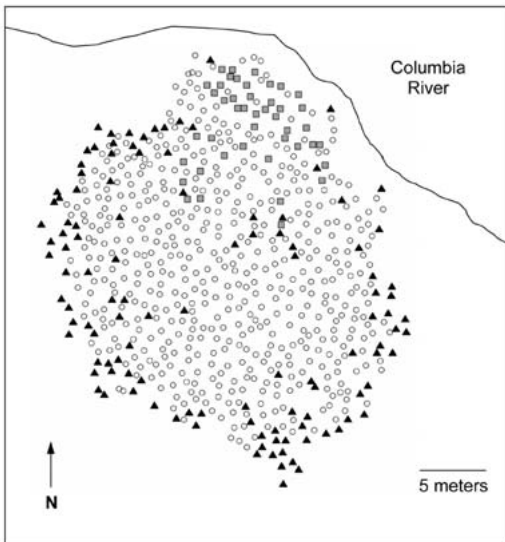**Table 1. Summary of characteristics of Caspian Tern nests (N = 192) monitored on Crescent Island in 2001.**

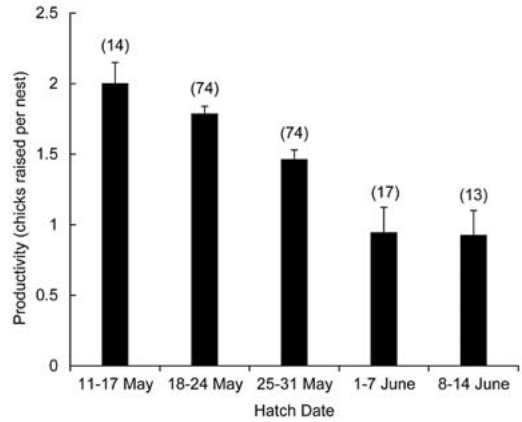|	Mean ± SD	Range
Productivity (chicks per nest)[a]	1.54 ± 0.65	0.00-3
Nest density (nests per m²)	0.97 ± 0.21	0.25-1.48
Nearest neighbor distance (m)	0.77 ± 0.15	0.35-1.50
Distance to colony edge (m)	3.73 ± 2.80	0.00-11.0
Hatch date (Julian days)	146.00 ± 6.72	131.00-165

[a]Measured at 20 days post-hatch.

Table 2. Productivity ± SD (N) of Caspian Tern nests monitored on Crescent Island, grouped by density, nearest neighbor distance, distance to colony edge, and timing of nest initiation.

	Productivity (chicks per nest)	
Nest density	HIGH	LOW
	1.60 ± 0.58	1.46 ± 0.72
	(108)	(84)
Nearest-neighbor distance	NEAR	FAR
	1.51 ± 0.67	1.57 ± 0.62
	(92)	(100)
Distance to colony edge	CENTER	EDGE
	1.67 ± 0.58	1.37 ± 0.69
	(109)	(83)
Hatch date	EARLY	LATE
	1.74 ± 0.54	1.20 ± 0.67
	(122)	(70)

Figure 2. Mean productivity ± SE (N) for Caspian Tern nests at the Crescent Island colony grouped by hatch date. Productivity differed significantly among groups ($\chi^2_4 = 42.9$, P < 0.001).

Table 3). Similarly, nearest-neighbor distance ($\chi^2_1 = 0.9$, n.s.) and distance to colony edge ($\chi^2_1 = 0.005$, n.s.) did not significantly affect productivity after accounting for the other variables in our inferential model. Hatch date was a significant factor after accounting for all other variables in the model ($\chi^2_1 = 9.7$, P < 0.01; Table 3).

Figure 1. Map of Caspian Tern nest locations relative to nest initiation on Crescent Island, 2001. Nests initiated by the first, third, and fifth week of egg laying are demarcated by a shaded square, open circle, and filled triangle, respectively.

DISCUSSION

Low disturbance rates at Crescent Island, and the observation that only one tern egg was lost to nest predators during the course of this study, support our assumption that nest predation was not an important source of egg or chick mortality at the Crescent Island colony. Contrary to our prediction, however, productivity of Caspian Terns at Crescent Island was not negatively associated with nest density. This suggests that intraspecific aggression did not cause significant mortality to chicks at Crescent Island, assuming that nest density and nearest-neighbor distance reflect the level of aggression experienced by chicks on the colony.

While EDGE nests were less productive than CENTER nests, distance to colony edge did not influence productivity after accounting for the effect of timing. This is due to the later initiation of EDGE nests, coupled with the strong negative relationship between productivity and nest initiation date. This suggests that analyses of edge effects on reproductive success of colonially nesting birds should account for nest initiation date to verify that position of the nest in the colony is the primary factor influencing nest success.

The relationship between timing of nest initiation and distance to the colony edge follows the central-periphery model of nest

Table 3. Poisson regression model of the main effects of nest density, nearest neighbor distance, distance to colony edge, and hatch date on productivity of Caspian Tern nests at Crescent Island in 2001. P-values are approximate two-sided values derived from Wald's tests for single coefficients.

Coefficients	Estimate	SE	Z-statistic	P-value
(Intercept)	5.070	1.69	2.99	0.003
Nest density	-0.030	0.37	-0.09	0.930
Nearest neighbor distance	0.130	0.41	0.31	0.760
Distance to colony edge	0.002	0.02	0.07	0.940
Hatch date	-0.030	0.01	-3.11	0.002

distribution (Coulson 1968; see Velando and Freire 2001). That is, in general, birds breeding in the center of a colony initiate nests earlier, and are thus more successful than those at the edge. The pattern of nest initiation at Crescent Island differed slightly from this general model, however, in that nest initiation started at the water's edge and expanded outward, with later nests filling in around the edges of the colony (Fig. 1). This suggests that patterns of nest initiation may be colony-specific and depend on local features. There was also some evidence that very late breeders initiated nests close to earlier, established nests (Fig. 1). This finding is consistent with the "central-satellite" distribution model proposed by Velando and Freire (2001). In that model, poorer-quality individuals initiate nests near a central, high-quality pair. Although this pattern only occurred in a small number of nests, these late breeders may be attempting to gain extra-pair fertilizations (Wagner *et al.* 1996), "commodities" (Danchin and Wagner 1997), or opportunities to acquire better sites and/or mates for the next breeding season (Aebischer *et al.* 1995; Velando and Freire 2001).

The strong negative relationship between hatch date and productivity demonstrates the importance of timing on the breeding success of Caspian Terns at this colony. Early nests were more productive, were in areas of higher nest density, and were generally further from the colony edge than late nests. The relationship between hatch date and productivity may be related to quality of adults, seasonal changes in food availability, or a combination of both. It has been demonstrated that early nesting birds are often older, more experienced individuals (e.g.,

Coulson and White 1958; Nisbet *et al.* 1984), and that seasonal declines in reproductive parameters, such as fledging success (Verhulst *et al.* 1995) and clutch size (Christians *et al.* 2001), may be attributable to quality of individuals alone. Within-cohort analyses (Perrins 1970) and food supplementation experiments (Brinkhof and Cavé 1997; Siikamäki 1998) have also provided evidence that declining food resources may provide the basis for seasonal declines in productivity.

At Crescent Island, seasonal declines in prey resources may have accounted for the strong effect of timing on breeding success. An analysis of Caspian Tern diet at Crescent Island demonstrated that during this study juvenile salmonids (*Oncorhynchus* spp.) comprised the majority of the diet (68%), and that the proportion of salmonids in the diet declined as the chick-rearing period progressed (Antolos *et al.* 2005). The decrease in salmonids in the diet of Crescent Island terns coincided with declines in the number of juvenile salmonids migrating through the mid-Columbia River late in the breeding season (Fish Passage Center 2003). This decline may signal a sharp drop in forage fish availability late in the nestling period, when chick food demand is greatest.

In addition, anecdotal evidence suggests that a major source of chick mortality at Crescent Island during this study was undernourishment. The following observations support this hypothesis: (1) Crescent Island tern chicks fledged at lower average mass than chicks at other Caspian Tern colonies in the Columbia River (D. E. Lyons and D. D. Roby, unpubl. data), (2) predation on tern chicks was never witnessed at Crescent Island during the 2001 breeding season, (3) no evi-

dence of nocturnal predation was found at this site, (4) there was no evidence of weather-related chick mortality, and (5) there were higher rates of kleptoparasitism by gulls at Crescent Island, compared to other Caspian Tern colonies in the Columbia River (Antolos 2003).

Our results indicate that variation in individual nest densities within the range observed at Crescent Island (0.25-1.48 nests per m²) does not negatively affect productivity of Caspian Terns. This information may be helpful for natural resource managers deciding minimum area requirements for breeding Caspian Terns at managed colony sites (e.g., at East Sand Island; Roby *et al.* 2002). Our data suggest that if colony area requirements are planned so that nest densities are maintained within the range observed at Crescent Island, density alone is not likely to affect the reproductive success of Caspian Terns.

LITERATURE CITED

Ackerman, S. M. 1994. American White Pelicans nest successfully at Crescent Island, Washington. Washington Birds 3: 44-49.
Aebischer, N. J., G. R. Potts and J. C. Coulson. 1995. Site and mate fidelity of Shags *Phalacrocorax aristotelis* at two British colonies. Ibis 137: 19-28.
Anderson, D. J. and P. J. Hodum. 1993. Predator behavior favors clumped nesting in an oceanic seabird. Ecology 74: 2462-2464.
Antolos, M. 2003. Breeding and foraging ecology of Caspian Terns (*Sterna caspia*) in the mid-Columbia River: predation on juvenile salmonids and management implications. M.S. thesis, Oregon State University, Corvallis.
Antolos, M., D. D. Roby and K. Collis. 2004. Breeding ecology of Caspian Terns at colonies on the Columbia Plateau. Northwest Science 78: 303-312.
Antolos, M., D. D. Roby, D. E. Lyons, K. Collis, A. F. Evans, M. Hawbecker and B. A. Ryan. 2005. Caspian Tern predation on juvenile salmonids in the mid-Columbia River. Transactions of the American Fisheries Society 134: 466-480.
Becker, P. H. 1995. Effects of coloniality on gull predation on Common Tern (*Sterna hirundo*) chicks. Colonial Waterbirds 18: 11-22.
Bent, A. C. 1921. Life histories of North American gulls and terns. U.S. National Museum Bulletin 113.
Birkhead, T. R. 1977. The effect of habitat and density on breeding success in the Common Guillemot (*Uria aalge*). Journal of Animal Ecology 46: 751-764.
Brinkhof, M. W. G. and A. J. Cavé. 1997. Food supply and seasonal variation in breeding success: an experiment in the European Coot. Proceedings of the Royal Society of London Series B 264: 291-296.
Brunton, D. H. 1997. Impacts of predators: center nests are less successful than edge nests in a large nesting colony of Least Terns. Condor 99: 372-380.
Butler, R. G. and W. Trivelpiece. 1981. Nest spacing, reproductive success, and behavior of the Great black-backed Gull (*Larus marinus*). Auk 98: 99-107.
Christians, J. K., M. Evanson and J. J. Aiken. 2001. Seasonal decline in clutch size in European Starlings: a novel randomization test to distinguish between the timing and quality hypotheses. Journal of Animal Ecology 70: 1080-1087.
Coulson, J. C. 1968. Differences in the quality of birds nesting in the centre and on the edges of a colony. Nature 217: 478-479.
Coulson, J. C. and E. White. 1958. The effect of age on the breeding biology of the Kittiwake *Rissa tridactyla*. Ibis 100: 40-51.
Cuthbert, F. J. and L. R. Wires. 1999. Caspian Tern (*Sterna caspia*). *In* A. Poole and F. Gill [Eds.], The Birds of North America, No. 403. The Birds of North America, Inc., Philadelphia, PA.
Danchin, E. and R. H. Wagner. 1997. The evolution of coloniality: the emergence of new perspectives. Trends in Ecology and Evolution 12: 342-347.
Davis, J. W. F. and E. K. Dunn. 1976. Intraspecific predation and colonial breeding in Lesser black-backed Gulls *Larus fuscus*. Ibis 118: 65-77.
Dexheimer, M. and W. E. Southern. 1974. Breeding success relative to nest location and density in Ring-billed Gull colonies. Wilson Bulletin 86: 288-290.
Fish Passage Center [online]. 2003. Historic daily passage data for the smolt monitoring project. <http://www.fpc.org/SMPDATA.html> (9 May 2003).
Götmark, F. and M. Andersson. 1984. Colonial breeding reduces nest predation in the Common Gull (*Larus canus*). Animal Behaviour 32: 485-492.
Hill, W. L., K. J. Jones, C. L. Hardenbergh and M. Browne. 1997. Nest distance mediates the costs of coloniality in Eared Grebes. Colonial Waterbirds 20: 470-477.
Houde, A. E. 1983. Nest density, habitat choice, and predation in a Common Tern colony. Colonial Waterbirds 6: 178-184.
Hunt, G. L., Jr. and M. W. Hunt. 1975. Reproductive ecology of the Western Gull: the importance of nest spacing. Auk 92: 270-279.
Hunt, G. L., Jr. and M. W. Hunt. 1976. Gull chick survival: the significance of growth rates, timing of breeding and territory size. Ecology 57: 62-75.
Kruuk, H. 1964. Predators and anti-predator behaviour of the Black-headed Gull (*Larus ridibundus* L.). Behaviour Supplement 11: 1-130.

Massoni, V. and J. C. Reboreda. 2001. Number of close spatial and temporal neighbors decreases the probability of nest failure and Shiny Cowbird parasitism in colonial Yellow-winged Blackbirds. Condor 103: 521-529.

Mayfield, H. F. 1975. Suggestions for calculating nest success. Wilson Bulletin 87: 456-466.

Nisbet, I. C. T., J. M. Winchell and A. E. Heise. 1984. Influence of age on the breeding biology of Common Terns. Colonial Waterbirds 7: 117-126.

Parsons, J. 1975. Seasonal variation in the breeding success of the Herring Gull: an experimental approach to pre-fledging success. Journal of Animal Ecology 44: 553-573.

Parsons, J. 1976. Nesting density and breeding success in the Herring Gull (*Larus argentatus*). Ibis 118: 537-546.

Patterson, I. J. 1965. Timing and spacing of broods in the Black-headed Gull *Larus ridibundus*. Ibis 107: 433-459.

Penland, S. 1981. Natural history of the Caspian Tern in Grays Harbor, Washington. Murrelet 62: 66-72.

Perrins, C. M. 1970. The timing of birds' breeding seasons. Ibis 112: 242-255.

Roby, D. D., D. P. Craig, K. Collis and S. L. Adamany. 1998. Avian predation on juvenile salmonids in the lower Columbia River. 1997 Annual report to the Bonneville Power Administration and U.S. Army Corps of Engineers, Portland, OR.

Roby, D. D., K. Collis, D. E. Lyons, D. P. Craig, J. Y. Adkins, A. M. Myers and R. M. Suryan. 2002. Effects of colony relocation on diet and productivity of Caspian Terns. Journal of Wildlife Management 66: 662-673.

Shuford, W. D. and D. P. Craig. 2002. Status assessment and conservation recommendations for the Caspian tern (*Sterna caspia*) in North America. U.S. Department of the Interior, Fish and Wildlife Service, Portland, OR.

Siegel-Causey, D. and S. P. Kharitonov. 1990. The evolution of coloniality. Current Ornithology 7: 285-330.

Siikamäki, P. 1998. Limitation of reproductive success by food availability and breeding time in Pied Flycatchers. Ecology 79: 1789-1796.

Velando, A. and J. Freire. 2001. How general is the central-periphery distribution among seabird colonies? Nest spatial pattern in the European Shag. Condor 103: 544-554.

Verhulst, S., J. H. van Balen and J. M. Tinbergen. 1995. Seasonal decline in reproductive success of the Great Tit: variation in time or quality? Ecology 76: 2392-2403.

Wagner, R. H., M. D. Schug and E. S. Morton. 1996. Condition-dependent control of paternity by female Purple Martins: implications for coloniality. Behavioral Ecology and Sociobiology 38: 379-389.

Wittenberger, J. F. and G. L. Hunt, Jr. 1985. The adaptive significance of coloniality in birds. Pages 1-78 *in* Avian Biology, Vol. VIII (D. S. Farner, J. R. King and K. C. Parkes, Eds.). Academic Press, Orlando, FL.