The Auk 117(3):634–639, 2000

INFLUENCE OF ENVIRONMENTAL AND DENSITY-DEPENDENT FACTORS ON REPRODUCTION OF LITTLE EGRETS

ROBERT E. BENNETTS,[1,3] MAURO FASOLA,[2] HEINZ HAFNER,[1] AND YVES KAYSER[1]
[1]*Station Biologique de la Tour du Valat, Le Sambuc, F-13200 Arles, France; and*
[2]*Dipartimento di Biologia Animale, Università, Piazza Botta 9, I-27100 Pavia, Italy*

ABSTRACT.—We evaluated the influence of environmental and density-dependent factors (intraspecific and interspecific) on clutch size, brood size, and nesting success of Little Egrets (*Egretta garzetta*) in the Camargue of southern France. We recorded these reproductive parameters in most years from 1970 to 1998. We used a generalized linear modeling approach (model selection based on AIC) to examine the environmental effects of spring rainfall, winter temperature, and wind on these parameters. We also examined density dependence of these parameters based on the total number of Little Egrets and the total number of tree-nesting herons nesting in these mixed-species colonies. Clutch size was positively associated with rainfall and negatively associated with the number of Little Egret nests in the Camargue. Brood size was negatively associated with the number of Little Egret nests, although rainfall was only significant as an interaction effect with these two effects. Nesting success was negatively associated with the number of tree-nesting herons, the proportion of each colony consisting of Cattle Egrets (*Bubulcus ibis*), wind speed, and several interactions among these variables. Virtually all of the reproductive parameters that we evaluated were negatively associated with the number of Little Egret nests or the number of tree-nesting herons. Anecdotal evidence suggests that Cattle Egrets displace Little Egrets at some centrally located nest sites. Such sites are better protected from strong winds, which are a common cause of nesting failure. *Received 20 November 1998, accepted 23 November 1999.*

DENSITY-DEPENDENT effects on avian reproduction are well known, although little evidence for such effects exists in wading birds (Butler 1994). In contrast, density-independent environmental factors are commonly reported to influence reproduction in this group. For example, Hafner et al. (1994) found that rainfall in winter and spring is correlated with clutch size and brood size of Little Egrets (*Egretta garzetta*). Extended periods of temperatures below freezing are correlated with wintering and subsequent breeding population size of Little Egrets (Hafner et al. 1994), although it is not known if subsequent effects influence reproductive success.

Since the mid-1980s, numbers of Little Egrets in the Camargue region of southern France have increased steadily (Hafner and Fasola 1997). Cattle Egret numbers (*Bubulcus ibis*) also have increased, from one nest in 1967 to a recent high of 3,532 nests in 1996 (H. Hafner unpubl. data). In the Camargue, anecdotal evidence suggests that Cattle Egrets occupy the center of colonies, where reproductive success of Little Egrets is higher (Hafner 1977). During nest building, Cattle Egrets frequently steal sticks from nearby nests (Valentine 1958), and sometimes they eject nest contents (Blaker 1969, Siegfried 1972). Given (1) an advantage of selecting certain nest sites, (2) increased numbers of Little Egrets and Cattle Egrets, and (3) aggressive behavior of Cattle Egrets, we hypothesized that intra- and interspecific density dependence related to nest-site acquisition could occur. Here, we evaluate the influence of environmental and density-dependent factors on clutch size, brood size, and nesting success of Little Egrets.

[3] E-mail: bennetts@tour-du-valat.com

METHODS

Study area.—Our study area was the Camargue (delta of the Rhone River in southern France), which comprises 180,000 ha and includes several colony sites and associated feeding areas used by Little Egrets (Hafner 1977, Hafner et al. 1982). The floodplain of the Rhone River has been confined within levees on either side of the delta since the early 1850s (Benoît 1933), and the habitat outside the delta complex generally is unsuitable for breeding or foraging (Hafner 1977). Thus, the spatial extent of the Camargue population of Little Egrets has remained largely the same for several decades (Hafner 1977, 1982). This population also is relatively isolated; the nearest major breeding areas are in Italy and Spain more than 400 km from the Camargue.

Breeding population size.—Little Egrets in the Camargue nest in trees, usually in mixed colonies with Cattle Egrets, Black-crowned Night-Herons (*Nycticorax nycticorax*), and Squacco Herons (*Ardeola ralloides*). Each year from 1967 to 1998, all colonies were located throughout the study area using a small aircraft (Hafner et al. 1994). From May to mid-July, each colony was censused weekly by the same observer (Hafner 1977). Each colony was partitioned into sectors of approximately 0.1 ha. Complete nest counts were conducted within each sector, and any new nests were added to the previous count during each subsequent visit. Based on repeated counts and marking of nests in a sample of sectors, we believe that overestimation was extremely unlikely and that the extent of underestimation was not substantial (e.g. <10% in the largest colonies).

Environmental variables.—We used the cumulative absolute value of daily minimum temperatures below 0°C (i.e. the sum of the negative values) as an indication of the severity of cold winter weather (Hafner et al. 1992, 1994). In accordance with Hafner et al. (1994), we used total cumulative rainfall between February and April as an indication of spring rainfall. A strong wind, known as the Mistral, occurs in the Camargue throughout the year and can be a substantial source of nesting failure (Valverde 1955, Hafner 1978). Thus, we used the cumulative sum of the maximum daily wind speed during the main nesting period (15 April to 15 June) as a measure of wind effects. Climatic data were provided by the Tour du Valat meteorological station, which is located in the center of the Camargue.

Reproductive parameters.—We assessed clutch size, brood size, and nesting success for a sample of colonies during most years (Table 1). Nests were marked along transects and their contents checked once a week. To reduce disturbance early in the breeding cycle, we recorded clutch size at 10% or fewer of the number of nests in large colonies and 20% or fewer in small colonies. We defined brood size as the number of chicks alive at 20 to 25 days of age. After this age, chicks can of escape by walking and may not be present at nests (H. Hafner unpubl. data). We considered a nest to be occupied with the laying of the first egg and successful if at least one young reached the age at which it was able to escape by walking. Because complete censuses were conducted weekly and nests were marked early during incubation, we did not expect a bias from finding nests in latter stages. Thus, we did not use the Mayfield (1961) estimator. Rather, nesting success was estimated as the proportion of occupied nests that was successful.

Data analysis.—Data were analyzed within a generalized linear modeling framework. We used log-linear models to assess effects of environmental and density-dependent explanatory variables on clutch size and brood size. We also included time (year) and colony effects as potential explanatory variables. We used logistic regression to explore the factors influencing nesting success. Model selection was based on Akaike's Information Criterion (AIC; Akaike 1973, Burnham and Anderson 1998). We checked the validity of a Poisson assumption using the model deviance divided by its degrees of freedom (SAS 1997, Burnham and Anderson 1998). We also checked for temporal autocorrelation by testing the association between the residuals of fitted models at times t and $t - 1$.

TABLE 1. Annual estimates of mean clutch size, mean brood size, and proportion of nests successful for Little Egrets in southern France. Number of nests is in parentheses.

Year	Clutch size	Brood size	Nesting success
1970	4.30 (156)	—	0.96 (142)
1971	4.39 (57)	—	0.90 (58)
1972	4.34 (215)	—	0.91 (115)
1973	—	—	—
1974	—	—	—
1975	—	3.02 (176)	—
1976	—	3.30 (152)	—
1977	—	3.19 (117)	—
1978	—	3.10 (80)	—
1979	—	3.05 (150)	—
1980	—	3.06 (178)	—
1981	—	2.90 (221)	—
1982	4.16 (58)	2.89 (189)	0.95 (57)
1983	—	3.09 (144)	—
1984	3.80 (51)	2.60 (279)	0.91 (54)
1985	—	3.31 (185)	—
1986	4.71 (135)	3.35 (155)	0.94 (156)
1987	4.43 (30)	3.27 (137)	0.88 (49)
1988	4.20 (97)	3.12 (136)	0.92 (122)
1989	3.83 (100)	2.98 (160)	0.88 (117)
1990	4.17 (106)	2.97 (207)	0.85 (148)
1991	3.86 (117)	2.79 (163)	0.63 (173)
1992	4.02 (120)	2.69 (199)	0.81 (155)
1993	3.85 (121)	3.02 (325)	0.89 (132)
1994	4.03 (121)	2.78 (297)	0.92 (122)
1995	4.13 (104)	2.63 (238)	0.78 (147)
1996	3.92 (79)	2.66 (277)	0.78 (151)
1997	3.45 (60)	2.42 (358)	0.79 (73)
1998	3.99 (116)	2.47 (283)	0.86 (121)

RESULTS

Our selected model indicated that mean clutch size was positively associated with rainfall ($\chi^2 = 11.67$, df = 1, $P < 0.001$) and negatively associated with the total number of Little Egret nests ($\chi^2 = 8.85$, df = 1, $P = 0.003$; Fig. 1). The model did not exhibit a substantial

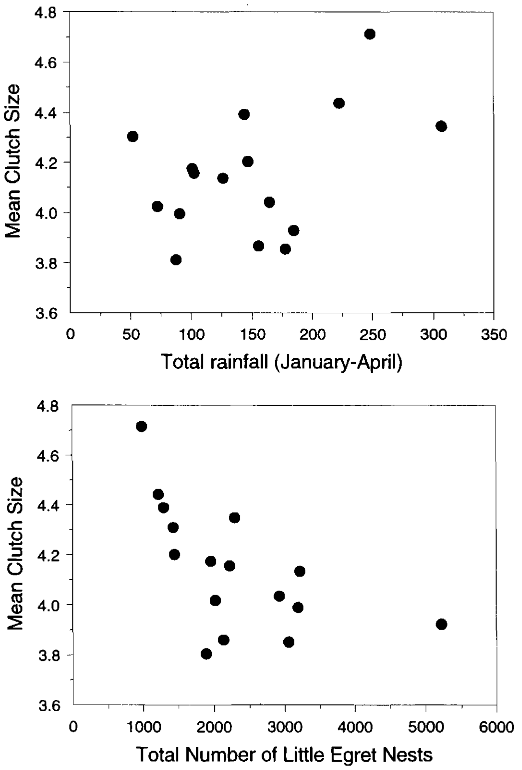

FIG. 1. Annual clutch size relative to total rainfall (upper) and total number of Little Egret nests in the study area (lower).

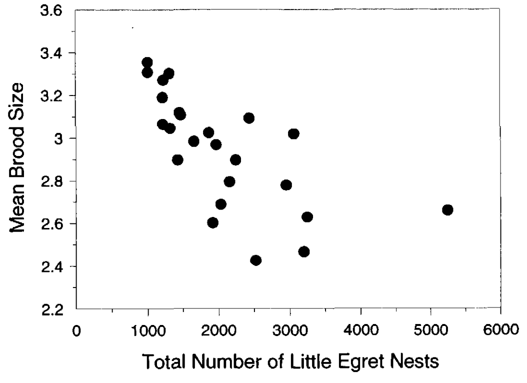

FIG. 2. Annual brood size relative to total number of Little Egret nests in the study area.

amount of overdispersion with respect to a Poisson assumption (deviance/df = 1.3), nor was there evidence of temporal autocorrelation of the residuals.

Brood size also was negatively associated with the total number of Little Egret nests ($\chi^2 = 18.36$, df = 1, $P < 0.001$; Fig. 2). Cumulative rainfall was not significant as a main effect ($\chi^2 = 0.25$, df = 1, $P = 0.617$) but was retained in our selected model because of its significance in an interaction term with the number of Little Egret nests ($\chi^2 = 8.31$, df = 1, $P = 0.004$). Our final model indicated a small degree of overdispersion with respect to a Poisson assumption (deviance/df = 2.3); however, adjusting for overdispersion using a quasi-likelihood framework (SAS 1997, Burnham and Anderson 1998) did not change which model was selected, and the significance of explanatory effects changed only slightly. As with clutch size, we found no evidence of temporal autocorrelation of the residuals.

Our final model of nesting success indicated an effect of the total number of tree-nesting herons, the proportion of the colony consisting of Cattle Egrets, wind speed, and several interactions among these variables (Table 2). The total number of tree-nesting herons and the proportion of Cattle Egrets in colonies were negatively associated with nesting success (Fig. 3). Wind speed was not significant as a main effect, but it contributed strongly to two inter-

TABLE 2. Maximum-likelihood analysis of variance table for final logistic regression model of nesting success of Little Egrets in southern France.

Source	χ^{2a}	df	P
Year	8.48	1	< 0.001
Total population size of tree-nesting herons (TPS)[b]	2.26	1	0.133
Proportion of colony consisting of Cattle Egrets (PCE)	18.29	1	<0.001
Wind[b]	0.87	1	0.350
TPS × PCE	33.15	1	<0.001
PCE × wind	29.56	1	<0.001
TPS × PCE × wind	41.86	1	<0.001

[a] Based on type 3 likelihood-ratio statistics and thus not dependent on order within model (SAS 1987).
[b] Not significant at $\alpha = 0.05$ as main effect, but retained because of significance in interactions.

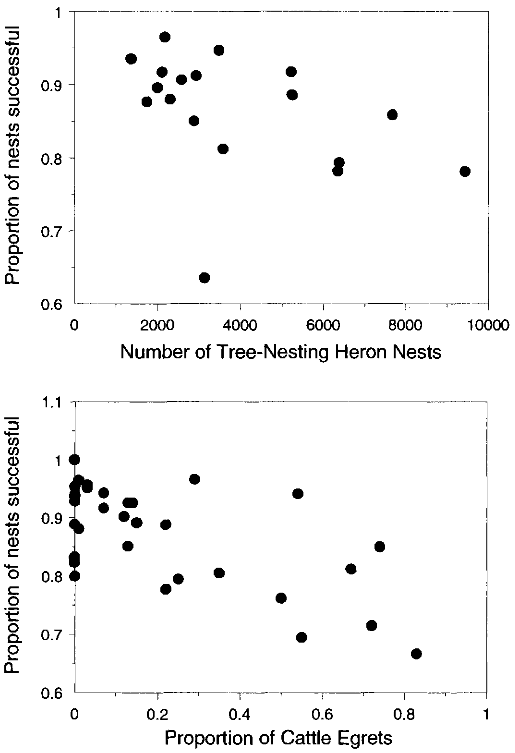

FIG. 3. Annual proportion of nests that were successful relative to total number of tree-nesting herons (upper) and proportion of each colony consisting of Cattle Egrets (lower).

action effects. In contrast to clutch and brood size, the residuals of our fitted model of nesting success exhibited temporal autocorrelation without the inclusion of an additional year effect, which was also supported by AIC and therefore included in our final model. An anomalous event (seen only once since 1967) occurred during 1986 where Eurasian Jackdaws (*Corvus monedula*) nesting in proximity to one small colony destroyed our entire sample of nests for that colony. Because the jackdaws probably used the disturbance of our visit to gain access to nests while the parents were off their nests, we excluded this colony from our analysis. Removal of this colony from analysis did not alter our general results but would have introduced an additional colony effect and colony × year interaction.

DISCUSSION

Environmental effects.—Severely cold winters reportedly affect winter and subsequent breeding population size of Little Egrets in the Camargue (Hafner et al. 1994). However, our analysis did not indicate a subsequent influence of winter temperature on reproductive parameters. An association between rainfall preceding the breeding season and reproductive success also has been reported for several species of herons (e.g. Ogden et al. 1980, Bancroft et al. 1988, Bildstein et al. 1990, Maddock and Baxter 1991), including the Little Egret (Hafner et al. 1994). Rainfall was the primary environmental influence we observed on clutch size and brood size. Years of higher rainfall correspond with a greater surface area of Little Egret foraging habitat (Hafner et al. 1994), and prolonged periods without surface water in freshwater marshes can result in prey die offs (Frederick and Collopy 1989). Although rainfall preceding the breeding season may have positive benefits related to foraging habitat, rainfall during the breeding season has been known to result in colony abandonment in some North American wetlands (e.g. Frederick and Collopy 1989). Such an effect was not apparent in the Camargue.

Wind had a significant effect on nesting success, but only as an interaction term with density- dependent effects. High winds can result in collapsed nest structures, particularly when nests are located on the edge of a colony where they have a more direct exposure without the sheltering effects of adjacent trees. Mistral winds in the Camargue typically are out of the north. Thus, nests on the north ends of colonies also are more likely to be susceptible to wind damage. During some years (e.g. 1991), high winds can cause a substantial decrease in overall nesting success.

Density-dependent effects.—Density-dependent reproduction has been observed in many animal populations (Sinclair 1989, Woiwod and Hanski 1992, Holyoak and Baillie 1996). Despite evidence for density-dependent effects on reproduction in other waterbirds (Gaston et al. 1983, Birkhead and Furness 1985, Hunt et al. 1986), evidence generally has been lacking for such effects on ardeids. Recently, Butler (1994) noted the general lack of evidence for density dependence in the reproduction of wading birds. Although our data are correlative, and inferences regarding causality are therefore limited, they are in contrast to Butler's assessment in that they indicate density-dependent effects on reproduction of Little Egrets in the Camargue. Virtually all of the reproductive parameters we evaluated were negatively associated with the number of nesting Little Egrets and/or other tree-nesting herons. In each case, the association was explained better by numbers of herons than by a linear trend over time (i.e. clutch and brood size), or was in addition to a linear trend (i.e. nesting success).

Competition for nest sites in the Camargue may occur because suitable undisturbed stands of trees are quite limited (Hafner 1982). Given the substantial increase in the number of Cattle Egrets in the Camargue since 1967, the potential for interspecific competition for nest sites also is likely to have increased, especially considering the aggressive nature of Cattle Egrets with respect to nest sites (Blaker 1969, Siegfried 1972). Our data suggest that nesting success of Little Egrets is density dependent only when considered in the interaction with the proportion of Cattle Egrets in nesting colonies. Prior to widespread distribution of Cattle Egrets in the Camargue, Hafner (1977) documented a relationship between nesting success of Little Egrets and the position of the nest relative to the center or edge of the colony. Nests on the periphery of a colony were more susceptible to damage from wind than those located more centrally (Hafner 1977). Anecdotal observations suggest that Cattle Egrets tend to occupy the more central locations of colonies in the Camargue and may even displace Little Egrets from these sites. This is currently being investigated, and if it occurs, it may provide a mechanism for the negative effect on nesting success. The phenomenon also would explain the interaction that we observed between the number and proportion of Cattle Egrets and wind.

Dhondt et al. (1992) postulated that density-dependent decreases in reproduction occurred because of more frequent occupation of relatively poor habitats at higher densities (thereby reducing overall breeding success). The spatial distribution of heron colonies within the Camargue has remained essentially the same throughout the study (Hafner 1977, 1982). Thus, increases in density have not resulted in spatial expansion of colonies into previously unused habitats. However, our results do not preclude the possibility that Little Egrets are using poorer nest sites within colonies.

ACKNOWLEDGMENTS

We appreciate the helpful comments of Gaëtan Lefebvre, Douglas Mock, Brigitte Poulin, and two anonymous reviewers. This work was carried out under license of the French Ministry of Environment and the CRBPO (French National Ringing Center). We are grateful for the support provided by Station Biologique de la Tour du Valat.

LITERATURE CITED

AKAIKE, H. 1973. Information theory and an extension of the maximum likelihood principle. Pages 267–281 *in* Proceedings of the 2nd International Symposium on Inference Theory (B. N. Petran and F. Csáki, Eds.). Akadémiai Kiadi, Budapest, Hungary.

BANCROFT, G. T., J. C. OGDEN, AND B. W. PATTY. 1988. Colony formation and turnover relative to rainfall in the Corkscrew Swamp area of Florida during 1992 through 1985. Wilson Bulletin 100:50–59.

BENOÎT, F. 1933. La Camargue. Henri Laurens Press, Paris.

BILDSTEIN, K. L., W. POST, J. JOHNSTON, AND P. C. FREDERICK. 1990. Freshwater wetlands, rainfall, and the breeding ecology of White Ibises in coastal South Carolina. Wilson Bulletin 102:84–98.

BIRKHEAD, T. R., AND R. W. FURNESS. 1985. Regulation of seabird populations. Pages 145–163 *in* Behavioural ecology (R. M. Sibly and R. H. Smith, Eds.). Blackwell Science Publishers, Oxford.

BLAKER, D. 1969. Behaviour of the Cattle Egret *Ardeola ibis.* Ostrich 40:75–129.

BURNHAM K. P., AND D. R. ANDERSON. 1998. Model selection and inference: A practical-theoretic approach. Springer-Verlag, New York.

BUTLER, R.W. 1994. Population regulation of wading ciconiiform birds. Colonial Waterbirds 17:189–199.

DHONDT, A. A., B. KEMPENAERS, AND F. ADRIAENSEN. 1992. Density-dependent clutch size caused by habitat heterogeneity. Journal Animal Ecology 61:643–648.

FREDERICK, P. C., AND M. W. COLLOPY. 1989. Nesting success of five ciconiiform species in relation to water conditions in the Florida Everglades. Auk 106:625–634.

GASTON, A. J., G. CHAPDELAINE, AND D. G. NOBLE. 1983. The growth of Thick-billed Murre chicks in colonies in Hudson Strait: Inter- and intra-colony variation. Canadian Journal Zoology 61: 465–475.

HAFNER, H. 1977. Contribution a l'étude de quatre espéces de herons (*Egretta garzetta* L., *Ardeola ralloides* Scop., *Ardeola ibis* L., *Nycticorax nycticorax* L.) pendant leur nidification en Camargue.

Ph.D. dissertation, University Paul Sabatier, Toulouse, France.

HAFNER, H. 1978. Le succès de reproduction de quatre espèces d'Ardeidés *Egretta g. garzetta* L., *Ardeola r. ralloides* Scop., *Ardeola i. ibis* L., *Nycticorax n. nycticorax* L. en Camargue. Revue Ecologie (Terre Vie) 32:279–289.

HAFNER, H. 1982. Creation of a breeding site for tree-nesting herons in the Camargue, southern France. Pages 216–220 *in* Managing wetlands and their birds (D.A. Scott, Ed.). International Waterfowl and Wetlands Research Bureau, Slimbridge, United Kingdom.

HAFNER, H., V. BOY, AND G. GORY. 1982. Feeding methods, flock size and feeding success in the Little Egret *Egretta garzetta* and the Squacco Heron *Ardeola ralloides* in Camargue, southern France. Ardea 70:45–54.

HAFNER, H., AND M. FASOLA. 1997. Long-term monitoring and conservation of herons in France and Italy. Colonial Waterbirds 20:298–305.

HAFNER, H., Y. KAYSER, AND O. PINEAU. 1994. Ecological determinants of annual fluctuations in numbers of breeding Little Egrets *Egretta garzetta* in the Camargue, S. France. Revue Ecologie (Terre Vie) 49:53–62.

HAFNER, H., O. PINEAU, AND J. P. WALLACE. 1992. The effects of climate on the size of the Cattle Egret (*Bubulcus ibis* L.) population in the Camargue. Revue Ecologie (Terre Vie) 47:403–410.

HOLYOAK, M., AND S. R. BAILLIE. 1996. Factors influencing the detection of density dependence in British birds. Oecologia 108:54–63.

HUNT, G. L., Z. A. EPPLEY, AND D. C. SCHNEIDER. 1986. Reproductive performance of seabirds: The importance of population and colony size. Auk 103:306–317.

MADDOCK, M., AND G. S. BAXTER. 1991. Breeding success of egrets related to rainfall: A six-year Australian study. Colonial Waterbirds 14:133–139.

MAYFIELD, H. F. 1961. Nesting success calculated from exposure. Wilson Bulletin 73:255–261.

OGDEN, J. C., H. W. KALE, AND S. A. NESBITT. 1980. The influence of annual variation in rainfall and water levels on nesting by Florida populations of wading birds. Transactions of the Linnaean Society of New York 9:115–126.

SAS INSTITUTE. 1997. SAS/STAT software: Changes and enhancements through release 6.12. SAS Institute, Inc., Cary, North Carolina.

SIEGFRIED, W. R. 1972. Breeding success and reproductive output of the Cattle Egret. Ostrich 43:43–55.

SINCLAIR, A. R. E. 1989. Population regulation in animals. Pages 197–241 *in* Ecological concepts (J. M. Cherrett, Ed.). Blackwell Science Publishers, Oxford.

VALENTINE, J. M. 1958. The Cattle Egret at Chincoteague, Virginia. Raven 29:68–95.

VALVERDE J. A. 1955. Essai sur l'Aigrette garzette (*Egretta g. garzetta*) en France. Alauda 23:147–171.

WOIWOD, I. P., AND I. HANSKI. 1992. Patterns of density dependence in moths and aphids. Journal of Animal Ecology 61:619–629.

Associate Editor: J. S. Sedinger