Ecological determinants of annual fluctuations in numbers of breeding Little Egrets (*Egretta garzetta* L.) in the Camargue, S. France

Heinz Hafner, Olivier Pineau, Yves Kayser

Résumé

Les Aigrettes garzettes qui nichent en Camargue ont été dénombrées chaque année entre 1968 et 1992. Pendant cette période, aucune tendance significative n'a pu être mise en évidence, même si d'une année à l'autre la population est passée du simple au double.
Une régression multiple a montré que le nombre d'aigrettes qui hivernent avec succès explique 53 % de la variation annuelle du nombre de nicheurs la saison suivante. Par contre, c'est le nombre de poussins envolés la saison précédant l'hivernage et la rigueur de l'hiver qui sont les deux variables responsables à 50 % de la variation de l'effectif des hivernants.
A la suite du froid rigoureux de janvier 1985 qui a décimé les hivernants, la population a rapidement comblé son déficit. Les conditions hydrologiques favorables dues aux pluies de l'hiver et du printemps ont permis aux quelques nicheurs de se reproduire avec succès. Les hivers suivants furent cléments et ont facilité la survie de nombreux oiseaux jusqu'à la saison de reproduction suivante.

Abstract

The number of Little Egrets breeding in the Camargue was determined annually from 1968 to 1992. The population shows no statistically significant trend over the 25 years, but fluctuated several times by a factor of 2 from one year to the next. Multiple regression analysis revealed that the number of Egrets remaining in the Camargue after the breeding season and surviving the winter in this area explains 53 % of the year to year variation in population size. The number of overwintering birds, in turn, depends on the number of young fledged during the preceding summer and winter severity, the two variables explaining 50 % of the variation.
After an important decline in 1985, due to a hard winter which caused the death of many Egrets (January 1985), the population recovered quickly. Fewer birds nested and favourable hydrological conditions due to winter-spring rainfall increased breeding success. Several consecutive winters were also mild and this allowed many Egrets to survive in the Camargue until the next breeding season.

ECOLOGICAL DETERMINANTS OF ANNUAL FLUCTUATIONS IN NUMBERS OF BREEDING LITTLE EGRETS (*EGRETTA GARZETTA* L.) IN THE CAMARGUE, S. FRANCE

Heinz HAFNER*, Olivier PINEAU* and Yves KAYSER*.

The Little Egret is a common breeding bird in the Camargue, delta of the river Rhône (Southern France). Each year 1000 to 2500 pairs nest in copses, usually together with Cattle Egrets (*Bubulcus ibis* L.), Night Herons (*Nycticorax nycticorax* L.), and Squacco Herons (*Ardeola ralloides* Scop.). Monospecific colonies of Little Egrets are rare and have only been found in the southern part of the delta, where brackish and saltwater lagoons form the main feeding area. One such monospecific colony existed from 1970 to 1976 and in 1983.

A proportion (0 to 30 %) of Camargue Little Egrets also winter in the Rhône delta and the neighbouring wetlands, depending on the severity of weather conditions during that part of the year. Migratory Little Egrets originating from the Camargue can move as far as tropical West-Africa, but the majority winter along the Mediterranean coast of France and Spain (Pineau, 1992). Over the past 25 years the breeding population has fluctuated considerably on three occasions, by a factor of 2 from one year to another. This paper aims to provide an insight into the variables at local scale (Camargue) affecting population size.

I. — *STUDY AREA AND METHODS*

Population size in summer and in winter

The number of occupied Egret nests was determined annually from 1968 to 1992. The 1800 km^2 area prospected each year stretches from the Plan du Bourg in the east to the île de la Camargue and the Petite Camargue to the west and includes a breeding area just to the west of the town of Aigues-Mortes (Fig. 1). Each year a small low flying plane was used to locate all the colonies in this area which is known to hold the total breeding population of the Camargue delta complex. In each breeding colony a census was carried out every 10 days between May 20 and July 31. Several visits are necessary during the breeding season because the chicks raised by early breeders fledge by the middle of June and late

* Station biologique de la Tour du Valat, Le Sambuc, F-13200 Arles.

broods are still found at the end of July. The census, which is based on direct and absolute nest counts through visual and auditive contacts, was carried out each year by the same observer. Counting errors increase with colony size, with up to 10 % underestimation in experimental plots, while overestimation is unlikely (Hafner, 1977).

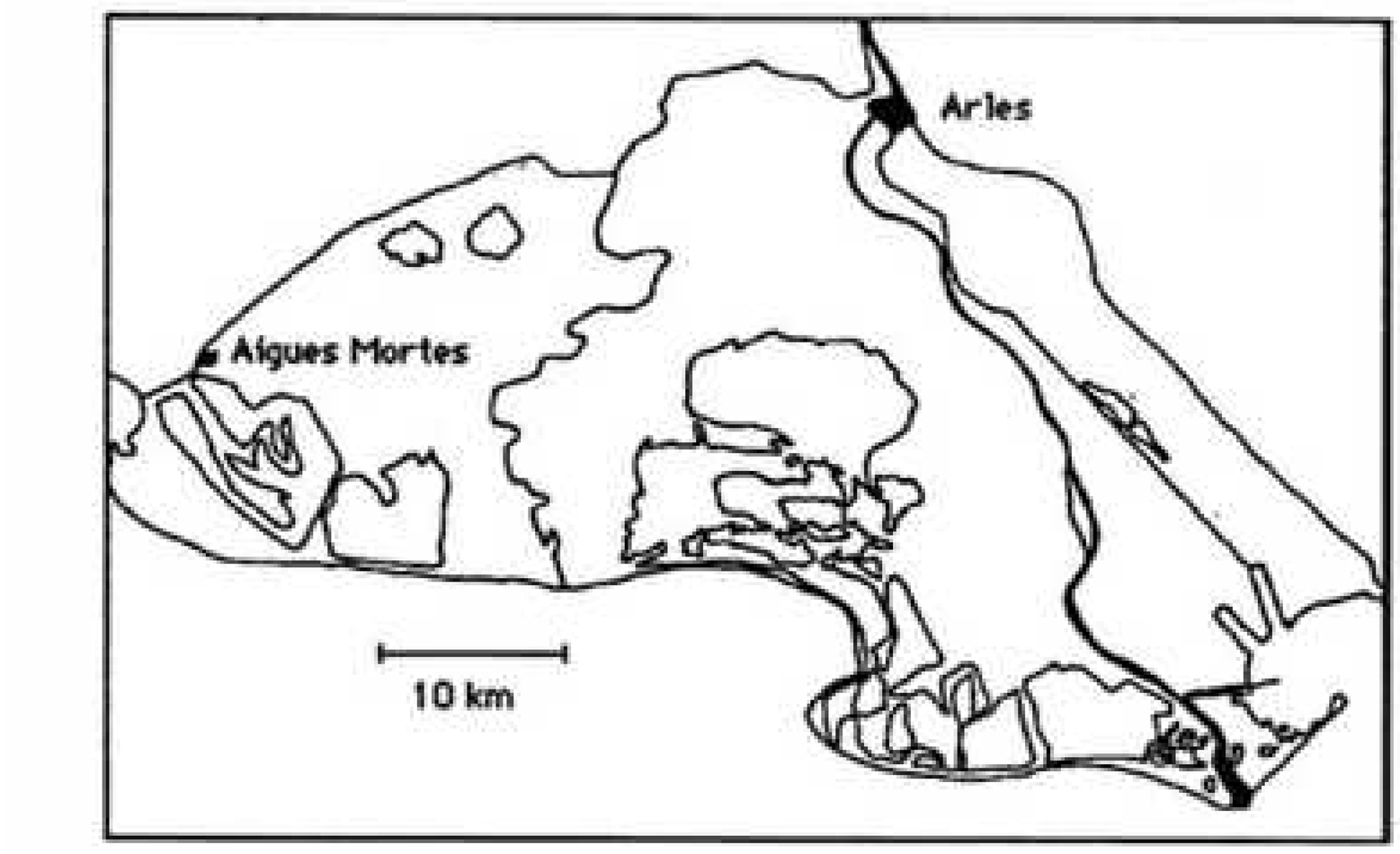

Figure 1. — The study area.

In order to gather information on the number of overwintering birds, monthly censuses were made from December 15 to February 20 at all known roosts in the area. Whenever possible, these were counted simultaneously by ornithologists from the « Station Biologique de la Tour du Valat », the« Réserve Nationale de Camargue » and the « Conservatoire de l'Espace Littoral et des Rivages Lacustres ». The lowest numbers of Little Egrets were usually recorded in January, sometimes in February. For each year, this minimum count is used as an index of the number of birds having survived the Camargue winter, and referred to as the number of overwintering birds .

Data on body condition

Chick condition was defined as the ratio of the actual body weight to the weight predicted from the regression of body weight on tarsus length for 4710 chicks measured in the Camargue between 1983 and 1992. Similarly, a total of 487 adult Egrets captured at the nest during the late stages of incubation (Pineau *et al.*, 1992) were weighed and measured over 9 breeding seasons. Adults vary considerably in size according to sex, wing length being the best independent measure of body size. Therefore the ratio body weight/wing length was used as an indicator of relative body condition of adults.

The regressions of body weight on tarsus length (chicks up to 25 days of age), and of body weight on wing length (adults) were linear :

Chicks : Weight (g) = 7.002 * Tarsus (mm) − 99.31 (R^2 = 0.88 ; $p < 0.001$).
Adults : Weight (g) = 3.621 * Wing (mm) − 534.16 (R^2 = 0.50 ; $p < 0.001$).

A body condition index of 1.1 thus means that the individual concerned had a body mass 10 percent in excess of the mean value for all birds of that size class.

Clutch size

In eight of the years it was possible to visit the colonies early in the year to obtain data on clutch size. Nests were marked in the different colonies and their content checked once a week. Clutch size was defined as the maximum number of eggs present before hatching occurred (mean incubation time is 22 days). In small colonies (< 50 pairs) most of the nests could be marked, while a minimum of 10 % of nests were marked in the large colonies.

Brood size

As the closest possible measure to fledging success, brood size was measured in the different colonies, just before the oldest chick in a brood was able to fly (at an age of about 30 days). The number of chicks present was determined by counting the number of chicks begging when a parent arrived to feed the brood. Eighteen years data (1975-1992) are available with a yearly mean sample size of 168 nests $\pm$ 52 S.D.). Each year, the sample reached around 10 % of the total population which ranged from 1015 to 2456 nests. The total number of young fledged per year was estimated by multiplying the weighted means (several colonies of different size) of brood size by the total number of nests.

Feeding ecology

To interpret the variation in reproductive success, data on feeding conditions and distribution were collected during several breeding seasons (Hafner *et al.*, 1982, 1986 ; Hafner & Britton, 1983 ; Reeders, 1983 ; Erwin *et al.*, 1985 ; Dugan *et al.*, 1986 ; Cezilly *et al.*, 1990 ; Kersten *et al.*, 1991 ; Hafner *et al.*, 1993). For most of the colonies, freshwater marshes are the major feeding sites. Two important colonies, however, are located near the extensive feeding areas, locally called « sansouire », to the east and south of the large central lagoon « Vaccarès » (Fig. 1). We defined « sansouire » as a low lying *Salicornietum* which, after heavy rainfall, floods and communicates with fish reservoirs such as canals, freshwater marshes or brackish lagoons from which fish can enter the sansouire. Flooded « sansouire » is often intermingled with temporary marshes. If the hydrological conditions allow exploitation of this habitat, it is widely used by the Egrets nesting in the « sansouire » colonies (Pineau *et al.*, in prep.).

Climatic variables

The data on climatic variables were provided by the Tour du Valat meteorological station. Data on population size, body condition, clutch size and brood size were examined in relation to rainfall (absolute values, mm) from autumn to spring (9 monthly blocks of rainfall : September-April, plus blocks for all possible combinations of consecutive months).

To examine the effects of winter severity, a *cold index* was calculated : the sum of the absolute values of the minimum daily temperature below 0° C between December 1st and February 28th.

Statistical analysis

Data on bird numbers and climatic variables were log-transformed : Log (x + 1) and submitted to linear and multiple stepwise regression analysis, using the least squares adjustment (Foucard and Lafaye, 1983). To relate clutch size and brood size to the amount of rainfall, the data on clutch size and brood size were converted into yearly weighted means, taking into account the size of the different colonies.

II. — *RESULTS*

The Camargue population

The population size over the 25 years 1968-1992 has not significantly declined or increased, but shows very large fluctuations over the period, with three peaks of over 2000 pairs in 1972, 1982-1983 and 1991-1992 (Fig. 2). One of the three strong declines (1976) was due, at least in part, to human disturbance during the incubation period followed by colony desertion (Hafner, unpublished). The lowest population levels recorded in 1985 and 1986 are the result of a severe winter (Hafner et *al.*, 1992).

The main factors affecting population size

The year to year variation in the size of the breeding population, and in the number of overwintering birds were investigated by multiple step-wise regression

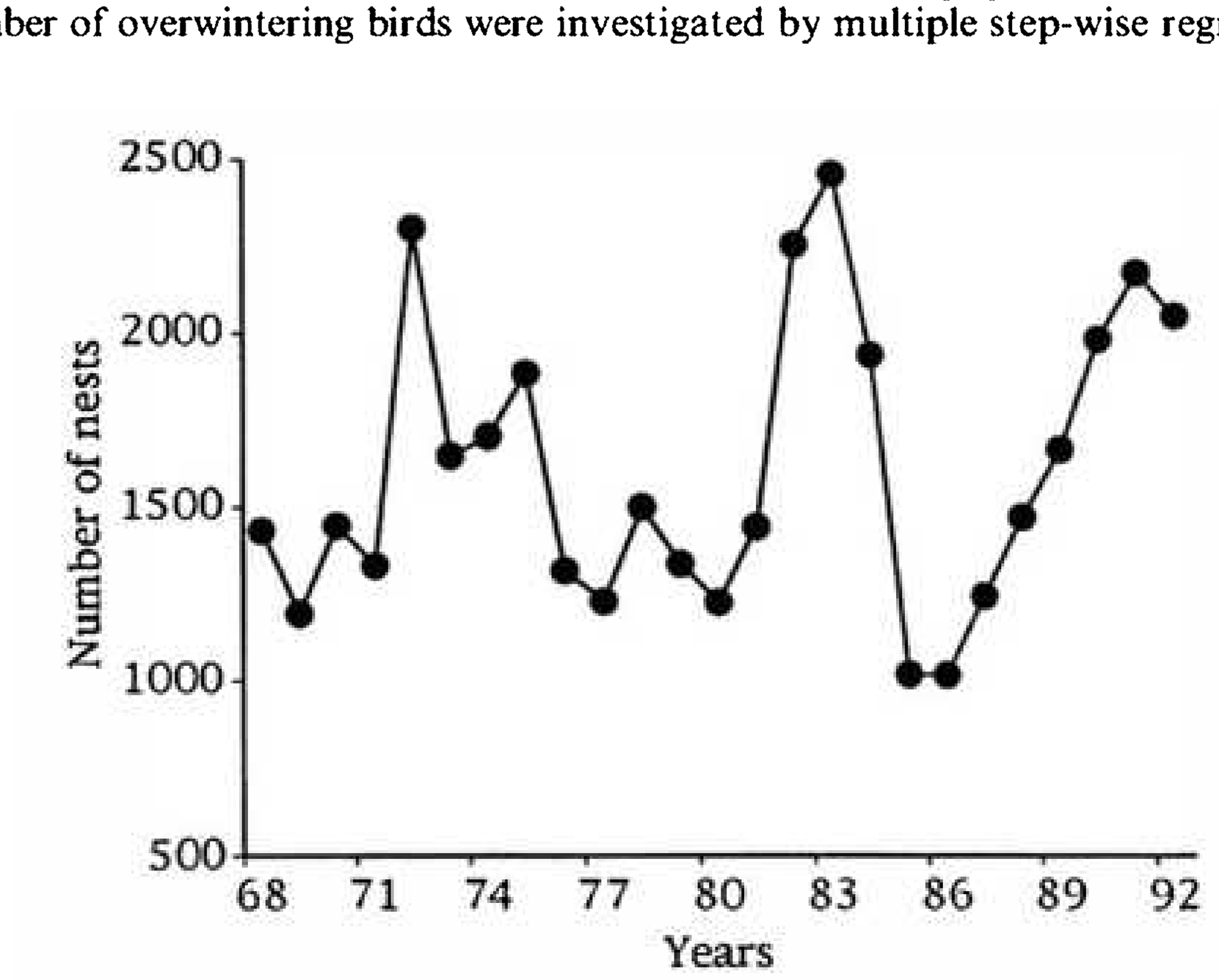

Figure 2. — Size of the Camargue population (1968-1992).

analyses, using as explicative variables : 1) the number of wintering birds, 2) the amount of rainfall at different periods, 3) the cold index, 4) the number of young fledged (n nests * weighted mean brood size) 1, 2 and 3 seasons previously, 5) the total number of birds at the end of the breeding season (n adults = n nests * 2, plus the number of young fledged) the previous season, but also 2 and 3 years earlier. Variation in the size of the breeding population was mostly explained by the number of birds overwintering in the Camargue during the winter preceding the breeding season. Its contribution is important ($R^2 = 0.53$; n = 17). The number of overwintering birds, in turn, appeared to depend on two factors : (1) the number of young fledged during the preceding summer ($R^2 = 0.24$) and (2) winter temperatures, the two variables combined explaining 50 % of the variation ($R^2 = 0.50$).

To summarize, the two main population parameters for predicting population size are (1) the number of overwintering birds recorded during the preceding winter, and (2) the number of young fledged the previous season. The number of young fledged two and three years previously did not affect the size of the population (Tab. I).

TABLE I

Correlation coefficients, r, for the relationship between the number of young produced and population size in subsequent years.

Log number of young	Log population size in year N
Year N − 1	r = 0.63, n = 17, = 0.007
Year N − 2	r = -0.08, n = 16, n.s.
Year N − 3	r = -0.47, n = 15, n.s.

Nineteen years data are available for illustrating the relationship between the number of overwintering birds and the size of the breeding population the following summer (Fig. 3).

Reproductive output

Reproductive success as measured by the size of the brood shortly before fledging shows strong variation from year to year and in some years from one colony to another (Hafner et *al.*, 1986 and 1993). To identify the different causes of variation implies separate analyses for each colony.

Here we examine the relationship between winter-spring rainfall and overall reproductive output, as the size of many feeding areas depends primarily on rainfall. Mean yearly clutch size correlated strongly with the amount of rainfall in January-February (Fig. 4), suggesting an early season effect of hydrological conditions. The black dots (Fig. 4 and 5) represent all the colonies investigated, the white dots the « sansouire » colonies only.

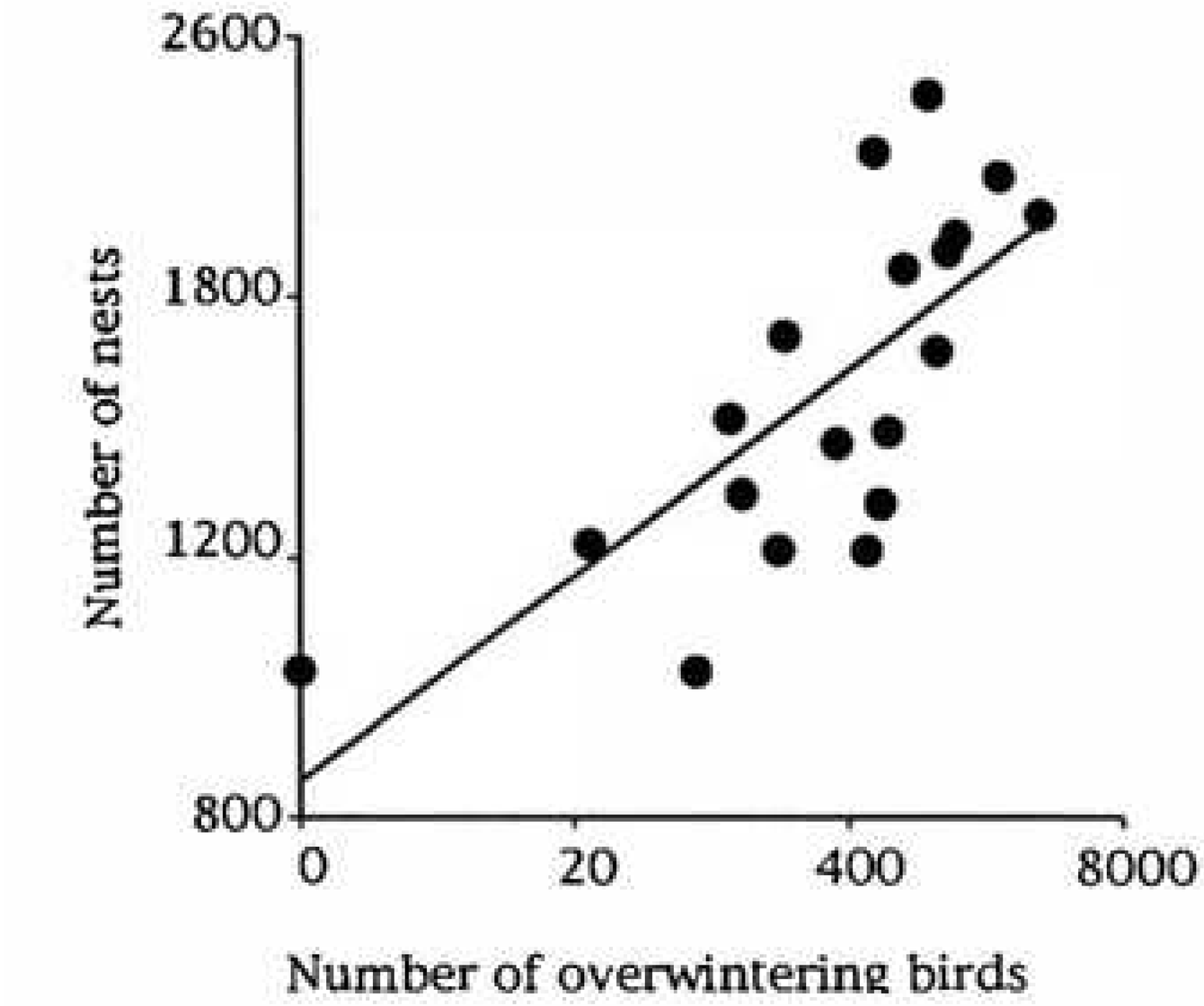

Figure 3. — The number of nests as a function of the number of birds present during the preceding winter (n = 19, r = 0.73, p < 0.001).

Brood size correlated to the amount of rainfall between February 1 and April 30 (Fig. 5). Mean brood size in the « sansouire » colonies correlated better to rainfall than the mean brood size for all the colonies. It should be noted however that the difference between the two slopes was not significant (F = 2.045,1 and 29 df, p = 0.16). These analysis suggest that rainfall improves conditions for successful breeding and that this is particularly true for the « sansouire » colonies.

A representative sample of direct measures of feeding conditions can hardly be obtained over the extensive foraging area used by these birds. However, the body condition of the incubating adults might be a reasonable indicator of feeding conditions. Indeed, the index of mean adult condition and mean chick condition did correlate significantly to the amount of rainfall in April (n = 9 (9 years), r = 0.78, p = 0.013, and r = 0.67, p = 0.049 respectively).

III. — *DISCUSSION*

From 1968 to 1992, the Camargue population of Little Egrets showed large fluctuations (Fig. 2). A very important decline was recorded in 1985, as a result of a severe winter (Hafner, 1992), and this was followed by a constant rate of recovery. In this population, the number of nests correlated strongly with the number of young fledged the previous year, but not 2 or 3 years previously. Reproductive output thus plays an important and immediate role in population regulation, but in this unstable environment, breeding success is influenced by environmental factors.

Rainfall before the breeding season seems to be an important factor acting on feeding conditions. There are two possible explanations. Abundant winter-spring

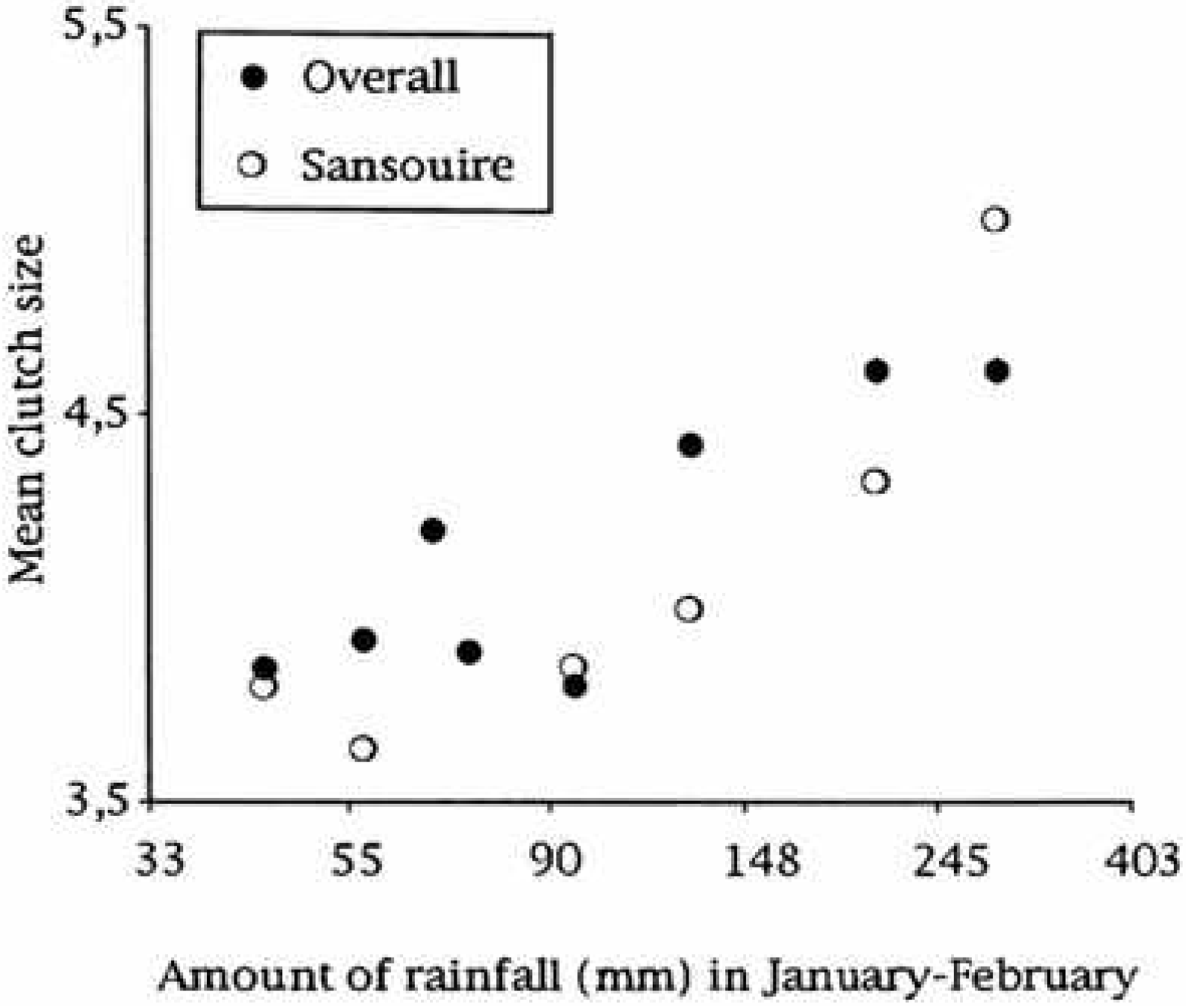

Figure 4. — Yearly mean clutch size as a function of the amount of rainfall preceding the breeding season (overall n = 8, r = 0.87, p = 0.005 ; sansouire colonies n = 6, r = 0.89, p = 0.018).

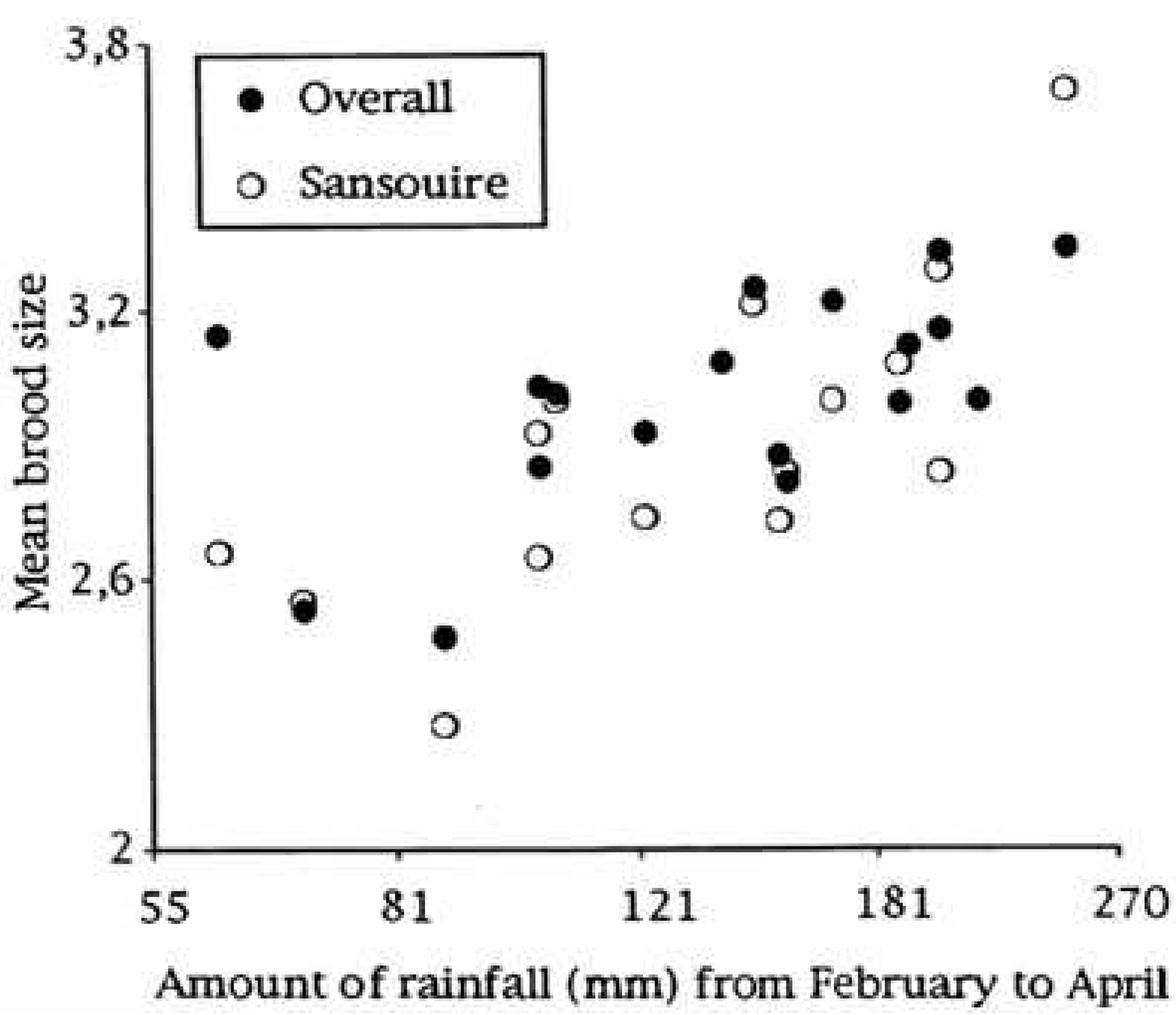

Figure 5. — Yearly mean brood size as a function of spring rainfall (overall n = 18, r = 0.56, p = 0.015, sansouire colonies, n = 15, r = 0.74, p = 0.002).

rainfall might increase the area of shallow water around the edges of marshes, early in the breeding season, when a large proportion of the major part of the marshes is too deep to be exploited by Egrets (Hafner, 1977). This increase in feeding area might enable the birds to be in a better condition and lay larger clutches than when this period of the year is dry. The second possible mechanism is that high water levels in winter and spring lead to communications between permanent water bodies, such as canals, which act as fish reservoirs, and the temporary water bodies. These communications allow the colonisation and subsequent spawning by fish in the « sansouire » and temporary marshes (Pont et al. 1991 ; Rosecchi and Crivelli, 1992.), increasing the prey populations the Egrets will exploit later in the season when they are rearing chicks. These two mechanisms are not mutually exclusive and Figures 4 and 5 provide some evidence that both may contribute to the eventual breeding success.

These results are in agreement with those obtained by Maddock and Baxter (1991), who related rainfall patterns to breeding success in four Egret species in Australia. The greatest fluctuations in breeding success occurred in the Little Egret, with highest success in the wet season, and lowest in the dry. A similar, but weaker relationship occurred in the Great Egret *Egretta alba* and the Intermediate Egret *Egretta intermedia,* but not in the Cattle Egret *Bubulcus ibis,* the latter being less dependent upon aquatic habitats.

In the Camargue, rainfall before the breeding season appeared to have a beneficial effect on the body condition of incubating Little Egrets, and on the number and the condition of young produced per brood. This presumably reflects a dependence of breeding success on feeding conditions via hydrological factors acting upon prey populations prior to the chick rearing period. Evidence that food is a limiting factor during the breeding season exists for a number of altricial birds (see reviews by Drent and Daan, 1980 ; Martin, 1987) and egrets seem to be no exception.

In the Camargue, a cold winter (Hafner *et al.*, 1992) causes an immediate significant decline in the population. The rapid increase which follows such an event (Fig. 2) indicates a strong recovery potential of the population. The important contribution of overwintering birds to population size variation supports the recent findings of Pineau (1992) indicating that the majority of Camargue Little Egrets are not long distance migrants. However, the few long distance migrants could also contribute to population recovery, particularly after a harsh winter.

To summarize, the number of birds overwintering successfully in the Camargue is a good predictor of the size of the breeding population the following year. The number of overwintering birds depends on the number of young fledged in the previous breeding season. Periodically, a harsh winter leads to the death of many potential recruits and, consequently, fewer birds survive to exploit the available food resources. This results in a high number of young fledged and the population will grow rapidly if the subsequent winters are mild.

SUMMARY

The number of Little Egrets breeding in the Camargue was determined annually from 1968 to 1992. The population shows no statistically significant trend over the 25 years, but fluctuated several times by a factor of 2 from one year to the next.

Multiple regression analysis revealed that the number of Egrets remaining in the Camargue after the breeding season and surviving the winter in this area explains 53 % of the year to year variation in population size. The number of overwintering birds, in turn, depends on the number of young fledged during the preceding summer and winter severity, the two variables explaining 50 % of the variation.

After an important decline in 1985, due to a hard winter which caused the death of many Egrets (January 1985), the population recovered quickly. Fewer birds nested and favourable hydrological conditions due to winter-spring rainfall increased breeding success. Several consecutive winters were also mild and this allowed many Egrets to survive in the Camargue until the next breeding season.

RÉSUMÉ

Les Aigrettes garzettes qui nichent en Camargue ont été dénombrées chaque année entre 1968 et 1992. Pendant cette période, aucune tendance significative n'a pu être mise en évidence, même si d'une année à l'autre la population est passée du simple au double.

Une régression multiple a montré que le nombre d'aigrettes qui hivernent avec succès explique 53 % de la variation annuelle du nombre de nicheurs la saison suivante. Par contre, c'est le nombre de poussins envolés la saison précédant l'hivernage et la rigueur de l'hiver qui sont les deux variables responsables à 50 % de la variation de l'effectif des hivernants.

A la suite du froid rigoureux de janvier 1985 qui a décimé les hivernants, la population a rapidement comblé son déficit. Les conditions hydrologiques favorables dues aux pluies de l'hiver et du printemps ont permis aux quelques nicheurs de se reproduire avec succès. Les hivers suivants furent cléments et ont facilité la survie de nombreux oiseaux jusqu'à la saison de reproduction suivante.

ACKNOWLEDGEMENTS

Our thanks go to L. Hoffmann without whose long-term commitment this 25 year study would not have been possible. We are grateful to J.P. Wallace who assisted both in the field and in the office from 1983 to 1987, and to J. Boutin, L. Brun, Y. Cherain, E. Coulet, A. Johnson, H. Kowalski, R. Lamouroux, J.L. Lucchesi, A. Mante and J. Walmsley for helping to count Egret roosts. We are indepted to B. Blohorn and the family de Bernis Calvière who allowed us to work on their estates. All capture and marking of birds was carried out under licence from the French National Ringing Center (C.R.B.P.O.) and the French Ministry of Environment. R. Drent helped during various stages of this work, often until deep into the night, and V. Boy provided statistical advice. A. Johnson and J. Skinner improved the English and J. Blondel, A. Crivelli and J. Skinner made usefull comments and suggestions.

REFERENCES

CÉZILLY, F., BOY, V. & HAFNER, H. (1990). — Group foraging in Little Egrets (*Egretta garzetta*) : from field evidence to experimental investigation. *Behav. Process,* 21 : 69-80.

DRENT, R.H. and DAAN, S. (1980). — The prudent parent : Energetic adjustments in avian breeding. *Ardea,* 68 : 225-252.

DUGAN, P.J., HAFNER, H. & BOY, V. (1986). — Habitat switches and foraging success in the Little Egret (*Egretta garzetta*). In Ouellet, H. (Ed.) *Proc. 19th International Ornithological Congress,* Vol.2 : 1869-1877. Ottawa, Canada.

ERWIN, R.M., HAFNER, H. & DUGAN, P. (1985). — Differences in the feeding behavior of Little Egrets *Egretta garzetta* in two habitats in the Camargue, France. *Wilson Bull,* 97 : 534-538

FOUCARD, T. and LAFAYE, J.Y. (1983). — *Régression linéaire sur microordinateurs.* Masson, Paris.

HAFNER, H. & BRITTON R.H. (1983). — Changes of foraging site by nesting Little Egrets (*Egretta garzetta* L.) in relation to food supply. *Colonial Waterbirds,* 6 : 24-30.

HAFNER, H. (1977). — *Contribution à l'étude écologique de quatre espèces de hérons* (Egretta g. garzetta *L.*, Ardeola r. ralloides *Scop.*, Ardeola i. ibis *L.*, Nycticorax n. nycticorax *L.)*. Thèse d'Université, Université Paul Sabatier, Toulouse.

HAFNER, H., BOY, V. & GORY, G. (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., DUGAN, P.J., & BOY, V. (1986). — Use of artificial and natural wetlands as feeding sites by Little Egrets (*Egretta garzetta* L.) in the Camargue, Southern France. *Colonial Waterbirds* 9 : 149-154.

HAFNER, H., DUGAN, P.J., KERSTEN, M. & WALLACE, J.P. (1993). — Flock feeding and food intake in Little Egrets (*Egretta garzetta* L.) : The effects on food provisioning and reproductive success. *Ibis,* 135 : 25-32.

HAFNER, H., PINEAU, O. & WALLACE J.P. (1992). — The effects of winter climate on the size of the Cattle Egret (*Bubulcus Ibis* L.) population in the Camargue. *Rev. Ecol. (Terre Vie)* 47 : 403-410.

KERSTEN, M., BRITTON, R.H., DUGAN, P.J. & HAFNER, H. (1991). — Flock feeding and food intake in Little Egrets : The effects of prey distribution and behaviour. *Journal of Animal Ecology,* 60 : 241-252.

MADDOCK, M. and BAXTER G.S. (1991). — Breeding success of Egrets related to rainfall : a six year Australian study. *Colonial Waterbirds,* 14 : 133-139.

MARTIN, E.Th. (1987). — Food as a limit on breeding birds : a life-history perspective. *Ann. Rev. Ecol. Syst.,* 18 : 453-487.

PINEAU, O. (1992). — Key wetlands for the conservation of Little Egrets breeding in the Camargue. In Finlayson, C.M., Hollis, G.E. & Davis, T.J. (eds). *Managing Mediterranean Wetlands and their Birds. Proc. IWRB Conf. Grado,* 1991. *IWRB Spec. Publ.,* 20 : 210-214.

PINEAU, O., HAFNER, H. & KAYSER, Y. (1992). — Influence of capture and wing-tagging on the Little Egret (*Egretta garzetta*) during the breeding season. *Rev. Ecol. (Terre Vie),* 47 : 199-204.

PINEAU, O., KAYSER, Y. and HAFNER, H. (in prep.). — Foraging distribution of Little Egrets breeding in the Camargue. Proc.Symposium Conservation of Colonial Waterbirds in the Mediterranean Region, 1993. *Annual Meeting of the Colonial Waterbird Society, Arles (France), 6-10 October 1993.*

PONT, D., CRIVELLI, A.J. and GUILLOT, F. (1991). — The impact of Three-spined Sticklebacks on the zooplankton of a previously fish-free pool. *Freshwater Biology,* 26 : 149-163.

REEDERS, H.H. (1983). — Spatial and temporal distribution of prey species of the Little Egret *Egretta garzetta* in a French Mediterranean wetland. *Report 170.* Wageningen, Netherlands : Agricultural University.

ROSECCHI, E. and CRIVELLI, A.J. (1992). — Study of a Sand Smelt (*Atherina boyeri* Risso 1810) population reproducing in fresh water. *Ecology of Freshwater Fish,* 1 : 77-85.