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Environmental impacts on wetland birds: long-term monitoring programmes in the Camargue, France

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Wetlands in the Mediterranean area have become a rare habitat due to human impact. To model the ecology and breeding biology of birds depending on that habitat, we describe long-term studies on two wetland birds (Little Egret *Egretta garzetta* and Greater Flamingo *Phoenicopterus (ruber) roseus*) in the Camargue, France. The hydrological conditions in natural Mediterranean wetlands depend largely on the pattern of rainfall (winter) and evapotranspiration (summer), but have been substantially altered by human activities. In natural conditions, these wetlands are very diverse and therefore sustain a high diversity of breeding birds. At the same time their unpredictable nature favours opportunistic breeding and wintering strategies of their inhabitants. Colonial waterbirds depend on wetlands both for safe nesting sites and for foraging. Availability of suitable nesting sites may limit breeding numbers. Availability and diversity of wetland habitats as foraging sites affect the number and density of breeding species that an area can sustain. Unfavourable feeding conditions can reduce the number of birds that attempt to breed and the number and quality of offspring the birds produce. Apart from local environmental factors, dispersal between wetlands in the western Mediterranean and existence of a non-breeding pool also affect breeding numbers in the Camargue. Thus, the persistence of wetland birds in the Mediterranean depends both on a network of habitat types on a local scale and a network of wetlands on a regional scale.

Key words: *Egretta garzetta*, *Phoenicopterus (ruber) roseus*, wetland habitats, wintering strategies

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Wetlands in the Mediterranean area, such as river deltas or coastal floodplains, are very patchily distributed. These wetlands have been destroyed and degraded to a great extent by dams for flood control, by agriculture, aquaculture, industrial and urban developments and by tourism (Hoffman *et al.* 1996). Due to the long history of human presence throughout the region, few wetlands have remained unaltered and the process of degradation is still continuing.

Colonially nesting waterbirds rely on intact wetlands both for safe nesting sites and for food resources. As a consequence of the diminishing wetland habitat in the Mediterranean, many bird species that depend on

these habitats only occur in widely separated and isolated populations and nine of the 31 species of colonially nesting waterbirds of this region are now considered threatened or endangered (Hoffmann *et al.* 1996).

In order to address the problems that wetland birds face, there is a need for information on their basic ecological requirements and the factors that affect their numbers. The causal relationships between environmental factors and fluctuations in populations can be understood through detailed studies over a long time period or, more reliably, through experimental studies. Endangered populations, however, do not lend themselves to either of these methods. However, populations

of rare species share many features of their ecology with more common species breeding in the same habitat and these species can, therefore, be used to collect information for the management and conservation of rarer species.

Throughout this paper we will refer to two long-term studies on Little Egret *Egretta garzetta* and Greater Flamingo *Phoenicopterus (ruber) roseus*, conducted in the Camargue, France, over the last c. 30 years (Hafner 1977, Hafner *et al.* 1994, Johnson 1989a, Johnson *et al.* 1991). These two species represent the general characteristics of many birds breeding in wetlands, such as colonial nesting and flock foraging, but differ in their specific habitat requirements and general life history. Little Egrets breed in mixed-species colonies located in trees and forage in a wide range of habitat types. They usually start breeding in their second year of life and have an annual survival rate of 70% (Voisin 1985). Populations at the northern edge of the breeding distribution, such as the Camargue population, are usually described as migratory, leaving the breeding grounds in autumn to winter in southern Spain and tropical West Africa.

Greater Flamingos typically breed at irregular intervals in large colonies and depend heavily on brackish and saline habitats for foraging. It is a long-lived species with high annual survival (93%) and many individuals do not start breeding until they are seven or eight years old (Cézilly *et al.* 1996, Pradel *et al.* 1997). In winter, flamingos disperse throughout the Mediterranean region but do not show any regular migration patterns.

Although neither group is actually considered to be threatened in the Camargue, the amount of information accumulated on them over the past decades allows us to gain important insights into ecological factors affecting the populations of wetland birds. The two studies are also by no means the only valuable set of long-term data available and other could have been selected, but the choice is mainly based on our personal involvement.

In the following text we will use the term population as a geographic unit of reproduction (Krebs 1994). Individuals from within a population are more likely to breed with each other than with any other individuals from outside that population. Successful persistence of populations requires (1) safe nesting sites, (2) adequate feeding areas within foraging range of the nest site, and (3) suitable habitats as stop-over sites during migration and as winter sites (Dugan 1983). We will use the two long-term studies on Little Egrets and Greater Flamingos to look briefly at the ecological requirements

of these populations. With the knowledge of their basic ecological requirements we then want to address the issue of which of these factors are most likely to affect the size of the two populations. Bearing in mind that the two species may use a network of different wetlands throughout the Mediterranean, populations in the Camargue may also be affected by environmental changes elsewhere in the region.

METHODS

Study area

The Camargue is a vast alluvial landscape of about 140,000 ha situated in the delta of the river Rhône (Fig. 1). It comprises a very rich mosaic of habitats (Blondel & Isenmann 1981). The area of natural wetland habitats in the Camargue has decreased by 39.8% to 50,000 ha mainly during the 1960s and 1970s (Lemaire *et al.* 1987). The northern part of the delta is heavily cultivated and today the only wetlands remaining are artificial, for example rice fields and fish farms.

Natural wetlands, such as seasonal brackish and oligohaline marshes, are concentrated in the Natural Reserve of the Camargue located around the central basin of the Vaccarès system (Tamisier & Grillas 1994). The extent of these wetlands was formerly determined by flooding from the river and the amount of rainfall. In the Mediterranean region, the main period of rainfall occurs during the winter months, whereas during the hot summer months evapotranspiration largely exceeds precipitation. In the Camargue the evapotranspiration is further increased by the common occurrence of strong winds. As a consequence of this rainfall deficit, salinity in these habitats is naturally high and many of the smaller water bodies completely dry out over the summer. Thus, the hydrological conditions of the wetlands largely depend on both the amount of winter rainfall and the action of the wind that can transport important amounts of water between interconnected water bodies (Heurteaux 1992). This gives this habitat type a very variable and unpredictable character.

The marshes surrounding the central basin are heavily affected by dyking and water pumping. To manage the wetlands for hunting, tourism and conservation, large areas in this zone are often flooded throughout the agricultural irrigation system in late summer (Tamisier & Grillas 1994). Both the resulting prolonged flooding season and the concomitant drop in salinity improves the primary production in these wetlands (Tamisier & Grillas 1994). Thus, in this zone the original character of the wetlands has changed from a variable

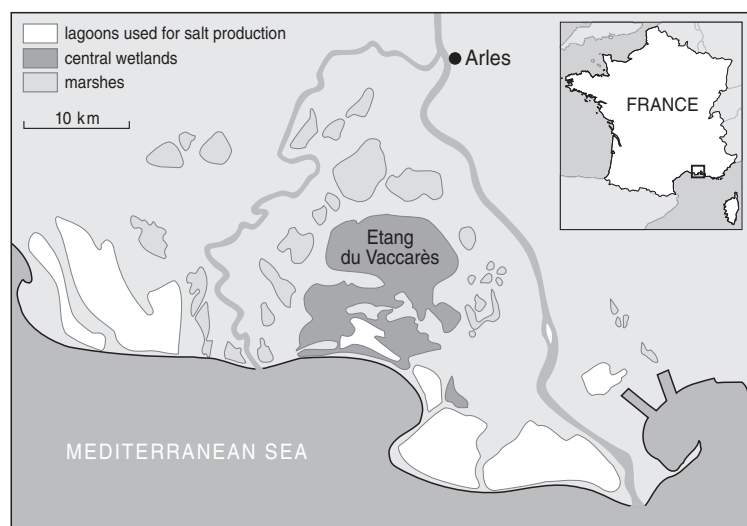


Figure 1. Map of the Camargue in the south of France, showing the different types of wetlands. The central wetlands preserved more or less their natural character of unpredictability. Marshes surrounding the central part are often managed with less variable water levels and salinities. The south-western and south-eastern parts are covered by lagoons used for commercial salt production.

and unpredictable habitat to one of a homogeneous and predictable nature.

Finally, the south-eastern and south-western corners of the delta are covered by large complexes of lagoons that are exploited for commercial salt production. So, within a relatively small geographical range the Camargue offers a large variety of habitat types.

Monitoring of populations

The ecology of Little Egrets and Greater Flamingos has been studied in the Camargue since the late 1960s (Hafner 1977, Hafner *et al.* 1982, Hafner & Britton 1983, Hafner *et al.* 1986, 1993, Erwin *et al.* 1985, Dugan *et al.* 1986, Johnson 1989a, Johnson *et al.* 1991, Kersten *et al.* 1991, Cézilly *et al.* 1995, Kazantzidis *et al.* 1996). Each year the whole area is searched from the air for breeding colonies. The size of the colonies are established by counting the nests during incubation either from the ground (egrets) or from aerial photographs (flamingos). Breeding success is inferred from counts of young birds at the end of the chick rearing period. Each year since the late 1970s and early 1980s, several hundred young of both species have been weighed, measured and individually marked. Throughout the year suitable habitat, both in the Camargue and elsewhere, is regularly checked for individually marked birds. The ringing programme provides information on the habitat utilisation and movements of birds as well as estimates of demographic parameters such as mortality and age of first breeding.

Throughout most of the period during which the two populations were monitored, additional information on feeding conditions, both in the Camargue and

elsewhere in the Mediterranean region, are available. Food availability can be directly assessed through sampling of prey species at the feeding sites. This method is very labour intensive and it is difficult to obtain data over a large geographical area. Since waterbirds rely exclusively on the aquatic ecosystem for their animal food, hydrological parameters, such as water levels, amount of rainfall and river discharge data, provide reliable indicators of feeding conditions for these birds (Kushlan 1989, Bildstein *et al.* 1990, Cézilly *et al.* 1995). The more rainfall and the higher the water level, the larger will be the area covered by water and thus the area available for foraging. We measured yearly variation in the extent of available feeding area for egrets from the amount of rainfall during winter. This was taken from weather stations in the Camargue (Tour du Valat) and southern Spain (Sevilla). For flamingos the feeding area was estimated from the water level in the centre of the Vaccarès system. The advantage of the latter is that it combines the effects of rainfall, wind and evaporation in determining the extent of the flooded area (Heurteaux 1992), whereas weather data are more readily available for larger geographical ranges.

RESULTS

Nesting sites

Many waterbirds in the Camargue breed in a small number of distinct colonies. For example Little Egrets use five to ten different localities each year, whereas the Greater Flamingos breed at a single site. Such breeding aggregations are particularly vulnerable to disturbance

and degradation of their nesting site, because a single localised factor can endanger the breeding success of an entire population. Little Egrets in the Camargue breed in several distinct, traditional mixed-species colony sites throughout the area. Egrets build nests in trees and, for successful breeding, the nesting trees need to be surrounded by water that provides protection against terrestrial predators. The frequently occurring strong winds in the delta are an important cause of nesting failure. Nesting trees, therefore, require protection from wind by surrounding stands of mature trees (Hafner 1982). Due to human impact, this habitat type is disappearing from the Camargue and good nesting sites are becoming rare.

Flamingos have been nesting in the Camargue for centuries using various sites in the southern lagoons, which are now part of the industrial salt pans. Suitable colony sites need to be surrounded by water throughout the breeding season as protection against terrestrial predators. In the Rhône Delta only a few such islands still exist within the lagoon system. Moreover, sites used repeatedly quickly erode, which leads to breeding failure and abandonment of the nesting site (Hoffmann 1964). During the last 50 years, flamingos in the Camargue, in contrast, have bred at only a few different sites. However, no breeding occurred there between 1964 and 1968, presumably reflecting a lack of suitable nesting sites (Rendon Martos & Johnson 1996). An artificial breeding island in one of the evaporation lagoons of the salinas was then constructed in 1970 and flamingos started to use the new site from 1974 onwards. Flamingos have been breeding successfully at this site every year since then (Rendon Martos & Johnson 1996). The vulnerability of colonially breeding birds to unusual events is best illustrated by the flamingos. In 1987 a red balloon drifted into the colony and in 1989 an escaped Black Swan *Cygnus atratus* repeatedly visited the breeding island. Both events led to the breeding failure of a significant number of pairs and caused increased emigration from the Camargue breeding site (Cézilly *et al.* 1995, Nager *et al.* 1996). The size of the artificial nesting island may also set a limit to the number of birds that are able to breed (Cézilly *et al.* 1996, Nager *et al.* 1996). In years with high nesting density, some flamingos, mainly young individuals, are observed to nest on a nearby dike. These nesting attempts usually failed.

Feeding habitats

Suitable nesting sites must also be surrounded by profitable feeding areas. Hafner & Fasola (1992) have quantified the extent of different foraging habitats in

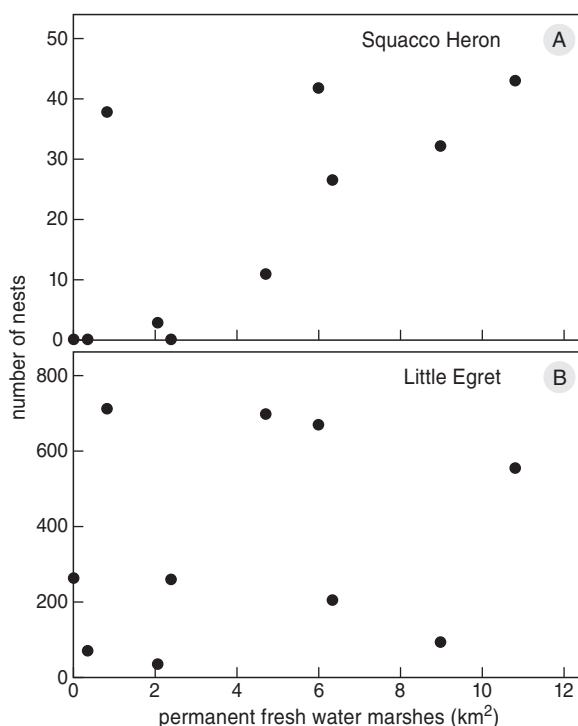


Figure 2. Number of nests of Squacco Herons (A) and Little Egrets (B) in relation to the surface area of permanent fresh water marshes available within 5 km of the colony site. The Squacco Heron heavily depends on availability of this habitat (Spearman correlation $r = 0.71$, $n = 10$, $P = 0.023$), whereas Little Egrets occur in similar numbers in colonies with little or lots of permanent freshwater marshes available ($r = 0.07$, $n = 10$, NS).

the surroundings of major colonies of herons in Algeria, Mediterranean France, Greece, Israel, Italy, Spain and Tunisia. The survey distinguished between brackish and freshwater habitats. The latter category also includes artificial wetlands such as ricefields, which are now also important feeding areas for herons (Kazantzidis *et al.* 1996). Within freshwater habitats, one also has to distinguish between permanent and temporary wetlands. Temporary marshes that are drying out provide an especially rich source of food to breeding birds and post-fledgling juveniles of Little Egret (Hafner 1977, Kersten *et al.* 1991). Colony size, expressed as the maximum number of nests of each heron species censused, was determined at the same time as the assessment of surface area of the different feeding habitats. Counts were made of Purple Heron *Ardea purpurea*, Grey Heron *A. cinerea*, Squacco Heron *Ardeola ralloides*, Great White Egret *Casmerodius albus*, Little Egret, Cattle Egret *Bubulcus ibis* and Black-crowned Night Heron *Nycticorax nycticorax*. In general, areas with a

larger surface of freshwater marshes supported larger numbers of breeding pairs. Different species sharing the same colony site show preferences for different foraging habitats (Fig. 2). For instance, Little Egrets are generalised feeders that often forage in flocks in open freshwater and brackish water bodies. They are, therefore, found in colonies surrounded by extensive freshwater as well as brackish areas. In contrast, Squacco Herons are solitary foragers which hide in the vegetation, waiting for passing prey, and they only breed in colonies that have at least 200 ha of permanent freshwater marshes within a distance of 5 km. Consequently, diversity of breeding colonies is expected to increase with increasing diversity of habitats within the feeding range of a colony site. This is indeed observed for tree nesting herons in the Mediterranean region (Fig. 3).

Although their nesting site is located within the industrial salinas, Greater Flamingos depend on a much wider area of natural wetlands of the central Vaccarès system for feeding. The major foraging habitat of breeding flamingos in the Camargue consists of a complex of brackish lagoons and temporarily flooded salt marsh vegetation (*sansouire*). Yearly fluctuations in the

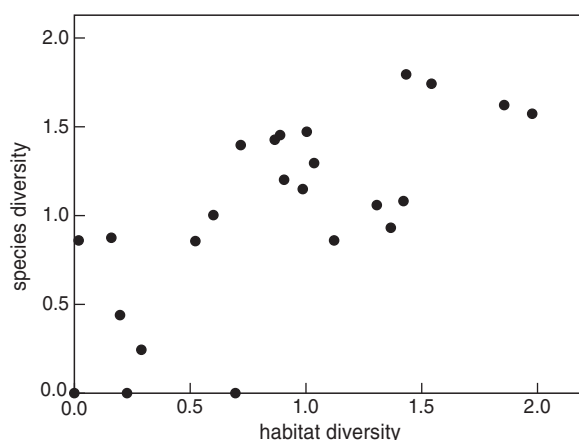


Figure 3. The composition of heron colonies in relation to habitat diversity. Species diversity in heronries increases when more different foraging habitats are available within the foraging range of the colony (reproduced with permission from Hafner & Fasola 1992).

extent of these habitat types can be readily measured by changes in the water levels of the central part of the Vaccarès system (Heurteaux 1992). As with herons, the size of the flamingo colony depends on the available foraging area. Less flamingos breed in years with low water levels, when a smaller area of foraging habitat is available (Cézilly *et al.* 1995). Flamingos may even forego breeding completely after winters with very low rainfall, as has happened in Spain in several years in the recent past (Johnson *et al.* 1991).

Wintering strategies

After breeding, Little Egrets disperse over a large area in search of suitable feeding grounds. Until the 1980s nearly all Little Egrets would leave the Camargue by winter time (Valverde 1956). They migrated to North and West Africa either eastwards through Italy (eastern migration route) or westwards through Spain (western migration routes) (Voisin 1985, Pineau 1992). From the 1980s onwards, the local wintering population has increased (Hafner *et al.* 1994) and a relatively higher proportion of birds ringed locally are recovered and sighted there in winter than before (Table 1). The Camargue breeding population has thus changed, in recent years, from a migratory population to a partially migrant one. In the 1970s, when few egrets wintered locally, the size of the wintering population in the Camargue increased after a dry year in southern Spain, their main migration direction (Fig. 4). In the late 1980s and 1990s, when an important proportion of breeding birds wintered locally, fluctuations in wintering

Table 1. Number of recoveries of Little Egrets, ringed as chick in the Camargue, during autumn and winter along the Mediterranean French coast, along the western migration route into tropical West Africa and along the eastern migration route into north-eastern Africa. There are two sets of ring recoveries available: (A) 1932–1983 (Voisin 1985) and (B) from the present ringing programme in the Camargue (1982–1994, Pineau 1992 and unpubl. data). Ring recovery rates may vary over time and between regions. To account for variation in recovery rates we compared the number of ring recoveries during winter with the ones during autumn for the three areas and the two time intervals separately. In more recent winters there is a significant increase in the proportion of birds recovered in the Camargue and surrounding areas, but no changes along the eastern and western migration routes.

Dataset		Number of ring recoveries in		Test
		Autumn	Winter	
Coastal Mediterranean France				
A	1932–1983	33	4	$\chi_1^2 = 42.84, P < 0.001$
B	1982–1994	13	52	
Western migration route				
A	1932–1983	4	12	$\chi_1^2 = 0.08, \text{NS}$
B	1982–1994	7	13	
Eastern migration route				
A	1932–1983	12	5	$\chi_1^2 = 1.29, \text{NS}$
B	1982–1994	3	5	

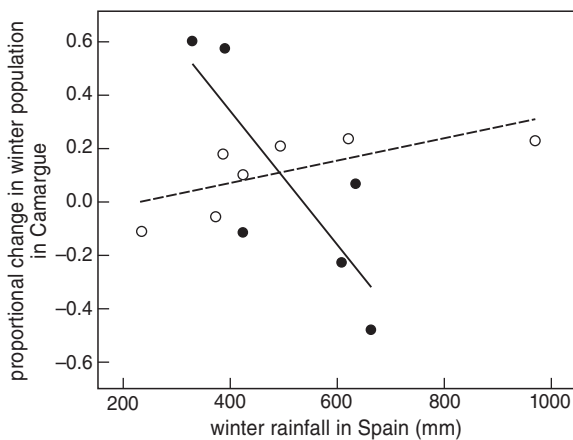


Figure 4. Changes in numbers of Little Egrets wintering in the Camargue in relation to rainfall in Spain in the preceding winter. Changes in the winter population were calculated as $\log_{10}(N_x) - \log_{10}(N_{x-1})$. In 1974–1980, hydrological conditions in Spain affected the local wintering population; it increased after dry winters (closed symbols and solid line, $r = -0.81$, $n = 6$, $P = 0.05$). In 1988–1995, this is not the case anymore (open symbols and broken line, $r = 0.68$, $n = 7$, NS). The interaction between the two time intervals is significant ($F_{1,9} = 14.50$, $P = 0.004$).

numbers became less pronounced and were not related any more to the amount of rainfall in southern Spain (Fig. 4).

Many Greater Flamingos also move to Spain and northern Africa after the breeding season. The main wind direction during the post-fledgling period in autumn determines whether juvenile flamingos that leave the Camargue move either to northern Africa or to Spain (Green *et al.* 1989). In subsequent winters, flamingos will return to the same area that they chose in their first year. However, as with egrets, the number of flamingos spending their winter in the Camargue has increased (Johnson 1989a,b, Johnson *et al.* 1991).

Breeding numbers, breeding success and survival

The number of breeding pairs of the populations of both Little Egret and Greater Flamingo fluctuates widely from year to year (Fig. 5). Note that there were several years of total absence of breeding flamingos in the Camargue (1964–68). Changes in population density are the outcome of various processes such as reproduction, mortality and dispersal. Fluctuations in the number of breeding birds are linked to the extent of available feeding area, such as in the Squacco Heron and the Greater Flamingo. Larger numbers of birds breed where more food or larger foraging areas are available. In contrast, we did not find a correlation

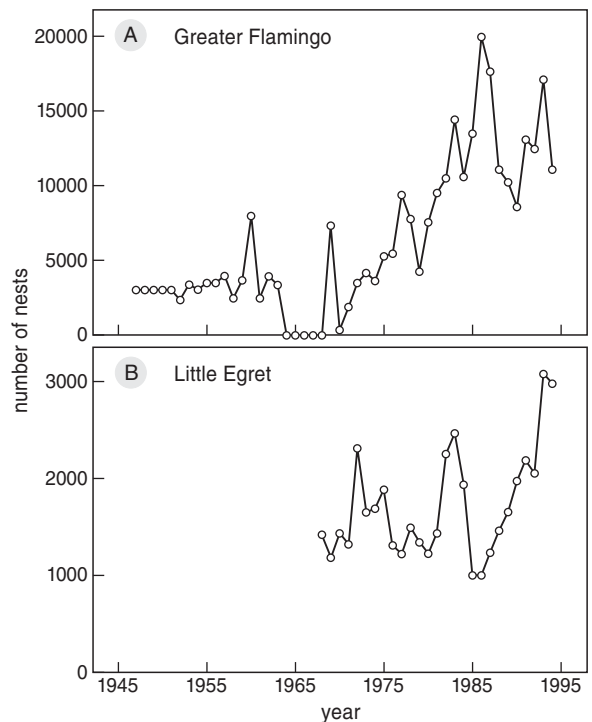


Figure 5. Annual number of nests of Greater Flamingo (A) and Little Egret (B) counted in the Camargue.

between breeding numbers of Little Egrets in the Camargue and local feeding conditions (Fig. 2). Fluctuations in the Camargue breeding population, however, are correlated with the amount of rainfall in southern Spain (Fig. 6). More birds are breeding in the Camargue after dry winters in Spain.

In addition, the reproductive output is affected by the feeding conditions. In breeding seasons after winters with high amounts of winter rainfall, breeding Little Egrets are in better condition, lay larger clutches and raise more fledglings (Hafner *et al.* 1994). Flamingos only lay one egg, and the probability of raising their young to fledging is independent of feeding conditions. The chicks' growth, however, is better in years with higher water levels, and may, as a result, increase the birds' chances of returning as a breeding bird in later years (Cézilly *et al.* 1995).

Other important factors that affect population size are the survival of breeding birds and the recruitment of young birds into the breeding population. These processes are usually difficult to study and require long-term information on individually marked birds (Clobert & Lebreton 1991, Lebreton & Clobert 1991). The most important period of mortality is usually considered to be the winter period which limits the birds' resource

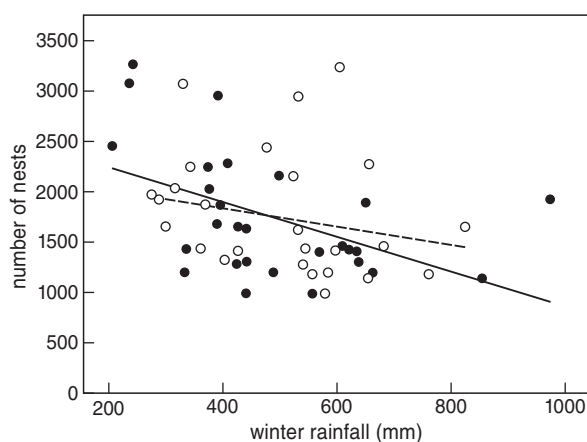


Figure 6. The influence of winter rainfall in the Camargue and southern Spain on number of breeding Little Egrets in the Camargue. About the same number of birds bred after dry or wet winters in the Camargue (open symbols and broken line, $r = -0.20$, $n = 28$, NS), but more egrets bred in the Camargue after dry winters in Spain (measured in Sevilla, closed symbols and solid line, $r = -0.47$, $n = 28$, $P = 0.01$).

acquisition. In January 1985, along the northern Mediterranean coast, an unusually severe cold spell occurred. All wetlands in the Camargue and surroundings were frozen over for a period of 15 days. This had a major impact on the survival of locally wintering birds, many of which were found dead. The large mortality during this winter explains the sharp drop of breeding numbers of Little Egrets between 1984 and 1985 (Hafner *et al.* 1994, see also Fig. 5). As a result of the cold spell, annual survival rate of flamingos breeding in the Camargue dropped from the average value of 93% to only 76% in 1985 (Cézilly *et al.* 1996). Survival of young flamingos between one and three years old was affected even more severely (Johnson *et al.* 1991). In contrast to the egrets, however, breeding numbers of flamingos did not drop after this severe winter (Fig. 5), despite the high mortality.

DISCUSSION

The fundamental objective of the research programme described here is the understanding of the biology of Little Egrets and Greater Flamingos in the Camargue and elsewhere in the Mediterranean region, and to gain insight into how Mediterranean wetlands support these, and other, bird populations. Both Little Egret and Greater Flamingo show the general characteristics of many wetland birds and will thus share them with

other, less well studied species. A common picture which emerges for both populations is that the numbers of breeding pairs fluctuate widely from year to year and are linked to environmental conditions. There are, however, some differences between the species in the way in which the fluctuations and environmental conditions are linked.

Large and diverse heron colonies require both safe nesting sites in trees and a mosaic of different habitat types in the immediate neighbourhood of the colony site. Among the herons, Little Egrets represent the type of generalist forager, using various different feeding habitats. It therefore may not be surprising that their breeding numbers are not affected by the extent of natural freshwater habitats, as reflected by the amount of local rainfall, because they can utilise alternative feeding sites such as brackish lagoons. Still, Little Egrets breed more successfully in summers following wetter winters (Hafner *et al.* 1994) which may suggest that the natural freshwater habitats provide better quality feeding sites. The harshness of the winter in the Camargue is another important environmental factor that affects the Little Egret's breeding numbers, especially since an increasing proportion of the population uses the Camargue as a wintering ground.

The number of breeding Greater Flamingos depends on the extent of their foraging habitat: the larger the area of *sansouires* flooded, the more flamingos attempt to breed in the Camargue. Their breeding success is affected by both disturbance at the nesting site and the extent of foraging habitat: a large number of pairs abandoned their nest after disturbances and successful pairs raise higher quality offspring in years with more favourable feeding conditions. Large numbers of flamingos spend the winter in the Camargue and many birds known to have bred here died during exceptionally cold weather. In contrast to egrets, however, cold winters had no effect on the number of breeding flamingos in the following summer. Why are there such large differences between the two species? For a fuller understanding of the breeding populations of Little Egrets and Greater Flamingos in the Camargue, more information on the use of alternative sites and on the turnover of individual birds is needed.

Both populations roam over most of the western Mediterranean region and other breeding populations are in their range. Thus, environmental events occurring in other wetlands and exchanges with other populations are likely to affect the numbers in the Camargue. For example, several European populations of wetland birds, such as Purple Heron and White Stork *Ciconia ciconia* were negatively affected by the drought

period in tropical western Africa where they spend their winter (Den Held 1981, Cavé 1983, Kanyamibwa *et al.* 1990). Little Egrets do not depend solely on wintering areas in tropical western Africa, but many birds from the Camargue also spend their winter in southern Spain (Pineau 1992). In the late 1970s most egrets left the Camargue in autumn, except in years following dry winters in Spain. This suggests that when dry conditions in Spain made the wetlands there unsuitable for wintering egrets, more birds remained or returned to the Camargue in search of alternative wintering sites. From the mid-1980s onwards, however, the wintering population in the Camargue steadily increased and changes in numbers became independent of the rainfall in southern Spain. The reason for this change of wintering strategy of Little Egrets is unknown. It could indicate that conditions in Spain had become less favourable, independent of the amount of rainfall, either through degradation of the wetlands or an increased competition with populations from Spain and western France that use the same wintering sites. Alternatively, the change in wintering strategy might also be caused by improved wintering conditions in the Camargue. Recent changes in the management of many wetland habitats have improved their primary production (Tamisier & Grillas 1994) and possibly increased the carrying capacity of the Camargue for wintering egrets. These two explanations are not mutually exclusive.

Not only the wintering numbers of Little Egrets are correlated with rainfall in southern Spain, but also their breeding numbers. More egrets were breeding in the Camargue after dry winters in Spain. After one particularly dry winter in Spain in 1992/1993, a large increase in breeding numbers was observed in the Camargue. That this increase resulted from immigration of egrets originating from Spain was corroborated by sightings of breeding birds ringed in Spain. The findings of frequent exchanges of individuals between wetlands suggest that these populations are linked to each other and form a meta-population on a regional scale. The Camargue population is therefore affected by both local and regional processes. Possibly, the Camargue received individuals from other populations, because the local population is currently below its carrying capacity due to changes in wetland management.

Breeding numbers of Greater Flamingos were largely affected by local factors and not by conditions elsewhere. A larger number of flamingos breed in the Camargue when foraging conditions are more favourable. Although there is some exchange of breeding birds between the Camargue and Spain, the other

important breeding area of flamingos in the western Palearctic, dry conditions in Spain that prevent local breeding do not result in increased immigration into the Camargue during these years (Nager *et al.* 1996).

Cold winter weather affected survival of locally wintering birds (Cézilly *et al.* 1996), but did not affect the breeding numbers in the following summer. When calculating the time-specific probabilities of new, previously unknown breeders in that colony, an unusually high proportion of first-time breeders was observed in 1985, after the severe winter (Pradel *et al.* 1997). This means that the losses of adult breeding birds had been compensated for by an unusually high recruitment rate of new breeders into the population. In the subsequent two years a lower frequency of first-time breeders than usual was observed (Pradel *et al.* 1997), indicating that a pool of potential recruits was depleted and first needed to re-form. The short-term perturbation caused by the exceptional cold spell thus altered the composition of the breeding population for up to three years, but not the breeding density. These changes were only detectable using resightings of marked individuals. Further support to the hypothesis of limited access to breeding for young flamingos in the Camargue is given by the observation that flamingos there start breeding at a later age on average than flamingos at the Spanish nesting site (Nager *et al.* 1996). Thus, environmental effects on breeding numbers of flamingos seem to be buffered by the existence of a large pool of non-breeding birds. The presence of such a large non-breeding population, however, may arise in the first place from a general shortage of suitable nesting areas in the region.

Successful persistence of populations requires safe nesting sites and adequate feeding areas within foraging range of the nest site. Both the size and the diversity of breeding colonies increase with increasing availability and diversity of habitats within the feeding range of the colony. Moreover, since the ecology of wetland birds is opportunistic, they move over a larger region and both local and regional factors affect the populations. All over the Mediterranean, however, human impact on wetlands decreases the number of sites allowing undisturbed and continuous breeding. To maintain a rich diversity of wetland birds, it is therefore essential to conserve an array of different habitat types and a minimum surface of each one of them. The whole integrity of a wetland complex on a regional scale needs to be conserved and not only selected key habitats.

For conservation and management purposes there is therefore an increasing need to assess ecosystem condi-

tions and changed over a landscape scale. Thus, coordinated counts over very large geographical areas are required to distinguish between local fluctuations and general trends within such meta-populations. In addition to the analysis of the resightings of individually marked birds, genetic studies can also contribute to our understanding of the extent of dispersal on a larger geographical scale. To understand the source of population fluctuations we need to examine interactions between environmental variables, bird numbers and breeding parameters. Provided a sufficiently large run of years is available, relationships between changes in population size and biotic and abiotic variables can be examined. Long-term data sets on breeding parameters and resightings of individually marked birds provide a sensitive indicator of changes in reproduction and survival that can then be related to variations in environmental factors. Such research is currently mainly concentrated on seabirds. However, other habitats can impose different constraints on bird populations. For instance, Mediterranean wetlands are characterised by a larger degree of variability than marine systems in hydrological conditions that may profoundly affect bird populations. The Little Egret and the Greater Flamingo studies may therefore be considered complementary to the traditional long-term studies on seabirds (Cézilly 1997).

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REFERENCES

- Bildstein K.L., Post W., Johnston J. & Frederick P. 1990. Freshwater wetlands, rainfall and the breeding ecology of White Ibises in Coastal South Carolina. *Wilson Bull.* 102: 84–98.
- Blondel J. & Isenmann P. 1981. Guide des oiseaux de Camargue. Delachaux & Niestlé, Neuchâtel-Paris.
- Cavé A.J. 1983. Purple Heron *Ardea purpurea* survival and drought in tropical West Africa. *Ardea* 71: 217–224.
- Cézilly F. 1997. Demographic studies of wading birds. *Colonial Waterbirds* 20: 121–128.
- Cézilly F., Boy V., Green R.E., Hirons G.J.M. & Johnson A.R. 1995. Interannual variation in Greater Flamingo breeding success in relation to water levels. *Ecology* 76: 20–26.
- Cézilly F., Viallefont A., Boy V. & Johnson A.R. 1996. Annual variation in survival and breeding probability in Greater Flamingos. *Ecology* 77: 1143–1150.
- Clobert J. & Lebreton J.-D. 1991. Estimation of demographic parameters in bird populations. In: Perrins C.M., Lebreton J.-D. & Hirons J.-D. (eds) *Bird population studies*. Oxford University Press, Oxford, pp. 75–104.
- den Held J.J. 1981. Population changes in the Purple Heron in relation to drought in the wintering area. *Ardea* 69: 185–191.
- Dugan P.J. 1983. The conservation of herons during migration and in the wintering areas: a review of present understanding and requirements for future research. In: Evans P.R., Hafner H. & L'Hermite P. (eds) *Shorebirds and large waterbirds conservation*. Commission of the European Community, Brussels, pp. 141–153.
- Dugan P.J., Hafner H. & Boy V. 1986. Habitat switches and foraging success in the Little Egret (*Egretta garzetta*). *Proc. Int. Ornithol. Congr.* 19: 1869–1877.
- Erwin R.M., Hafner H. & Dugan P.J. 1985. Differences in the feeding behaviour of Little Egrets *Egretta garzetta* in two habitats in the Camargue, France. *Wilson Bull.* 97: 534–538.
- Green R.E., Hirons G.J.M. & Johnson A.R. 1989. The origin of long-term cohort differences in the distribution of Greater Flamingos *Phoenicopterus ruber roseus* in winter. *J. Anim. Ecol.* 58: 543–555.
- 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.). PhD dissertation, University Paul Sabatier, Toulouse.
- 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. & Fasola M. 1992. The relationship between feeding habitat and colonially nesting Ardeidae. In: Finlayson C.M., Hollis G.E. & Davis T.J. (eds) *Managing Mediterranean wetlands and their birds*. IWRB Special Publication No. 20, Slimbridge, UK, pp. 194–201.
- 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 effect on food provisioning and reproductive success. *Ibis* 135: 25–32.
- Hafner H., Kayser Y. & Pineau O. 1994. Ecological determinants of annual fluctuations in numbers of breeding Little Egrets *Egretta garzetta* in the Camargue, S. France. *Revue d'Ecologie (Terre Vie)* 49: 53–62.
- Heurteaux P. 1992. Modifications du régime hydrique et salin des étangs du système de Vaccarès (Camargue, France) liées aux perturbations anthropiques des cinquante dernières années. *Annales de Limnologie* 28: 157–174.
- Hoffmann L. 1964. La production des flamants en 1962 et 1963. *Revue d'Ecologie (Terre Vie)* 18: 331–333.
- Hoffmann L., Hafner H. & Salathé T. 1996. The contribution of colonial waterbird research to wetland conservation in the Mediterranean region. *Colonial Waterbirds* 19 (Special Publication 1): 12–30.

- Johnson A.R. 1989a. Population studies and conservation of Greater Flamingos in the Camargue. In: Spaans A.L. (ed.) Wetlands en watervogels. Pudoc, Wageningen, pp. 49–63.
- Johnson A.R. 1989b. Movements of Greater Flamingos *Phoenicopterus ruber roseus* in the western Palearctic. *Revue d'Ecologie (Terre Vie)* 44: 75–94.
- Johnson A.R., Green R.E. & Hirons G.J.M. 1991. Survival rates of Greater Flamingos in the west Mediterranean region. In: C.M. Perrins, J.-D. Lebreton & G.J.M. Hirons (eds) Bird population studies. Oxford University Press, Oxford, pp. 249–271.
- Kanyambwa S., Schierer A., Pradel R. & Lebreton J.-D. 1990. Changes in adult survival rates in a western European population of the White Stork *Ciconia ciconia*. *Ibis* 132: 27–35.
- Kazantzidis S., Hafner H. & Goutner V. 1996. Comparative breeding ecology of the Little Egret (*Egretta g. garzetta*) in the Axios delta (Greece) and the Camargue (France). *Revue d'Ecologie (Terre Vie)* 51: 313–327.
- 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. *J. Anim. Ecol.* 60: 241–252.
- Krebs C.J. 1994. Ecology. Fourth edition. Harper Collins, New York.
- Kushlan J.A. 1989. Avian use of fluctuating wetlands. In: Sharitz R.R. & Gibbons J.W. (eds) Freshwater wetlands and wildlife. Dept Energy Symposium Series No. 61. Dept Energy Office of Scientific and Technical Information, Oak Ridge, Tennessee, USA, pp. 593–604.
- Lebreton J.-D. & Clobert J. 1991. Bird population dynamics, management, and conservation: the role of mathematical modelling. In: C.M. Perrins, J.-D. Lebreton & G.J.M. Hirons (eds) Bird population studies. Oxford University Press, Oxford, pp. 105–125.
- Lemaire S., Tamisier A. & Gagnier F. 1987. Surface, distribution et diversité des principaux milieux de Camargue. Leur évolution de 1942 à 1984. *Revue d'Ecologie (Terre Vie)* Suppl. 4: 47–56.
- Nager R.G., Johnson A.R., Boy V., Rendon Martos M., Calderon J. & Cézilly F. 1996. Temporal and spatial variation in dispersal in the Greater Flamingo (*Phoenicopterus ruber roseus*). *Oecologia* 107: 204–211.
- 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. IWRB Special Publication No. 20, Slimbridge, UK, pp. 210–214.
- Pradel R., Johnson A.R., Viallefont A., Nager R.G. & Cézilly F. 1997. Local recruitment in the Greater Flamingo: a new approach using capture-mark-recapture data. *Ecology* 78: 1431–1445.
- Rendon Martos M. & Johnson A.R. 1996. Management of nesting sites for Greater Flamingos. *Colonial Waterbirds* 19 (Special Publication 1): 167–183.
- Tamisier A. & Grillas P. 1994. A review of habitat changes in the Camargue: an assessment of the effects of the loss of biological diversity on the wintering waterfowl community. *Biol. Conserv.* 70: 39–47.
- Valverde J.A. 1956. Essai sur l'Aigrette Garzette en France (*Egretta garzetta*). *Alauda* 24: 1–36.
- Voisin C. 1985. Migration et stabilité des populations chez l'Aigrette garzette *Egretta garzetta*. *L'Oiseau et RFO* 55: 291–311.

SAMENVATTING

Net als elders in Europa zijn natuurlijke wetlands in het Middellandse Zeegebied schaars geworden als gevolg van menselijk handelen. De hydrologie van de resterende stukken wordt sterk bepaald door neerslag (in de winter) en verdamping (in de zomer), maar ook daar heeft de mens een grote invloed op gekregen. De Camargue, gelegen in de delta van de Rhône, is daar een voorbeeld van. In de afgelopen halve eeuw is de omvang van het natuurlijke moeras met 40% afgenomen tot 50.000 ha. Het noordelijke deel van de delta is in cultuur gebracht, vooral ten behoeve van rijstvelden en viskwekerijen. Aan de hand van Kleine Zilverreiger *Egretta garzetta* en Flamingo *Phoenicopterus (ruber) roseus*, beide onderwerp van studie in de Camargue sinds de late jaren zestig, brengen de auteurs de complexiteit van het leven in een moeras tot uitdrukking. Beide soorten vertoonden grote aantalschommelingen. In het geval van de Flamingo's was daarvoor de omvang van het foerageergebied, in het bijzonder de brakke lagunes en tijdelijk overstroomde zoutvlaktes (sansouire) in het centrale Vaccarès systeem, van doorslaggevende betekenis. Bij de Kleine Zilverreiger speelde dat geen rol. Bij deze soort werd echter een correlatie gevonden met droogte in Zuid-Spanje: in droge Spaanse winters groeide het aantal broedparen in de Camargue. De Flamingo's kunnen alleen op enkele eilandjes broeden in de industriële zoutpannen gelegen in de zuidelijke lagunes. Overal elders zouden ze het slachtoffer van grondpredatoren worden. En zelfs op de eilandjes hoeft maar weinig te gebeuren of het gaat mis. Een rode ballon en een ontsnapte Zwarte Zwaan *Cygnus atratus* bijvoorbeeld zorgden voor een aanzienlijke verstoring en broeduitval. Ook Kleine Zilverreigers zijn kwetsbaar gebleken, doordat zij afhankelijk zijn van bomen omringd door water om in te broeden. Dit type habitat vermindert onder invloed van mensen. Beide soorten trokken na de broedtijd altijd naar overwinteringgebieden in Spanje en Noord- en West-Afrika, maar sinds de late jaren tachtig is het aandeel lokale overwinteraars sterk toegenomen. Zodoende is de overleving tegenwoordig minder gekoppeld aan droogte in Spanje of Afrika, maar wel aan streng winterweer op de broedplaats. Forse wintersterfte hoeft overigens niet tot een populatiedaling te leiden, omdat de verliezen worden gecompenseerd door een grote instroom van jonge rekruten (die anders als niet-broeders hadden moeten wachten). Hierdoor verandert de leeftijdssamenstelling van de lokale broedvogelpopulatie voor ten minste drie jaar alvorens de oude situatie is hersteld. Deze studie laat duidelijk zien dat begrip van een lokaal moerassysteem een lange adem vereist, en bovendien een brede geografische blik (in dit geval geheel Zuid-Europa en grote delen van Afrika).