SPATIAL RELATIONSHIPS BETWEEN TREE-NESTING HERON COLONIES AND RICE FIELDS IN THE CAMARGUE, FRANCE

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ABSTRACT.—Habitat composition around nesting sites is one of the important factors that drive the colonial dynamics of waterbirds. Using a Monte Carlo procedure, we compared the changes that occurred over a period of 25 years (1975–1999) in (1) the distribution and composition of tree-nesting heron colonies and (2) the distribution and amount of rice cultivated in the Camargue region of southern France. During the period of 1967–1999, 25 sites in the Camargue were each occupied for at least one breeding season by colonies of tree-nesting herons. Total number of nests, number of nests per colony, and number of colonies varied among the four species considered. During the same period, the proportion of the study area planted with rice fluctuated widely. Overall, nests of all species tended to be located at sites surrounded by a large area of rice fields. However, examination of the results revealed a difference among species in selection of nest colony sites: Cattle Egret (Bubulcus ibis), Squacco Heron (Ardeola ralloides), and Black-crowned Night Heron (Nycticorax nycticorax) seemed more inclined to nest on sites surrounded by rice fields; whereas Little Egrets’ (Egretta garzetta) nest choice was not consistently related to availability of rice fields. That pattern was especially noticeable at a small scale (i.e. <5-km radius around the colony). Our spatial analysis supports previous findings on the effects of rice farming on the colony dynamics of tree-nesting herons. We conclude that different landscape scales are an important consideration for understanding colony site selection and need to be taken into account in the planning and design of agri-environmental development schemes.

Résumé.—La composition de l’habitat est un des facteurs importants qui influencent la dynamique coloniale des oiseaux d’eau. Nous avons utilisé une analyse Monte Carlo pour comparer les changements observés sur une période de 25 ans dans la distribution et la composition des colonies de quatre espèces d’hérons coloniaux arboricoles, et dans la distribution et l’étendue de riz cultivé en Camargue, France. De 1967 à 1999, 25 sites différents ont été occupés au moins une fois par les hérons pendant la saison de reproduction. Le nombre total de nids, le nombre de nids par colonie et le nombre de colonies ont varié différemment selon les espèces considérées. Pendant la même période, la superficie en riz cultivée en Camargue a énormément fluctué. Globalement, les nids de toutes les espèces étaient localisés sur des sites entourés d’une large proportion de rizières. Cependant, un examen détaillé montre une hiérarchie parmi les 4 espèces de hérons en relation avec leur sélection de colonies de reproduction basée sur la distribution des rizières. Le Héron garde-boeuf (Bubulcus ibis), le Héron crabier (Ardeola ralloides) et le Héron bihoreau (Nycticorax nycticorax) semblent plus niché dans des sites entourés de rizières, alors que le choix du site par l’Aigrette garzette (Egretta garzetta) n’est pas forcément relié à la disponibilité des rizières autour du site. Cette différence est particulièrement remarquable à petite échelle (i.e. < 5 km de rayon autour de la colonie). Nos analyses spatiales confirment les résultats d’études précédentes sur les effets de la riziculture sur la dynamique coloniale des hérons arboricoles en Camargue. Cette étude soulève la nécessité de considérer différentes échelles paysagères pour comprendre la sélection des sites de colonies qui doit être particulièrement prise en compte dans la mise en place de mesures agri-environnementales.

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Multiple factors drive colony site dynamics in waterbirds, depending on species and on habitat quality (Kharitonov and Siegel-Causey 1988, Fasola and Alieri 1992, Boulinier and Lemel 1996, Erwin et al. 1998). Habitat composition around nesting sites has been far the most studied of those factors (for a review, see Fasola and Alieri 1992, Baxter and Fairweather 1998). Because reproduction is a time of high energy demand (Drent and Daan 1980), availability of suitable foraging sites will directly influence colony location, colony size, and reproductive parameters.

Today, cultivated lands represent ≤30% of the world’s terrestrial habitats (Fisher et al. 2000) and ~50% of habitats in Europe (Pain and Dixon 1997). Agro-ecosystems are often part of the main ecosystems in which bird species accomplish all or part of their life-cycles (Fuller et al. 1995, Pain and Dixon 1997, Perkins et al. 2000). Rice fields are among the most widespread of those human-made habitats, totaling 11% of the Earth’s farmlands. Having replaced many natural wetlands on all continents, rice fields have become the only wetlands available for waterbirds in some regions (Fasola and Ruiz 1997). Examining how those artificial wetlands contribute to their ecology is therefore essential to understanding the population dynamics and distribution of colonial waterbirds (Hafner and Fasola 1992, Fasola and Alieri 1992, Fasola and Ruiz 1997, Tourenq et al. 2001). It is also important from a conservation perspective because management decisions and policies require identification of species’ needs and of the processes affecting those needs (Bennetts et al. 1998).

The Camargue region of southern France, one of the main wetland complexes of the western palearctic, is a major breeding ground for colonial waterbirds (Heath and Evans 2000) in Europe and also a major area of rice production on the continent (Fasola and Ruiz 1997). Of the species that extensively use rice fields in the Camargue, tree-nesting herons are the most studied (Bredin 1984, Hafner et al. 1986, Hafner and Fasola 1992, Tourenq et al. 2000). Many studies on coloniality of tree-nesting herons in the world have focused on the relationship between colony size and availability of foraging sites around the colony (Gibbs et al. 1987, Gibbs 1991, Fasola and Alieri 1992, Hafner and Fasola 1992, Baxter and Fairweather 1998). However, little attention has been given to the relationship between colony location and spatial distribution of foraging sites (but see Gibbs et al. 1987, Gibbs 1991, Fasola and Alieri 1992). Authors of previous studies (Hafner and Fasola 1992, Parejo and Sánchez-Guzmán 1999, Tourenq et al. 2000) have suggested a significant positive correlation between the number of breeding pairs of some tree-nesting heron species in a colony and the proportion of rice fields around the colony site. We further investigated that relationship by examining changes in the distributions of rice fields and tree-nesting heron colonies in the Camargue over a 25-year period.

Methods

Study area.—Our study area was the delta of the Rhone River in southern France, known as the Camargue (43°30’N, 4°30’E; Sandoz and Chauvelon 1998), a 142,000-ha wetland complex that is home to ≤14 colonies of tree-nesting herons each year. Natural habitats cover some 60,000 ha (~41% of total surface) and salt pans some 21,000 ha (~15% of total surface), the latter located in the southern part of the delta. Some 24,000 ha (~16% of total surface) are used for rice farming and 26,000 ha (~18% of total surface) for dry crops. Finally, an industrial complex located in the southwestern part (Fos-sur-Mer metal transformation and refineries) covers ~9% of the delta’s total surface area (Tourenq et al. 2000).

Rice is traditionally cultivated in flat areas, which are usually flooded just before sowing (end of April through early May). Germination takes place 7–15 days later and rice plants emerge from water ~30 days after sowing. They develop stems in June and attain their maximum height in August. Harvest takes place in September–October after rice fields are completely dried some days before harvesting. During the period considered (1967–1999), the total area planted to rice fluctuated widely in the study area (see below). From 1967 to 1981, rice cultivation decreased by ~85%, from 26,770 to 4,400 ha. After 1981, cultivation increased again, reaching in 1993 approximately the same value as in the late 1960s (24,000 ha). A decrease of ~20% has been registered since. In addition to that variation in total surface-area cultivated, agricultural practices have changed in the area, with increasing mechanization of seeding and, since 1985, use of laser technology to level rice fields. Those changes resulted in water levels, which had previously been highly variable, being consistently maintained at 10 cm maximum water depth during the flooding phase (end of April through early May), which corresponds to the breeding season of tree-nesting herons (Fasola and Ruiz 1997, Tourenq et al. 2000).
Four species of herons breed in dense interspecific tree colonies in the Camargue: Little Egret (EGRETA GARGANZELLA), Cattle Egret (BUBULCUS IBIS), Black-crowned Night Heron (NYCTICORAX NYCTICORAX), and Squacco Heron (ARDLEA RALLOIDES). The ecology of these species has been extensively studied (for a review, see Kushlan and Hafner 2000). Little and Cattle egrets exhibit great variability in habitat use, but Little Egrets use aquatic habitats (permanent and temporary; fresh and salt water) more often than Cattle Egrets, which forage mainly on wet or dry pastures and on agricultural lands. In the Camargue, Black-crowned Night and Squacco herons are exclusively freshwater species, but the Black-crowned Night Heron exhibits a wider habitat use than the Squacco Heron: the former feeds in artificial canals, ponds, meanders, and permanent or temporary freshwater marshes; whereas the Squacco Heron feeds almost exclusively in open freshwater marshes and frequently in rice fields.

Each year from 1967 to 1999, all colonies were located and mapped throughout the delta, using a small aircraft at an elevation of 100 to 300 m (Hafner et al. 1994). From May to mid-July, each colony was censused weekly. Censuses were based on direct nest counts and were carried out each year by the same observer (H. Hafner). Counting error increased with colony size, with up to 10% underestimation of larger colonies, overestimation being unlikely (Bennetts et al. 2000). Number of pairs of each species was defined as the maximum number of pairs at the time installation of the last pair was observed.

Monitoring spatial dynamics of rice fields. — Digitized aerial photographs of the study area (scale 1:20,000) were orthorectified, georeferenced, and stored (Sandoz and Chauvelon 1998). Digitization of 18,500 agricultural blocks and of natural areas and marshes was done with MapInfo (MapInfo Corporation). That procedure provided a grid map of the Camargue with >2,000,000 quadrats. Each quadrant (26 × 26 m) was assigned to one of two classes: rice or nonrice. Land use was updated every year during the study with the help of classified satellite images (Landsat). Because of cloud cover, some satellite images were not available; high-quality images were obtained for only 11 of the 25 years between 1975 (date of the first satellite image) and 1999. Those years were 1975, 1981, 1985, 1987, 1989, 1991, 1993, 1994, 1995, 1998, and 1999. For years without satellite images, data on rice cover were obtained from the Centre Français du Riz, Arles, an agronomic organization that centralizes data on rice cultivation in France.

Statistical analysis. — For any given year, observed nest distribution in relation to rice fields was compared with theoretical nest distribution expected under the null hypothesis that birds build their nests at random (i.e. without taking rice-field distribution into account) among the pool of colony sites available across the study area. That comparison was made both for each species separately and for all four species combined. First, for each species, a linear correlation analysis was used to examine the relationship between surface area of rice fields available in a 5-km radius around each colony site and the relative tendency of the species to nest in that colony. That relative tendency, ranging between −1 and 1, was computed as the proportion of nests present within that plot minus the overall proportion of nests in all colony sites for the year and the species considered. A null value for the correlation signified that the species was distributed randomly within colonies (i.e. without taking into account the proportion of rice surface available). Second, we used numeric simulations to determine expected random nest distributions (Monte Carlo procedure; see Manly 1997). In those simulations, we considered that each year both the available sites for nesting and the total number of breeding pairs (i.e. total number of nests built) of each species depend on factors that are only loosely tied to rice-field distribution. For example, it is likely that the colony site locations depend more on presence of suitable groups of trees than on a given density of rice surrounding the site. In contrast, the number of nests that a species builds at a site in a given year may be independent of (null hypothesis) or depend in some way on (alternative hypothesis) the current rice-field distribution around the site. Consequently, in our numeric simulations, the number and locations of colony sites and the total number of nests per species were considered fixed for any given year, and set to the values observed for that year. Nest locations were drawn at random from among the various sites available in each year.

Two types of computer simulation were run. In the simpler procedure, nests of each species were distributed at random among all available colony sites, without any further constraint. In the other procedure, each site was constrained so that it could not hold more nests (all species combined) than the maximum number ever counted at that site during the census period (1967–1999). That “site-saturation constraint” was implemented as follows. First, all nests, irrespective of the species involved, were distributed at random over the available sites, but no site was allowed to contain more nests than the maximum number observed at that site. Second, each nest at each site was allocated to one of the four species according to their relative proportions on the whole study area.

For each of those two procedures and for each of the 11 years for which we had reliable data about rice distribution, 5,000 distributions of the nest locations were computed. From those distributions, expected means and confidence intervals of two complementary variables were derived, under the null hypothesis that nests were distributed at random among available sites (with or without the site-saturation
constraint). One variable was distance between a nest and the closest rice quadrat. The other variable was rice surface available for a nest (computed as the number of rice quadrats) within a given radius. Three radii were considered (1, 5, and 10 km; 10 km being the mean greatest foraging distance from a colony site for heron species of the size studied; Kushlan and Hafner 2000). Expected mean distance between a nest and the closest rice quadrat, and expected mean of rice surface available for a nest within a given radius (under the null hypothesis of a random nest distribution), were then compared to the observed mean values using normal z-tests (a normal z-test corresponds to a student t-test with an infinite number of degrees of freedom; confidence intervals were not estimated from the observed sample but from theoretical simulations run under the null hypothesis).

**Results**

Variation in heron abundance and distribution.—During the 1967–1999 period, 25 sites in the Camargue were each occupied for at least one breeding season by colonies of tree-nesting herons. Since the 1960s, yearly number of colonies in the Camargue has steadily increased for all four species. However, both total number of nests and mean number of nests per colony varied among species (Fig. 1). Total number of Little Egret nests increased by ~80% during the study period ($r^2 = 0.43$, $F = 23.9$, df = 1 and 31, $P < 0.0001$; Fig. 1), but their average number of nests per colony did not exhibit any trend and was highly variable ($r^2 = 0.02$, $F = 0.8$, df = 1 and 31, $P = 0.37$). Cattle Egret numbers increased from a single nest observed in 1967 to a recent high of 4,497 nests in 1999; mean number of nests per colony increased by ~300% over the same period ($r^2 = 0.63$, $F = 54.1$, df = 1 and 31, $P < 0.0001$; Fig. 1). Number of Black-crowned Night Heron nests declined substantially during the mid-1980s (75% decrease from 1967 to 1986) and increased again during the mid-1990s. However, mean number of Black-crowned Night Herons per colony has decreased by ~85% over the entire period ($r^2 = 0.68$, $F = 66.4$, df = 1 and 31, $P < 0.0001$; Fig. 1). Squacco Herons have exhibited a slight increase over the past three decades, but of lesser magnitude than the increases of Little and Cattle egrets ($r^2 = 0.29$, $F = 12.9$, df = 1 and 31, $P = 0.001$; Fig. 1). Mean number of Squacco Herons per colony has not exhibited any clear trend ($r^2 = 0.07$, $F = 2.4$, df = 1 and 31, $P = 0.12$).

Relationship between rice fields and heron abundance in colonies.—Proportion of Little Egret nests within colonies decreased with rice-field surface area (i.e. number of rice quadrats) in a 5-km radius around each colony site ($r^2 = 0.24$, $F = 25.7$, df = 1 and 79, $P < 0.0001$; Fig. 2A). Proportion of Cattle Egret nests within colonies tended to increase with rice-field surface area in a 5-km radius around each colony site ($r^2 = 0.14$, $F = 13.6$, df = 1 and 79, $P < 0.0001$; Fig. 2A). Relationships between proportions of Squacco and Black-crowned Night herons and rice-field surface area within a 5-km radius around colonies were weaker ($r^2 = 0.07$, $F = 5.6$, df = 1 and 79, $P = 0.02$ and $r^2 = 0.04$, $F = 3.2$, df = 1 and 79, $P = 0.08$, respectively; Fig. 2B).

Heron nests generally closer to rice fields than would be expected by chance (Fig. 3A, B). Differences in expected and observed mean distances between a nest and the closest rice quadrat were significant for all years and species considered (z-test, $P < 0.01$), except for the Little Egret in 1994 (z = 0.09, NS). Little Egrets differed from Cattle Egrets, Squacco Herons, and Black-crowned Night Herons in that they did not consistently nest closer to rice than expected by chance. That difference was more apparent during the period between 1989 and 1995.

Use of colony sites was influenced by the proportion of rice fields within radii of 1, 5, and 10 km around colony sites. Squacco Heron abundance within a colony was positively correlated with increased proportion of rice fields around the colony, especially during the period between 1991 and 1995. The relationship was weaker for Little Egrets: from the late 1980s, a negative relationship was observed between Little Egret abundance in a colony and the extent of rice fields around the colony site within a 5-km radius. The two remaining species, Cattle Egret and Black-crowned Night Heron, are intermediate, with the positive relationship of their abundance in the colony to the extent of rice fields around the site also showing a peak between 1991 and 1995. Although the pattern is clearest for the 1-km radius, it remains similar when the 5- and 10-km radii are considered (Fig. 4).

**Discussion**

Heron nests in the Camargue tend to be located at sites surrounded by a high proportion of rice quadrats (i.e. a large area of rice fields).
Fig. 1. Variations in surface area planted to rice and in number of colonies and number of pairs of Little Egret, Cattle Egret, Black-crowned Night Heron, and Squacco Heron (∗10) in the Camargue, France, for years 1967–1999.
Fig. 2. Difference between proportion of nests of each heron species at each site (local proportion) and overall (global) proportion of nests of each species at all colony sites for the years 1967–1999, considering rice-field surface area available in a 5-km radius around each colony site. Null values signify that species are distributed randomly within colonies. (A) Little Egret and Cattle Egret, (B) Squacco Heron and Black-crowned Night Heron.
Fig. 3. Comparison of observed and expected distance between a nest and the closest rice quadrat, in colonies of tree-nesting herons in the Camargue, France, with (A) and without (B) “site-saturation constraint.” Values above or below the x-axis indicate, respectively, that nests were farther from or nearer to rice than expected by chance.
Fig. 4. Comparison of observed and expected heron abundance in colonies and in rice fields within a radius of 1 km (A), 5 km (B), and 10 km (C) around colony sites. Values above or below the x-axis indicate, respectively, that nests were surrounded by more or less rice than expected by chance.
However, close examination of the four species we studied revealed differences in colony-site selection. Cattle Egrets, Squacco Herons, and Black-crowned Night Herons nested on sites surrounded by rice fields, whereas Little Egrets’ nest choice was not consistently related to availability of rice fields. Little Egrets also differed from Cattle Egrets, Squacco Herons, and Black-crowned Night Herons in that they did not nest more closely to rice fields than expected. The negative relationship between proportion of Little Egret nests within a colony and available rice-field surface area was especially noticeable at the 5-km scale.

Although Little Egrets in the Camargue include rice fields in the wide range of habitats they use (Hafner et al. 1986), they tend to avoid cultivated habitats, such as rice fields, and forage in natural marshes during parts of the year (Lombardini et al. 2001, Tourenq et al. 2001). The Cattle Egret, in contrast, uses farmed areas extensively and is commonly observed in rice fields year-round (Lombardini et al. 2001). Finally, Black-crowned Night and Squacco herons are exclusively freshwater species (Hafner and Fasola 1992) that prefer natural marshes but will occasionally use rice fields.

Habitat associations changed temporally in relation to availability of rice fields. A random distribution of heron nests was observed at spatial scales of <5 km during the 1980s, when the area of rice cultivation was lowest. Increases in species occurrences within colonies in relation to abundance of rice fields around colony sites were observed in the early 1990s, when both rice acreage and number of heron colony sites increased in the landscape. New colony sites were established when sites both with and without a high proportion of rice in their surroundings were still available; birds thus had opportunities to “choose” among different site types. Finally, the latter half of the 1990s corresponded to a period of saturation of colony sites in the Camargue, with intense intra- and interspecific competition (Bennetts et al. 2000, Hafner et al. 2001, L. Dami unpubl. data). Birds might have then been forced to occupy sites regardless of the proportion of rice fields in their vicinity—hence the decrease in species segregation with respect to variation in abundance of rice fields around colony sites.

Surface area and quality of freshwater habitats have been reported as factors limiting size and diversity of breeding heron populations in the Mediterranean region (Hafner and Fasola 1992). The region is characterized by a succession of dry (summer) and wet (fall–spring) periods. Hafner et al. (1994) reported a significant effect of rainfall amount prior to the breeding season on number of tree-nesting herons. During dry years, foraging sites may be restricted to rice fields, which are flooded from spring to fall, whereas temporary freshwater marshes dry during the same period. Colony sites in an environment rich in rice fields may be more attractive during those periods of drought. Our data set included two years of drought, 1989 and 1998, with respectively 24% and 60% less precipitation than the mean calculated since 1963 (623 mm; P. Chauvelon unpubl. data). However, we did not find clear evidence of an effect of drought on spatial distribution of colonies, a result consistent with the absence of a rainfall effect on temporal population and colonial patterns of tree-nesting herons reported in Tourenq et al. (2000).

With the worldwide loss of natural wetlands and their replacement by artificial wetlands, the effects of rice farming on waterbirds have been increasingly studied (Fasola and Ruiz 1997, Tourenq et al. 2001, Elphick 2000). Heron colony dynamics, in particular, have been said to be influenced by the proportion of rice fields in the landscape mosaic (Hafner and Fasola 1992, Parejo and Sánchez-Guzmán 1999, Tourenq et al. 2000). However, as evident from our study, the relationships between waterbirds and rice farming are complex and vary temporally among regions and species. Our spatial analysis supports previous results on the effects of temporal variation in rice acreage on dynamics of tree-nesting herons in the Camargue (Tourenq et al. 2000). That study suggests that when rice habitat proportion falls below some level in the landscape, herons cease to select colony sites in the way that optimizes their access to rice fields—which might mean that herons sample the landscape to select colony sites at scales larger than those used in the study. In other words, when a suitable habitat becomes less common, herons may increase the scale at which they assess the landscape.

Agro-environmental schemes are currently under revision in the Camargue. Decisions to be made involve a new structuring of the territory at the levels of field (evolution of agricultural
practices), farm (diversity of production systems) and landscape (dynamics between agricultural and rural uses). Until now, ecological and socio-economic evaluations have not taken into account those three levels simultaneously. Mathevet et al. (2003) suggest that a good understanding of the role played by agricultural policies in a region's development history and geography of development is fundamental to any conservation policy analysis. Examination of long-term data sets such as the one used here can provide new insights into how to interpret the effects of changes in the landscape mosaic on birds communities.

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