



The importance of rice fields for glossy ibis (*Plegadis falcinellus*): Management recommendations derived from an individual-based model

Gregorio M. Toral^{a,*}, Richard A. Stillman^b, Simone Santoro^a, Jordi Figuerola^a

^a Department of Wetland Ecology, Doñana Biological Station, CSIC, Avda. Américo Vespucio s/n 41092, Seville, Spain

^b School of Applied Sciences, Bournemouth University, Talbot Campus, Poole, Dorset BH12 5BB, UK

ARTICLE INFO

Article history:

Received 16 May 2011

Received in revised form 26 January 2012

Accepted 1 February 2012

Available online 22 February 2012

Keywords:

Wetland
Agriculture
Crayfish
Waterbird
MORPH

ABSTRACT

Artificial wetlands provide alternative habitats for waterbirds. The Doñana rice fields (SW Spain) are extensively used as a foraging site by the glossy ibis (*Plegadis falcinellus*). The aim of this study was to develop an individual-based model to predict the possible effects of glossy ibis' population growth, reductions in the rice cultivated area, and changes on the phenology of the management processes of the paddies on the mortality rate of the glossy ibis population. We test the hypothesis that the glossy ibis breeding population of Doñana can obtain its energy requirements during the non-breeding season by feeding on rice fields alone. Our results show that the glossy ibis population growth is not currently limited by rice field availability. However, a reduction of 80% would cause mortality rate increases above the observed mortality (5.9% per year), with values around 10% per year for populations between 50,000 and 100,000 birds. A reduction of 90% of the rice field area would cause mortality rate increase above the observed value for populations greater than 20,000 birds, reaching 60% per year with a population of 100,000 birds. Cultivated area in Doñana suffers temporary reduction on its area during drought periods. Taking into account the fact that the glossy ibis population for 2011 may exceed 22,900 birds, large scale changes in the area of rice fields due to habitat transformations and/or drought periods may have important effects on the viability of the glossy ibis population in Doñana.

© 2012 Elsevier Ltd. All rights reserved.

1. Introduction

In the current scenario of loss of natural marshes, the surface area of artificial wetlands has increased in many areas, providing alternative habitats for waterbirds (Elphick and Oring, 1998; Elphick, 2000; Tourenq et al., 2001; Ma et al., 2004). Rice fields have been proven to be of great value for waterbirds in different regions of the world (Fasola and Ruiz, 1996; Elphick, 2000; Maeda, 2001; Czech and Parsons, 2002; Sánchez-Guzmán et al., 2007; Toral and Figuerola, 2010) and are thus considered the world's most important agricultural crop for waterbirds (King et al., 2010). Furthermore, in areas suffering drought periods (like the Mediterranean basin) this crop could play an important role as a refuge for waterbirds when natural marshes dry (Tourenq et al., 2001; Rendón et al., 2008). However, since the scarcity of water in those areas could also threaten the viability of rice fields, it is important to understand how future reductions in the area of rice fields could affect waterbird populations.

In the northern hemisphere the glossy ibis (*Plegadis falcinellus*) has a near cosmopolitan distribution, including areas in Africa, America, Asia, Australia and Europe (Figuerola et al., 2004). In the

Iberian Peninsula the glossy ibis became extinct as a breeding species at the beginning of the 20th century. Three failed recolonization attempts of the area by glossy ibis occurred in Doñana marshes during 1930–1935, 1940–1942 and 1958 (Figuerola et al., 2004). New breeding colonies were established in the marshes of the Doñana National Park (SW Spain, Fig. 1) and Ebro Delta (Catalonia, NE Spain) in 1996 (Santoro et al., 2010). The colony of Doñana has rapidly increased (Fig. 2) to become the largest colony in Western Europe (Figuerola et al., 2004) and held more than 3500 pairs in 2007 (Máñez and Rendón-Martos, 2009), and about 5300 pairs in 2010 (Máñez pers. com.). However, the concentration of this important breeding colony in a few locations in the Doñana marshes increases the risk of extinction due to any exceptional event that affects Doñana (for example no breeding occurred in 1999 and 2005 due to severe droughts). At present, the glossy ibis is considered IUCN Vulnerable in Spain (Figuerola et al., 2004) and is a species of conservation concern in Europe, where it is in decline (Delany and Scott, 2006).

Rice is an important food for many avian species (Lourenço and Piersma, 2008; Stafford et al., 2010). Glossy ibis consistently exploit rice agriculture throughout their range (del Hoyo et al., 1992; Hancock et al., 1992; Taylor and Schultz, 2010). There are a few detailed studies of glossy ibis diet carried outside Europe (Acosta et al., 1996; Davis and Kricher, 2000). The only study in Europe, performed in Doñana, indicates that during the breeding

* Corresponding author. Tel.: +34 654442904; fax: +34 954621125.

E-mail addresses: grego@ebd.csic.es (G.M. Toral), rstillman@bournemouth.ac.uk (R.A. Stillman).

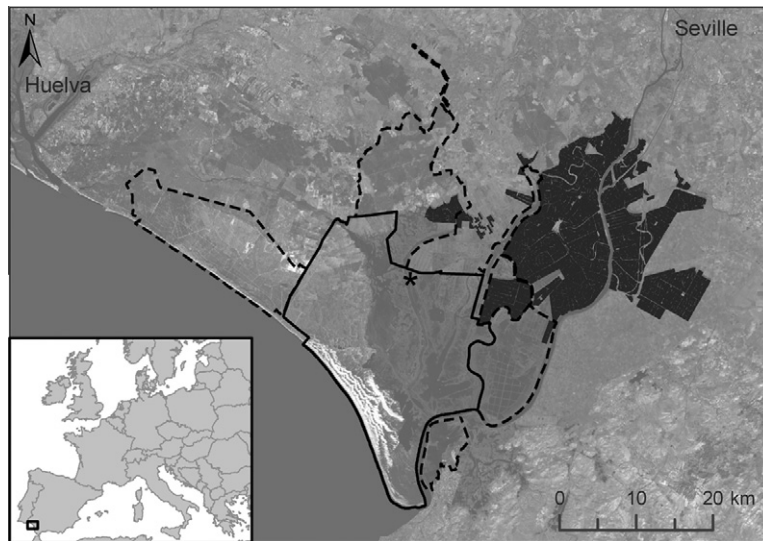


Fig. 1. Location of the study area showing rice fields (black) and the boundaries of the Doñana National Park (solid line) and Doñana Natural Park (dashed line). The symbol (*) indicate the location of the main breeding colony of glossy ibis.

season the glossy ibis diet is dominated by aquatic Coleoptera and Odonata (Macías et al., 2004). However, during the non-breeding season in Doñana, glossy ibises feed on the waste rice grains present in the paddy fields after the harvest (pers. obs.). This shift in the diet between the breeding and non-breeding season has been also observed in the glossy ibises feeding in rice fields in Cuba, and confirmed by looking at stomach contents (Acosta et al., 1996).

During the non-breeding season (from September to February), most of the glossy ibis leave the marshes of Doñana and go to surrounding rice fields, where they feed on rice grains in post-harvested ploughed rice paddies. While feeding on rice fields, glossy ibis use a roost in a well conserved area situated inside the rice field area, near the river Guadalquivir. Evaluating the quality of Doñana rice fields as a foraging site for this species and the possible negative effects of future reductions in the area cultivated on the mortality rates of this growing population is essential to inform the appropriate management decisions.

Individual-based models, comprised of fitness-maximising individuals, are a potential tool for predicting the mortality rates and body conditions of birds under different scenarios (Stillman et al., 2005a). Individual-based models based on the MORPH software (Stillman, 2008) have been successfully used to predict the effects

of changes in the environment in a variety of species of shorebirds and wildfowl and have successfully predicted changes in mortality rates due to loss of habitat (e.g. Stillman and Goss-Custard, 2010; Stillman et al., 2005b; Durell et al., 2006). MORPH models have been shown to be of great value when assessing conservation objectives of waterbirds (Stillman et al., 2010). The key feature of these models is that they are based on the assumption that individuals within animal populations always behave in order to maximise their own chances of survival and reproduction, no matter how much the environment changes (Stillman, 2008). The decisions made by model animals are based on optimal foraging theory and game theory, which are thought to provide a reliable basis for prediction (Goss-Custard, 1993; Sutherland, 1996; Goss-Custard and Sutherland, 1997). Therefore, animals in these individual-based models are expected to respond to environmental change in the same ways as real animals would (Goss-Custard, 1993; Sutherland, 1996; Goss-Custard and Sutherland, 1997). Using this model, population level parameters are predicted from the fates of all individuals in the population (Stillman et al., 2005a).

In this paper we demonstrate how a MORPH individual-based model can be used to assess the quality of rice fields as a foraging site during the non-breeding season for the glossy ibis. The MORPH software has not previously been used to assess the quality of an artificial habitat. Furthermore, to our knowledge, this is the first individual-based model developed for the glossy ibis. We test the hypothesis that the current and future glossy ibis population of Doñana can obtain their energy requirements during the non-breeding season feeding on rice grains in the rice fields surrounding the Doñana National Park. We first test if the current rice field area is able to support an increased population of glossy ibis as, at present, it is still growing (Santoro et al., 2010). We then model loss of habitat and changes in the phenology of the management of the paddies to predict the effect of environmental change on mortality rates. We consider the implications of our results for the conservation of the species in Doñana.

2. Materials and methods

2.1. Study site

The rice fields of Doñana (Fig. 1) are the largest rice field area in Spain. They are situated near the marshes of the Doñana National Park, a 55,000 ha wildlife reserve north of the Guadalquivir estuary

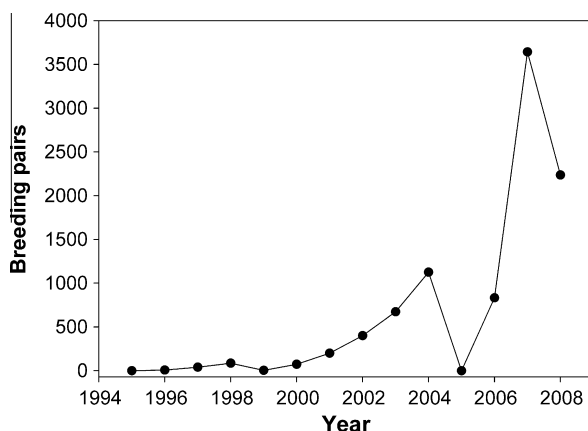


Fig. 2. Increases in the breeding season population of glossy ibis in Doñana, Southwest Spain (based on Santoro et al. (2010) and unpublished data from the Natural Processes Monitoring Team of the Doñana Biological Station (<http://www-rbd.ebd.csic.es/Seguimiento/seguimiento.htm>).

in Andalucía (SW Spain). The climate is Mediterranean sub-humid with rainy winters and dry summers. For more details of the area see Serrano et al. (2006), Rendón et al. (2008) and Kloskowski et al. (2009). Of the 180,000 ha of fresh and brackish marshes present in 1900, 36,000 ha were transformed into rice fields between 1926 and 1997 (García-Novo and Martín-Cabrera, 2006; Rendón et al., 2008). Additionally, other types of transformation have reduced the area of natural marshes to 30,000 ha at present (Enggass, 1968; García-Novo and Martín-Cabrera, 2006). Between September and January the habitat structure of rice fields change quickly as paddy fields are harvested and thus undergo a series of management processes. A few days after a paddy field is harvested, usually at the end of September, it is ploughed whilst still wet to favour the decomposition of the stubble, which is mixed with the soil. Subsequently, the paddy field is flooded with a variable amount of water (depending on the farmer and the amount of rain that has fallen) and stays flooded until it dries up, usually in December–January.

2.2. The model

We used MORPH to develop our individual-based model. As MORPH has been described in detail elsewhere (Durell et al., 2006; Stillman, 2008), we limit ourselves to a detailed account of the model's parameterization for glossy ibis. The parameters were derived from previous literature and newly collected data. A sensitivity analysis (see Appendix A) was performed to calibrate the model and to understand the impact of variations in each parameter on the model outputs. We optimised model complexity and reduced uncertainty by using multiple patterns observed in the real system as suggested by Grimm et al. (2005). We look at the observed patterns that seem to characterise the system and its dynamics and then included the appropriate variables and processes so that those patterns emerge from the model. We evaluated how the different models (with different parameter values) reproduce observed behaviour patterns of glossy ibis and selected the model that produced the most accurate predictions (Grimm et al., 2005) (see Appendix A). MORPH tracks the location, behaviour, and ultimate fate of each individual in a population and incorporates variation in the foraging abilities among individuals. The model follows the behavioural decisions of each individual as it attempts to meet its daily energy requirements. Individuals that exceed their energy requirements add to their body stores until a maximum is reached. Individuals that cannot meet their requirements deplete their body stores to survive, but die of starvation if they deplete these stores completely.

2.3. Model parameters

An overview of the equations and default settings of the individual bird parameters in the model is given in Table 1. The model comprised all of the rice field area available in Doñana. Based on the cultivated area in 2005 (37,442 ha), the model encompassed 67 patches, one of them representing the roost and the rest representing 66 IPGs (Integral Production Groups), which are groups of paddies that have parallel control and management under the Integrated Production System. Patches size ranged from 53 to 1236 ha ($\bar{X} = 567 \pm 183$ ha). The distance from the patches to the roost ranged from 227 to 26,499 m ($\bar{X} = 9712 \pm 4390$ m). We assumed that the initial population consisted of 7000 adult birds (breeding population size in 2007). Only adult birds were considered in the model. We believe that this assumption is appropriate, as the age of first breeding in this species at Doñana is 1 year (Máñez and Rendón-Martos, 2009). In practice, to reduce the time taken to run simulations, in the model each forager represented 35–500 identical individuals (super-individuals sensu, Scheffer et al.,

1995). Foragers (but not individuals) differed in their foraging abilities and behaviour. The initial size of body store (Table 1) was calculated using data from the CRC handbook of avian body masses (Dunning, 1993).

The MORPH model source code and user guide are available as an online appendix to a study that has already been published (Stillman, 2008). The parameter files used in this study are available as online appendices (Appendix B and C).

2.3.1. Time period

The model simulated glossy ibis feeding on rice fields during the non-breeding season (150 days) from 20th September, when all the paddies are sown, to 18th February, when all the paddies are dry and birds return to the marshes of the Doñana National Park, which usually have been flooded by winter rainfall (although they can be dry during severe drought periods). The model mimicked how paddies are harvested, ploughed while containing some water, and subsequently dry. The days on which each patch was harvested, ploughed and became dry were randomly selected for each simulation from within the corresponding range of dates observed in the field during the crop seasons of 2005–2006 and 2006–2007. Glossy ibis migrated to the model following a uniform distribution of arrival dates during the period between the day on which the first patch was ploughed and 1st November, the month when the highest number of glossy ibis is observed in rice fields of Doñana (Toral pers. obs.). Birds emigrated from the model following a uniform distribution of emigration dates during the period between 10 days after the first patch became dry and the day on which the last patch became dry. Paddies became accessible to birds once they were ploughed and remained accessible until they became dry. Birds fed on patches during daylight, and went to the roost during the night. The duration of daylight was calculated from the location of the rice fields (<http://www.usno.navy.mil/USNO/astronomical-applications/data-services/rs-one-year-us>) and ranged from 9 h 35 min to 12 h 15 min. In the model, time was divided into discrete 1 h time steps, during which environmental conditions and the distribution of birds remained constant.

2.3.2. Distribution of food supply through the winter

To evaluate the density and biomass of food resources, core samples were taken from 24 ploughed paddies at six locations across the rice field area (four replicated paddies on each location). Five replicate cores were taken in each paddy. Samples were collected using a 69 mm diameter core, penetrating approximately 10 cm into the mud. To account for seasonal changes in food supply, paddies were sampled three times during the course of winter, October–November 2007, December–January 2008, and March 2008, resulting in a total of 360 cores. Samples were filtered and sieved through 0.5 mm mesh. The number of rice grains per core was counted. We then measured the mean dry mass (after drying for 24 h at 60 °C) and ash-free dry mass (after burning off organic matter for 4 h at 450 °C) of rice grains in each core. The area of paddies was calculated using ArcGIS 9.2 (ESRI, 2002) from which the density of rice grains was calculated. We used Generalised Linear Models to test whether the location of paddies had an effect on the density and ash-free dry mass of rice grains. We used Wilcoxon tests to explore whether rice grain ash-free dry mass or density varied throughout the winter. Statistical analyses were performed using SAS and SPSS.

Rice energy density was assumed to be 16.51 kJ/g (Santiago-Quesada et al., 2009).

2.3.3. Feeding behaviour of glossy ibis

Observations of a total of 56 ringed adults of glossy ibis feeding in four rice paddies between 14 December 2007 and 7 February 2008 were made to measure the mean feeding rate of the species.

Table 1
Summary of individual bird parameters used in the model.

Parameter	Value/function
Number of individuals	200 super-individuals each representing 35–500 identical birds = 7000 to 100,000 individuals
Initial size of body store (g)	Drawn from a normal distribution, with a mean of 634 g and an SD of 59 g
Target size of body store (g)	Drawn from a normal distribution, with a mean of 634 g and an SD of 59 g
Starvation body mass	418 g
Intake rate (g s ⁻¹)	0.15
Efficiency of assimilating resource component	Assimilation efficiency * efficiency to convert carbohydrates into fat = 0.90 * 16.51/33.4
Energy expenditure when feeding or roosting (kJ h ⁻¹)	35
Energy expenditure when moving (kJ m ⁻¹)	4.21
Energy density of bird reserves	Amount of energy (kJ) contained in a gram of bird fat reserves = 33.4 kJ g ⁻¹ (value measured in shorebirds by Kersten and Piersma, 1987).
Rule for knowledge of site	Birds always know food supply in every patch
Survival	If body store <418 g at the end of time step, the individual dies.

Each individual was observed over 5 min and feeding observations were recorded onto a digital voice recorder. Birds were observed feeding on rice grains, taking one grain at a time. The formula applied in the model for the functional response of the glossy ibis was defined according to Goss-Custard et al. (2006). Maximum intake rate was based on the maximum daily energy assimilation calculated from body mass using standard equations (Kirkwood, 1983). We used the value of assimilation efficiency (90%) corresponding to black-tailed godwits (*Limosa limosa*) eating rice grains (Santiago-Quesada et al., 2009) since glossy ibis' value is currently unknown. The feeding rate of glossy ibis was determined through a combination of observations during this study and a meta-analysis of the functional responses of shorebirds (Goss-Custard et al., 2006), a group of birds that are structurally similar to glossy ibis and have similar foraging behaviour. The rate at which glossy ibis feed in the model (FR, measured as rice grains s⁻¹) was determined by the abundance of food in a patch and calculated using the following equation (Goss-Custard et al., 2006):

$$F = \frac{F_{\max} N}{N_{50} + N} \quad (1)$$

where $F_{\max}$ = maximum intake rate when rice grains are superabundant, N = rice density in the patch (grains m⁻²) and N_{50} = grains density (grains m⁻²) at which feeding rate is 50% of its maximum. We used the mean feeding rate measured for glossy ibis in the rice fields, based on the frequency of swallowing movements (0.15 g s⁻¹) as $F_{\max}$, assuming that birds were feeding at their maximum rate (Goss-Custard et al., 2006). We used the value of N_{50} corresponding to redshank (*Tringa tetanus*) feeding on *Hediste diversicolor* (46.1 items m⁻²) (Goss-Custard et al., 2006) since this was the prey species in the meta-analysis with the closest ash-free dry mass (0.006 g) to that of rice grains.

The amount of energy expended per time step by birds when feeding or roosting (Table 1) was based on body mass using the all bird equation of Nagy et al. (1999). The energy expenditure when flying (Table 1) was based on body mass and wing length using the formula derived by Castro and Myers (1988). We used the value of flight speed (45.4 km/h) measured on glossy ibis by Bruno and Andreas (2001) to calculate the energy expenditure by kilometre of flight.

2.3.4. Decision rules

Birds' decision rules depended on the energy assimilation achievable on each available patch. Model birds were assumed to have perfect knowledge of the food supply on each patch. The distance (m) from the centroid of each patch to the roost was measured using ArcGIS 9.2. During each time step the birds calculated the energy they could obtain by feeding for 6 h in a patch, taking into account the energy spent while feeding and

the energy spent to fly to the patch. Model birds then moved to the patch that maximised their energy assimilation. We used a value of 6 h as ringed individual glossy ibis were observed to remain feeding within the same paddy up to 5 h 30 min. We did not use a shorter time as a sensitivity analysis (see Appendix A) showed that this resulted in the model birds avoiding patches furthest away from the roost, whereas these patches were used by the real birds.

2.3.5. Mortality rates

Since the establishment of the colony in 1996, a high proportion (25–80%) of the chicks of glossy ibis have been marked every year with pvc rings. Observed mortality rate (5.9% per year) was indirectly estimated by the analysis of capture-mark-resight (CMR) data from 5 years (September 2000–August 2005). We consider that this estimate might be slightly higher than the real mortality rate as this population showed a consistent site fidelity (unpublished data) during the period of study (for details, see White and Burnham, 1999). In the individual-based model, the only source of mortality considered was starvation. Illegal hunting is other possible cause of mortality for this species in the wild. However, we have not included it in the model since we think that it is a minor cause of mortality that does not affect the population and it is also very difficult to measure. A model bird died if it failed to maintain its body mass above a starvation body mass of 418 g. This value was calculated by regression of the mass against known starvation mass of seven waterbird species of increasing size (see Stillman et al. (2005a) for the starvation masses of these waterbirds).

2.3.5.1. Simulations.

Once the model was calibrated, we simulated two possible scenarios of environmental change:

1. To determine the effect of possible habitat loss and increased population on site quality, we ran simulations combining populations ranging from 10,000 to 100,000 birds (using intervals of 5000) and habitat loss of 0%, 50%, 80% and 90% (Fig. 3).
2. To determine the effect of changes in the date the paddies were ploughed, we ran simulations with increasing length of the base interval between harvest-day and plough-day (range from 10 to 50 days. The plough-day for each patch was randomly selected from this interval; the mean observed interval was 31 days). We ran two separate groups of simulation: one with a population of 25,000 birds and another with a population of 75,000 birds.

The characteristics of each individual were randomly generated at the start of each simulation. As a result, predicted mortality rates varied slightly between replicate simulations using the same parameter values. Therefore, model results were based on the average predictions of 50 replicate simulations with each combination



Fig. 3. Reductions in the number of rice patches included in the individual-based model to simulate loss of habitat. Simulations without habitat loss included all the rice fields (A, 66 patches). Habitat loss was simulated by reductions of 50% (B, 33 patches), 80% (C, 12 patches) and 90% (D, 5 patches) of cultivated area.

of population, rice field area and interval between harvest-day and plough-day.

3. Results

3.1. Distribution of food supply through the winter

Rice density varied among locations. A post-hoc Tukey–Kramer test showed that half of the locations had a high density of rice (hereafter ‘high density’ patches) in October–November ($\bar{X} = 1056 \pm 687$ grains m^{-2} , $n = 12$ paddies) and the other half had low density of rice (hereafter ‘low density’ patches) ($\bar{X} = 212 \pm 200$ grains m^{-2} , $n = 12$ paddies). This distribution of the food supply was incorporated in the model, so that every patch had a 50% probability of being a ‘high density’ or ‘low density’ patch at the beginning of the simulation. Rice ash-free dry mass did not vary among locations and had a mean value of 0.0169 ± 0.0017 g ($n = 19$ paddies) during October–November. Rice density in ‘high density’ paddies decreased a 65% between the second and third sampling periods, with mean final value of 374 ± 244 grains m^{-2} ($n = 12$ paddies). Rice ash-free dry mass decreased between the first and second sampling periods, with mean final value of 0.0126 ± 0.0040 g ($n = 19$ paddies). These patterns of changes in rice density and ash-free dry mass were incorporated into the model. Depletion of rice due to consumption by the glossy ibis was also incorporated into the model.

3.2. Feeding behaviour of glossy ibis

The observed mean feeding rate was 0.15 ± 0.10 rice grains/s ($n = 56$). On only four occasions were glossy ibis observed to consume prey larger than a rice grain. Two of these were identified as the introduced red-swamp crayfish (*Procambarus clarkii*) and the other two could not be identified.

3.3. Observed mortality rates

The observed mean mortality rate derived from CMR data was $5.9 \pm 5.5\%$ ($n = 5$ years) per year. As the individual-based model encompassed a period of 150 days, the annual predicted mortality rate derived from the model was calculated as the sum of the mortality predicted by the model plus 3.5% (the mortality corresponding to the remaining 215 days of the year based on the observed annual mortality).

3.4. Predicted mortality rates

3.4.1. Increased population and reductions in the cultivated area

In simulations including all of the rice field area, an increase in population size up to 100,000 birds had no effect on predicted mortality rates (Fig. 4), showing that population growth was not limited by rice field availability. Simulated habitat reduction of 50% also had no effect on predicted mortality rates, even with a population of 100,000 birds. With a reduction of 80% in rice field area, the predicted mortality rate was higher than the observed mortality rate for populations above 25,000 birds, and it remained near 10% per year for populations between 50,000 and 100,000 birds. With a reduction of 90% of rice field area, the predicted mortality rate was higher than the observed mortality rate for populations above 20,000 birds, and increased with increasing population size, reaching 60% per year for a population of 100,000 birds.

3.4.2. Increased length of the interval between harvesting and ploughing

The length of the interval between harvesting and ploughing had no influence on predicted mortality rates, which were always below the observed value (Table 2). This lack of relationship was observed for the two tested population sizes (25,000 and 75,000 birds).

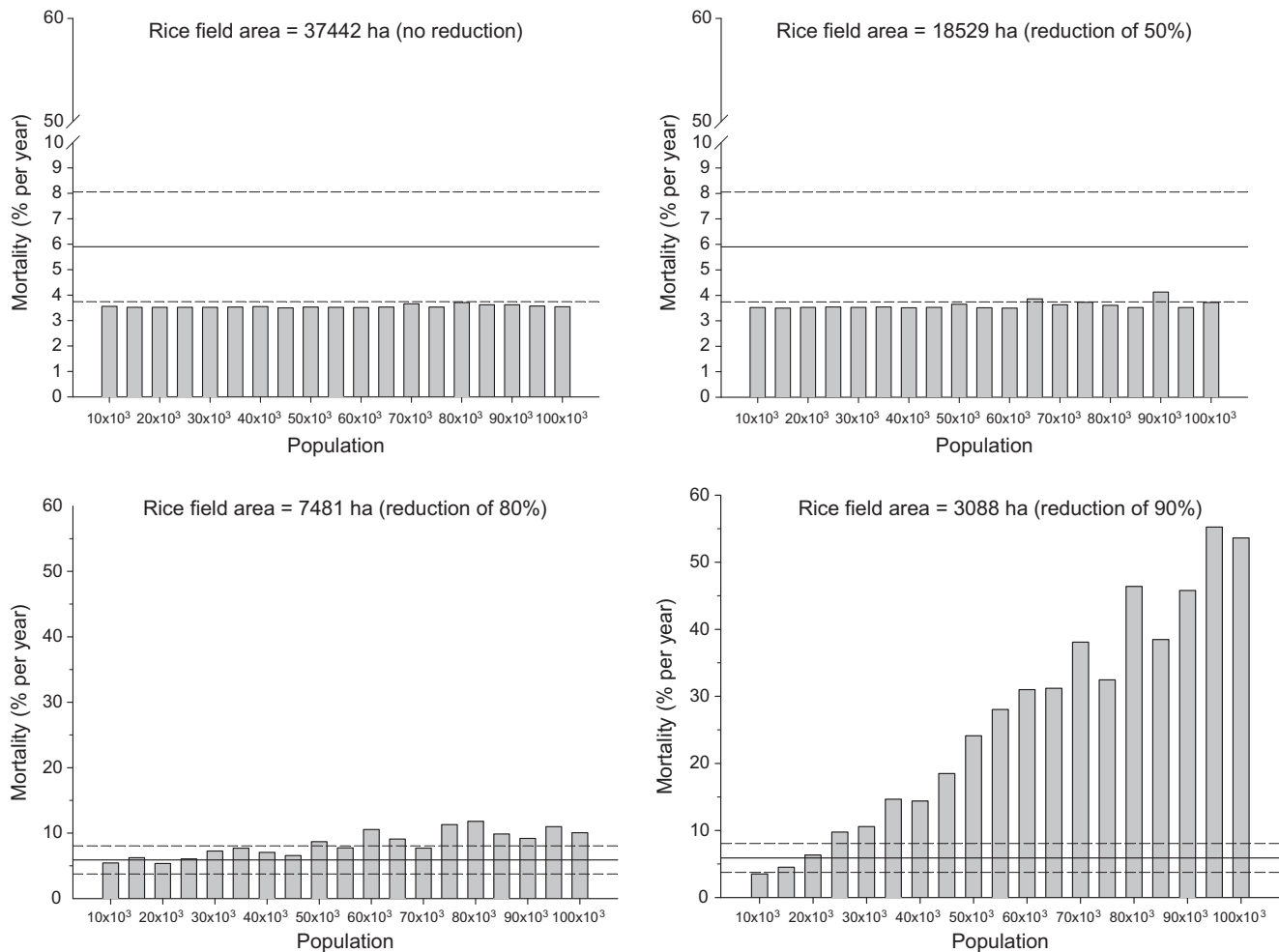


Fig. 4. Predicted mortality rates of glossy ibis in relation to rice field area and the population included in the model. Each bar shows the mean of 50 replicate simulations. Solid line represents observed mortality rate (5.9% per year). Dashed lines represent 95% confidence interval of mortality rate.

Table 2

Predicted mortality rates (% per year) of glossy ibis over a range of interval lengths between harvest-day and plough-day obtained for a population of 25,000 birds (Mortality A) and 75,000 birds (Mortality B).

Interval length	Mortality A	Mortality B
10	3.6	3.5
20	3.5	3.7
30	3.5	3.5
40	3.5	3.5
50	3.5	3.7

4. Discussion

Our results confirm the hypothesis that the current glossy ibis population of Doñana can obtain their energy requirements during the non-breeding season by feeding on rice grains in the rice fields surrounding the Doñana National Park. Furthermore, it is unlikely that the growth of the population will be limited by habitat availability during the non-breeding period. However, the model predicted that, a greater than 80% reduction in the area cultivated would cause increased mortality rate in a population of 25,000 birds, and that a greater than 90% reduction in area would cause increased mortality in populations of greater than 20,000 birds. The glossy ibis breeding population in 2010 reached 5267 breeding pairs (Manolo Máñez pers. com). As the mean productivity of this

species in Doñana is 2.1 chicks/breeding pair (Máñez and Rendón-Martos, 2009), it is expected that during the non-breeding season of 2011, more than 20,000 glossy ibises (including juveniles) will be feeding on rice fields. Thus, conservation planning is required to ensure that possible future reductions in rice field area do not affect this growing glossy ibis population.

We checked if simple energetic calculations (instead of our Morph individual based model) fail to predict glossy ibis mortality rates (analyses not shown). We based our calculations on the total amount of energy within the rice fields, the daily energy requirements of the glossy ibis and the assimilation efficiency. We found that simple energetic calculations failed to predict the mortality rate of glossy ibises, since no bird would die in a population of 100,000 feeding on the complete area of rice fields for more than 2 years (804 days), while both the observed and Morph predicted mortality rates are positive. These differences emerge from the fact that in the model, as in the real system, individuals compete for the same resource (rice grains) and a variation in the foraging abilities and initial body size among individuals is incorporated.

The Doñana glossy ibis breeding colony has been shown to be sensitive to changes in the marshes, as the birds failed to breed in 1999 and 2005 due to the scarcity of water caused by drought (Fig. 2). Drought periods in Doñana have already caused severe reductions in the area of rice cultivated during some years. For example, during 1993–1995 a severe drought period caused reductions of 80% and 90% of the rice cultivation area, reducing it to

2910 ha in 1993, 6400 ha in 1994 and only 1641 ha in 1995. During the last drought period in Doñana, the reductions on the rice field area were less severe but still important (40%), but future drought periods may cause new episodes of reductions in rice field area.

Glossy ibis is not the only species feeding on rice grains in the rice fields of Doñana. Recent work has shown that the Iberian rice fields provide a very profitable foraging habitat for black-tailed godwit (Masero et al., 2007; Lourenço and Piersma, 2008). During northward migration, large numbers of these birds stopover in Iberia, where they forage in large flocks that gather in rice field (Kuijper et al., 2006; Lourenço and Piersma, 2008). They forage almost exclusively on spilled rice grains and they can reduce rice availability by $50 \pm 20\%$ ($n = 10$) (Lourenço et al., 2010a). Furthermore, authors have reported that waterfowl using rice fields in winter feed heavily on waste rice (Manley et al., 2004; Mugica et al., 2006; Greer et al., 2009). Therefore, the mortality predictions of our model under habitat loss may be conservative, as depletion by other species may reduce the abundance of rice grains available to glossy ibis. However, although black-tailed godwits and several waterfowl species use flooded paddy fields in Doñana during the winter, they also use the artificial ponds of Veta la Palma, especially during dry winters (Rendón et al., 2008; Kloskowski et al., 2009), while glossy ibises are only occasional visitors (Toral pers. observ.).

The ash-free dry mass of rice grains in Doñana ($\bar{X} = 0.0169 \pm 0.0017$ g) is similar to the value of 0.02 g reported by other authors (Shimada, 1999; Shimada and Mizota, 2008). The heterogeneous distribution of waste rice seeds found in rice fields of Doñana is in accord with previous studies carried out in other rice cultivated areas (e.g. Lourenço and Piersma, 2008; Stafford, 2004). Glossy ibis use ploughed and flooded fields more than dry paddies (Toral et al., 2011). These habitat preferences shown by glossy ibises are similar to those described for black-tailed godwits foraging in rice fields (Lourenço and Piersma, 2008) and thus are likely to arise from the same cause: that flooded and ploughed rice fields have higher densities of rice grain. The range of densities of rice grains found in ploughed and flooded paddies in Doñana is similar to that found in rice fields of Portugal by Lourenço and Piersma (2008) and also to the values found in Japan by Amano et al. (2006), who reported a mean density of 1223 grains m^{-2} in 1999–2001. Giving-up density of (GUD) prey is the density of prey remaining in a patch at the time that a predator stops foraging within it (Brown, 1988). Our results showed that half the paddies in our model had a rice density below the presumed GUD for waterfowl feeding on rice (250 grains m^{-2} , Greer et al., 2009). The value is above the observed GUD for black-tailed godwits (Lourenço et al., 2010a). However, if we scale the size of a godwit to the size of an ibis, we would expect the GUD for ibises would be higher. Although this pattern of rice density has been found in other rice growing regions (Manley, 1999), further research is required to determine why rice density is very low in some paddies, and hence to recommend management to increase the amount of waste rice available for glossy ibis and other Doñana waders populations.

Stafford et al. (2006) reported that waste rice abundance in Arkansas, Louisiana, Mississippi and Missouri, declined by an average of 71% from early autumn to early winter, a percentage very similar to the decline we have found in Doñana rice fields (65%). This decline is due to both seed deterioration and feeding depletion (Greer et al., 2009). It could be said that the rice fields of Doñana have a food supply distribution similar to others rice fields regions around the world, meaning that the results obtained with the model developed in this study may be useful as a starting point to evaluate the viability of glossy ibis populations in other rice growing regions.

The introduced red-swamp crayfish (*P. clarkii*) may have positive effects as a new food resource for some bird populations in

Doñana (Tablado et al., 2010). This prey does not seem to be important in the diet of the glossy ibis during the breeding season (Macias et al., 2004). Although glossy ibis was only observed to consume red-swamp crayfish on two occasions during our field observations, glossy ibis consume this prey in rice fields during the non-breeding season (Tablado pers. comun.) and may also represent a new food resource for them.

Rice fields can play an important role in wetland bird conservation (Elphick and Oring, 1998; Elphick, 2000; Toral and Figuerola, 2010). The deterioration of natural wetlands in Europe makes rice field management a priority for waterbird conservation (Longoni, 2010). Previous work suggests that in some areas rice fields may be the primary foraging habitat available to waterbirds and that the use of rice habitats by some waterbird groups (e.g. long legged wading birds) is considered essential to sustaining their populations (Czech and Parsons, 2002). Masero et al. (2011) found that Extremadura's rice fields support at least 14% of the declining Western European population of black-tailed godwit during their northward migration, while the rice fields in Portugal are likely to receive 38–44% of the same population (Lourenço et al., 2010b). In Europe, species using rice fields as their preferred habitat during the non-breeding season present more positive population trends than species mainly using natural wetlands (Toral and Figuerola, 2010).

Changes in the Common Agriculture Policy may reduce the area of rice fields in southern Spain and in the rest of Europe. The 2003 reform of the Common Agriculture Policy introduced a number of modifications such as the withdrawal of support for farm production, which has meant a reduction in the subsidies received by rice farmers, who are now changing to alternative uses like solar farms, with the concomitant loss of habitat for waterbirds. Ibises may also be affected by changes in the rice harvesting techniques, since if they are greatly improved the availability of waste rice could decline dramatically, affecting survival rates of ibises without any declines in the area covered by rice fields. Furthermore, pesticides used by rice growers may have direct consequences for the animals foraging in the rice fields. Thus, ensuring that the current harvesting practices are maintained and applying an integrated pesticide management (which implies a strong reduction in the use of pesticides) should thus be part of any future management plans.

There are no data about the historic population of glossy ibis in Doñana. Although it is expected that the population of glossy ibis in Doñana continues growing, this important colony is vulnerable to any exceptional event occurring in Doñana (e.g. a strong drought period). Thus, it is important to design management actions aimed to conserve this colony even if it reaches a population of more than 20,000 individuals. Since this species feed on waste rice, it does not represent a threat to invertebrates or other birds, and does not damage the rice crop.

Areas of rice habitat have been designated as Important Bird Areas under BirdLife International's global scheme to recognise sites of high conservation value (Acosta et al., 2010). The rice fields of Doñana support internationally important numbers of birds (Elphick et al., 2010a). A complementary management action for the rice fields of Doñana in benefit of glossy ibises could be based on the fact that rice growers could use specific benefits to this species of conservation interest to promote their crop. This option is already being applied in Cambodia, where Ibis Rice™ – named for the critically-endangered giant ibis (*Pseudibis gigantea*) – is marketed by growers who agree to limit practices such as wetland conversion and waterbird hunting in an effort to protect rare waterbirds (<http://www.wildlifefriendly.org/ibis-rice>) (Elphick et al., 2010b). It is clear that agricultural practices have important effects on the conservation of European biodiversity (e.g. Genghini et al., 2006). Unfortunately, organic practices have been only tested in a very small area in Doñana rice fields. Since the conservation of

species in their natural habitat is related to the management of the adjacent artificial habitats, more attention should be paid to the rice fields of Doñana due to their importance for the conservation of the birds that use the marshes of the Doñana National Park.

5. Conclusions

Our results show that the glossy ibis population growth is not currently limited by rice field availability. However, large reductions in the area of rice fields due to habitat transformations and/or drought periods may have important effects on the viability of the glossy ibis population in Doñana. We think that rice fields of Doñana are necessary for glossy ibis to survive during the period between August and December, when most of the marshes of the Doñana National Park may be dry. Despite this, most of the rice fields of Doñana are outside protected areas. As has already been proposed in the case of Extremadura's rice fields (Masero et al., 2011), we strongly suggest the inclusion of Doñana rice fields as a special protection area for birds (SPA) under the European Union Directive on the conservation of wild birds (79/409/CEE). Considering the large number of solar energy plants being proposed in this area, some of them already built on former paddies, the inclusion of these rice fields as an SPA would avoid, or at least reduce greatly, the possibility that more of these infrastructures are built in rice fields.

Acknowledgements

This study was funded by the Regional Government of Andalucía (Junta de Andalucía) via the project *Las aves acuáticas de Doñana y el cultivo del arroz: la interacción entre la agricultura y la conservación de las zonas húmedas* and by the Spanish Ministry of Science and Innovation via project CGL2006-02247/BOS. Gregorio M. Toral was funded by an I3P-CSIC grant for the formation of researchers. We are grateful to Maricarmen Lozano and Inmaculada Cintado for processing the core samples for this study. We would also like to thank all the land-owners who allowed us to work in their rice fields. Pedro Lourenço and two anonymous referees really helped to improve the manuscript.

Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.biocon.2012.02.001.

References

- Acosta, M., Mugica, L., Mancina, C., Ruiz, X., 1996. Resource partitioning between Glossy and White Ibises in a rice field system in southcentral Cuba. *Colonial Waterbirds* 19, 65–72.
- Acosta, M., Mugica, L., Blanco, D., Lopez-Lanús, B., Dias, R.A., Doodnath, L.W., Hurtado, J., 2010. Birds of rice fields in the Americas. *Waterbirds* 33, 105–122.
- Amano, T., Ushiyama, K., Fujita, G., Higuchi, H., 2006. Foraging patch selection and departure by non-omnivorous foragers: a field example in white-fronted geese. *Ethology* 112, 544–553.
- Brown, J.S., 1988. Patch use as an indicator of habitat preference, predation risk, and competition. *Behav. Ecol. Sociobiol.* 23, 37–47.
- Bruno, B., Andreas, B., 2001. Flight characteristics of birds. *Ibis* 143, 178–204.
- Castro, G., Myers, J.P., 1988. A statistical method to estimate the cost of flight in birds. *J. Field Ornithol.* 59, 369–380.
- Czech, H.A., Parsons, K.C., 2002. Agricultural wetlands and waterbirds: a review. *Waterbirds* 25 (Special Publication 2), 56–65.
- Davis, W.E., Kricher, J., 2000. Glossy ibis (*Plegadis falcinellus*). In: Poole, A., Gill, F. (Eds.), *The Birds of North America*, vol. 545. The Birds of North America, Inc., Philadelphia.
- Delany, S., Scott, D., 2006. *Waterbird Population Estimates*, fourth ed. Wetlands International, Wageningen.
- del Hoyo, J., Elliott, A., Sargatal, J. (Eds.), 1992. *Lynx Edicions*, Barcelona.
- Dunning Jr., J.B., 1993. *CRC Handbook of Avian Body Masses*. CRC Press, Boca Raton, Florida.
- Durell, S., Stillman, R.A., Caldow, R.W.G., Mcgrorty, S., West, A.D., Humphreys, J., 2006. Modelling the effect of environmental change on shorebirds: a case study on Poole Harbour, UK. *Biol. Conserv.* 131, 459–473.
- Elphick, C.S., Oring, L.W., 1998. Winter management of Californian rice fields for waterbirds. *J. Appl. Ecol.* 35, 95–108.
- Elphick, C.S., 2000. Functional equivalency between rice fields and seminatural wetlands habitats. *Conserv. Biol.* 14, 181–191.
- Elphick, C.S., Taft, O., Lourenço, P.M., 2010a. Management of rice fields for birds during the non-growing season. *Waterbirds* 33, 181–192.
- Elphick, C.S., Baicich, P.J., Parsons, K.C., Fasola, M., Mugica, L., 2010b. The future for research on waterbirds in rice fields. *Waterbirds* 33, 231–243.
- Enggass, P., 1968. Land reclamation and resettlement in the Guadalquivir delta-las marismas. *Economic Geography* 44, 125–143.
- ESRI, 2002. *ArcGIS 9.2*. ESRI (Environmental Systems Research Institute), Redlands, California, USA.
- Fasola, M., Ruiz, X., 1996. The value of rice fields as substitutes for natural wetlands for waterbirds in the Mediterranean region. *Colonial Waterbirds* 19, 122–128.
- Figuerola, J., Mániz, M., Ibáñez, F., García, L., Garrido, H., 2004. Morito común *Plegadis falcinellus*. In: Madroño, A., González, C., Atienza, J.C. (Eds.), *Libro Rojo de las Aves de España*. Dirección General para la Biodiversidad. SEO/BirdLife, Madrid, pp. 74–76.
- García-Novo, F., Martín-Cabrera, C., 2006. Doñana: Agua y Biosfera. UNESCO/Ministerio de Medio Ambiente, Madrid.
- Genghini, M., Gellini, S., Gustin, M., 2006. Organic and integrated agriculture: the effects on bird communities in orchard farms in northern Italy. *Biodivers. Conserv.* 15, 3077–3094.
- Goss-Custard, J.D., 1993. The effect of migration and scale on the study of bird populations: 1991 Witherby lecture. *Bird Study* 40, 81–96.
- Goss-Custard, J.D., Sutherland, W.J., 1997. Individual behaviour, populations and conservation. In: Krebs, J.R., Davies, N.B. (Eds.), *Behavioural Ecology: An Evolutionary Approach*, fourth ed. Blackwell Science, Oxford, pp. 373–395.
- Goss-Custard, J.D., West, A.D., Yates, M.G., Caldow, R.W.G., Stillman, R.A., Bardsley, L., Castilla, J., Castro, M., Dierschke, V., Durell, S.E.A.L.D., Eichhorn, G., Ens, B.J., Exo, K.M., Udayangani-Fernando, P.U., Ferns, P.N., Hockey, P.A.R., Gill, J.A., Johnstone, I., Kalejta-Summers, B., Masero, J.A., Moreira, F., Nagarajan, R.V., Owens, I.P.F., Pacheco, C., Perez-Hurtado, A., Rogers, D., Scheiffarth, G., Sitters, H., Sutherland, W.J., Triplet, P., Worrall, D.H., Zharikov, Y., Zwarts, L., Pettifor, R.A., 2006. Intake rates and the functional response in shorebirds (Charadriiformes) eating macro-invertebrates. *Biol. Rev.* 81, 501–529.
- Greer, D.M., Dugger, B.D., Reinecke, K.J., Petrie, M.J., 2009. Depletion of rice as food of waterfowl wintering in the Mississippi alluvial valley. *J. Wildlife Manage.* 73, 1125–1133.
- Grimm, V., Revilla, E., Berger, U., Jeltsch, F., Mooij, W.M., Railsback, S.F., Thulke, H.H., Weiner, J., Wiegand, T., DeAngelis, D.L., 2005. Pattern-oriented modeling of agent-based complex systems: lessons from ecology. *Science* 310 (5750), 987–991.
- Hancock, J.A., Kushlan, J.A., Kahl, M.P., 1992. *Storks, Ibises and Spoonbills of the World*. Academic Press, London.
- Kersten, M., Piersma, T., 1987. High levels of energy expenditure in shorebirds: metabolic adaptations to an energetically expensive way of life. *Ardea* 75, 175–187.
- King, S., Elphick, C.S., Guadagnin, D., Taft, O., Amano, T., 2010. Effects of landscape features on waterbird use of rice fields. *Waterbirds* 33 (Special, Publication 1), 151–159.
- Kirkwood, J.K., 1983. A limit to metabolisable energy intake in mammals and birds. *Comp. Biochem. Physiol. A Physiol.* 75, 1–3.
- Kloskowski, J., Green, A.J., Polak, M., Bustamante, J., Krogulec, J., 2009. Complementary use of natural and artificial wetlands by waterbirds wintering in Doñana, south-west Spain. *Aquat. Conserv.* 19, 815–826.
- Kuijper, D.P.J., Wymenga, E., van der Kamp, J., Tanger, D., 2006. Wintering Areas and Spring Migration of the Black-Tailed Godwit. Bottlenecks and Protection Along the Migration Route. A&W Rapport No. 820, Altenburg and Wymenga, Ecologisch onderzoek, Veenwouden.
- Longoni, V., 2010. Rice fields and waterbirds in the Mediterranean region and the Middle East. *Waterbirds* 33, 83–96.
- Lourenço, P.M., Piersma, T., 2008. Stopover ecology of Black-tailed Godwits *Limosa limosa* in Portuguese rice fields: a guide on where to feed in winter. *Bird Study* 55, 194–202.
- Lourenço, P.M., Mandema, F.S., Hooijmeijer, J.C.E.W., Granadeiro, J.P., Piersma, T., 2010a. Site selection and resource depletion in Black-tailed Godwits *Limosa l. limosa* eating rice during northward migration. *J. Anim. Ecol.* 79, 522–528.
- Lourenço, P.M., Kentie, R., Schroeder, J., Alves, J.A., Groen, N.M., Hooijmeijer, J., Piersma, T., 2010b. Phenology, stopover dynamics and population size of migrating Black-tailed Godwits *Limosa limosa* in Portuguese rice plantations. *Ardea* 98 (1), 35–42.
- Ma, Z., Li, B., Zhao, B., Jing, K., Tang, S., Chen, J., 2004. Are artificial wetlands good alternatives to natural wetlands for waterbirds? – A case study on Chongming Island, China. *Biodivers. Conserv.* 13, 333–350.
- Macias, M., Green, A.J., Sanchez, M.I., 2004. The diet of the Glossy ibis during the breeding season in Doñana, southwest Spain. *Waterbirds* 27, 234–239.
- Maeda, T., 2001. Patterns of bird abundance and habitat use in rice fields of the Kanto Plain, central Japan. *Ecol. Res.* 16, 569–585.
- Manley, S.W., 1999. *Ecological and Agricultural Values of Winter Flooded Rice Fields in Mississippi*. Unpublished Ph.D. Dissertation. Mississippi State University Mississippi.
- Manley, S.W., Kaminski, R.M., Reinecke, K.J., Gerard, P.D., 2004. Waterbird foods in winter-managed ricefields in Mississippi. *J. Wildlife Manage.* 68, 74–83.

- Mañéz, M., Rendón-Martos, M. (Eds.) 2009. El morito, la Espátula y el flamenco en España. Población en 2007 y método de censo. SEO/BirdLife. Madrid.
- Masero, J.A., Santiago-Quesada, F., Sánchez-Guzmán, J.M., Albano, N., Abad-Gómez, J.M., Villegas, A., Corbacho, C., Costillo, E., 2007. Key issues influencing non-breeding season processes of Black-tailed Godwit *Limosa l. limosa*: spring staging ecology of Black-tailed Godwit at East Atlantic Flyway's rice fields. Wader Study Group Bull., vol. 114, pp. 14.
- Masero, J.A., Santiago-Quesada, F., Sánchez-Guzmán, J.M., Villegas, A., Abad-Gómez, J.M., Lopes, R.J., Encarnação, V., Corbacho, C., Morán, R., 2011. Long lengths of stay, large numbers, and trends of the Black-tailed Godwit *Limosa limosa* in rice fields during spring migration. Bird Conserv. Int. 21, 12–24.
- Mugica, L., Acosta, M., Denis, D., Jimenez, A., 2006. Prey availability of waterbirds in flooded fields of the Sur del Jibaro rice fields during the rice cultivation cycle. J. Caribbean Ornithol. 19, 97–103.
- Nagy, K.A., Girard, I.A., Brown, T.K., 1999. Energetics of free ranging mammals, reptiles and birds. Annu. Rev. Nutr. 19, 247–277.
- Rendón, M.A., Green, A.J., Aquilera, E., Almaraz, P., 2008. Status, distribution and long-term changes in the waterbird community wintering in Doñana, southwest Spain. Biol. Conserv. 141, 1371–1388.
- Sánchez-Guzmán, J.M., Moran, R., Masero, J.A., Corbacho, C., Costillo, E., Villegas, A., Santiago-Quesada, F., 2007. Identifying new buffer areas for conserving waterbirds in the Mediterranean basin: the importance of the rice fields in Extremadura, Spain. Biodivers. Conserv. 16, 3333–3344.
- Santiago-Quesada, F., Masero, J.A., Albano, N., Villegas, A., Sánchez-Guzmán, J.M., 2009. Sex differences in digestive traits in sexually size-dimorphic birds: insights from an assimilation efficiency experiment on Black-tailed Godwit. Comp. Biochem. Physiol. – Part A: Mol. Integrative Physiol. 152 (4), 565–568.
- Santoro, S., Mañéz, M., Green, A.J., Figuerola, J., 2010. Formation and growth of a heronry in a managed wetland in Doñana, southwest Spain. Bird Study 57, 515–524.
- Scheffer, M., Baveco, J.M., De Angelis, D.L., Rose, K.A., van Nes, E.H., 1995. Super-individuals a simple solution for modelling large populations on an individual basis. Ecol. Model. 80, 161–170.
- Serrano, L., Reina, M., Martín, G., 2006. The aquatic systems of Doñana (SW Spain): watersheds and frontiers. Limnetica 25, 11–32.
- Shimada, T., 1999. Comparison of the food abundance for wintering geese of different harvesting methods in rice fields near Lake Izunuma-Uchinuma. Strix 17, 111–117.
- Shimada, T., Mizota, C., 2008. Temporal and spatial changes in foraging distribution of an increasing population of wintering greater white-fronted geese over one decade (1997/98 to 2007/08): a case study for an area around Lake Izunuma-Uchinuma. Jpn. J. Ornithol. 57, 122–132.
- Stafford, J.D. 2004. Abundance and Conservation of Waste Rice for Wintering Waterfowl in the Mississippi Alluvial Valley. Unpublished Ph.D. Dissertation, Mississippi State University, Starkville, Mississippi.
- Stafford, J.D., Kaminski, R.M., Reinecke, K.J., Manley, S.W., 2006. Waste rice for waterfowl in the Mississippi Alluvial Valley. J. Wildlife Manage. 70, 61–69.
- Stafford, J.D., Kaminski, R.M., Reinecke, K.J., 2010. Avian foods, foraging, and habitat conservation in world rice fields. Waterbirds 33, 133–150.
- Stillman, R.A., West, A.D., Goss-Custard, J.D., McGrorty, S., Frost, N.J., Morrissey, D.J., Kenny, A.J., Drewitt, A.L., 2005a. Predicting site quality for shorebird communities: a case study on the Humber estuary, UK. Mar. Ecol. Prog. Ser. 305, 203–217.
- Stillman, R.A., Caldow, R.W.G., Durell, S.E.A.I.V.d., West, A.D., McGrorty, S., Goss-Custard, J.D., Perez-Hurtado, A., Castro, M., Estrella, S.M., Masero, J.A., Rodriguez-Pascual, F.H., Triplet, P., Loquet, N., Desprez, M., Fritz, H., Clausen, P., Ebbinge, B.S., Norris, K., Mattison, E., 2005b. Coast Bird Diversity-Maintaining Migratory Coastal Bird Diversity: Management through Individual-based Predictive Population Modelling. Centre for Ecology and Hydrology for the Commission of the European Communities.
- Stillman, R.A., 2008. MORPH - an individual-based model to predict the effect of environmental change on foraging animal populations. Ecol. Modell. 216, 265–276.
- Stillman, R.A., Goss-Custard, J.D., 2010. Individual-based ecology of coastal birds. Biol. Rev. 85, 413–434.
- Stillman, R.A., Moore, J.J., Woolmer, A.P., Murphy, M.D., Walker, P., Vanstaen, K.R., Palmer, D., Sanderson, W.G., 2010. Assessing waterbird conservation objectives: an example for the Burry Inlet, UK. Biol. Conserv. 143 (11), 2617–2630.
- Sutherland, W.J., 1996. From Individual Behaviour to Population Ecology. Oxford University Press, Oxford.
- Tablado, Z., Tella, J.L., Sánchez-Zapata, J.A., Hiraldo, F., 2010. The paradox of the long-term positive effects of a North American crayfish on a European community of predators. Conserv. Biol. 24 (5), 1230–1238. doi:10.1111/j.1523-1739.2010.01483.x.
- Taylor, I.R., Schultz, M.C., 2010. Waterbird use of rice fields in Australia. Waterbirds 33, 71–82.
- Toral, G.M., Figuerola, J., 2010. Unraveling the importance of rice fields for waterbird populations in Europe. Biodivers. Conserv. 19, 3459–3469.
- Toral, G.M., Aragonés, D., Bustamante, J., Figuerola, J., 2011. Using Landsat images to map habitat availability for waterbirds in rice fields. Ibis. doi:10.1111/j.1474-919X.2011.01147.x.
- Tourenq, C., Bennets, R.E., Kowalski, H., Vialet, E., Licchesi, J.-L., Kayser, Y., Isenmann, P., 2001. Are ricefields a good alternative to natural marshes for waterbird communities in the Camargue, southern France? Biol. Conserv. 100, 335–343.
- White, G.C., Burnham, K.P., 1999. Program MARK: survival estimation from populations of marked animals. Bird Study Suppl. 46, 120–138.