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Natural and human-mediated factors in the recovery and subsequent expansion of the Purple swamphen *Porphyrio porphyrio* L. (Rallidae) in the Iberian Peninsula

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Abstract. Instances of range contraction and population decline in bird species in Europe are more common than cases of recovery following decline. Here we report on the recovery and expansion processes of an endangered bird species in Europe, the purple swamphen (*Porphyrio porphyrio* L., Rallidae), with special reference to the Iberian Peninsula, its main distribution area in Western Europe. After a drastic decline during the first half of the 20th century, which restricted its range to a few areas in southern Spain, the Iberian population has recovered. Currently, the species occurs in a range similar to the one it had at the beginning of the 20th century, and has even colonized new areas. These processes seem to be the result of both human-mediated (effective protection of the species and suitable habitats; success of reintroduction programs as expansion focuses of birds colonizing nearby and distant regions [>300 km] wetlands) and natural factors (inter- and intra-seasonal cycles of wet and dry years). Thus, we found a significant relationship between rainfall and bird abundance and productivity, suggesting that such inter- and intra-seasonal cycles may have significant effects on demographic parameters that could be related to the expansion process. Finally the species shows remarkable adaptability, as proven by data on breeding success in recently colonized areas and the ability to breed shortly after reintroduction. We hypothesize that saturation of breeding habitats in established areas, a reasonable habitat continuity and favorable environmental conditions, and protection have facilitated the dispersion of birds.

Key words: conservation, Iberian peninsula, *Porphyrio porphyrio*, recovery and expansive processes, reintroduction programs, seasonal cycles

Introduction

Examples of bird species' recovery following population decline are scarce in the scientific literature in general, and in Spain in particular (Kleiman 1989; De Juana 1992; but see Sánchez-Lafuente et al. 1992; Matamala et al. 1994), either because specific actions for the recovery of populations are not contemplated for many endangered species or because successful results of existing recovery plans may be difficult to achieve. However, such examples may become useful 'tools' for population managers, because they allow to study both the reasons for the decline and subsequent recovery and the convenience and suitability of human-mediated actions. For example, reintroduction programs are being increasingly contemplated in many species' recovery plans (e.g. Barclay and Cade 1983; Bonnet et al. 1990; Mayol and Vicens 1995). However, in order to have a chance for success, they must fulfil a number of requirements (Heredia 1992) and be planned and executed considering the particular needs and characteristics of the target species.

This paper attempts to outline the recovery and expansion processes of the purple swamphen (*Porphyrio porphyrio* spp. *porphyrio*, Rallidae), a semi-precocial bird species endangered in its European range that maintains in the Iberian Peninsula its main population (Viedma and Giménez 1999). It inhabits primarily wetlands (mainly marshes, lagoons and reservoirs) with suitable water levels and emergent vegetation. During the breeding season (that may extend over the whole year in some areas), birds defend a territory where they build several nests to lay (clutch size ranges 3–8 eggs; Sánchez-Lafuente, unpub. data). Further information on the species' natural history may be consulted elsewhere (e.g. Rodríguez and Hiraldo 1975; Sánchez-Lafuente 1993; Sánchez-Lafuente et al. 1998).

In the Iberian Peninsula the species suffered a drastic decline in the first half of the 20th century (Sánchez-Lafuente et al. 1992), mainly because of the loss of habitats and excessive hunting. Its wide distribution range before 1900 was restricted to a few wetlands in the lower Guadalquivir River basin by the 1960's (Sánchez-Lafuente et al. 1992). Following its legal protection in 1973, the purple swamphen began an expansion process in which both natural and human-mediated factors (e.g. occurrence of artificial habitats and reintroduction programs) seem to be involved. Currently, the species occurs in a range similar to the one it had at the beginning of the 20th century, although it is still considered vulnerable (Blanco and González 1992; Viedma and Giménez 1999).

Specifically, our goals are:

(1) to present a case study of the recovery and expansion of an endangered species in Europe, with special reference to the Iberian Peninsula;
(2) to update the information available on its current distribution range in this area, analyzing bird density and breeding success in established vs. newly colonized areas
(3) to highlight the importance of natural and human-mediated factors involved in the recovery and expansion processes, especially the influence of environmental factors and the outcome of different reintroduction programs.

Methods

General methods

Data on the current distribution and breeding range of the species in the Iberian Peninsula have been collected from recent literature (see Appendix). In order to gather the latest information available we also requested personal communications from researchers and experienced ornithologists from different areas. Information on the reintroduction programs was provided by authorities and biologists responsible for such programs.

We estimated bird density for different areas, and compared breeding success in an established population (Alto Guadalquivir Natural Park, N2 in Figure 1B) and several new distribution areas in Central and Southern Spain, to receive information concerning two issues: suitability of new habitats to maintain birds and birds' ability to successfully colonize and breed in such habitats. Data from the new distribution areas were obtained from published sources (see Appendix), while data from Alto Guadalquivir were obtained from a 15-year study (1983–1998, 1997 not included) on the species' demography and reproductive biology.

Alto Guadalquivir Natural Park (663 ha) is an artificial wetland consisting of three reservoirs that eventually developed suitable conditions for the species (approximately 300 ha of flooded emergent vegetation; see Sánchez-Lafuente et al. 1998 for a more detailed description of the site). It was naturally colonized by the purple swamphen by 1980–1982, and exemplifies many of the artificial areas where the species currently occurs in Spain. From 1985–1990 and in 1998, censuses were conducted monthly; from 1991–1996, censuses were conducted fortnightly. For 1983 and 1984, only 5 and 2 censuses were available, respectively. In order to avoid differences caused by sampling effort, all censuses have been conducted by the same group of researchers under the same criteria. Overall, 235 censuses were carried out, with 3588 birds observed during more than 900 h of observation.

Bird densities were estimated from census data considering the whole extent of the habitat suitable for the species (ca. 300 ha). In some cases, bird densities were also estimated from nest densities (e.g. Sánchez-Lafuente et al. 1992; Tucker and Heath 1994), assuming that breeding pairs build a single nest per season within their territories. This is, however, not necessarily true (Sánchez-Lafuente 1992; see also Craig 1974 for *melanotus*), but the real number of nests built per territory remained unknown.

To compare breeding success between Alto Guadalquivir and newly colonized areas in Central and Southern Spain, we respectively used 114 records of breeding pairs/groups with 180 chicks observed, and 19 records with 39 chicks observed. In order to standardize our estimate for comparative purposes, breeding success was estimated as the number of chicks/pair, the most usual unit found in the literature surveyed. Although data from Alto Guadalquivir could be more detailed (clutch-size, chick survival, etc.) this was not always the case for newly colonized areas. Thus, breeding success was estimated only from census data, which may yield a conservative estimate of breeding success as it is unlikely that all chicks raised by a pair/group would be observed when conducting a census.

Time series analysis and other statistical methods

To exemplify the population trend in Alto Guadalquivir Natural Park, we have used an Auto-Regressive Integrated Moving Average model (ARIMA; Box and Jenkins 1976). Data were obtained from censuses conducted over a period of 15 years (see above). However, 1983 and 1984 were disregarded because censuses were not conducted every month, while from 1991–1996 we considered a single census per month (the one yielding the largest bird count). Thus, the final time series consisted of 156 monthly censuses over a period of 13 years (120 months were used for model construction and 36 for validation). Data were log-transformed to convert multiplicative, exponential trends to additive, linear ones. Also, in order to avoid the likelihood of slight seasonal trends (i.e. birds might be more easily observed in certain periods of the year) we conducted a seasonal decomposition on the transformed series (Makridakis et al. 1983).

Non-seasonal ARIMA models are defined by 3 parameters: [p, d, q]; where p is the number of autoregressive terms, d the number of non-seasonal differences and q the number of lagged forecast errors in the prediction equation (i.e. moving average terms). Most time series consist of elements that are serially dependent in the sense that one can estimate one or several coefficients describing consecutive elements of the series from specific, time-lagged (i.e. previous) elements. For the purpose of analysis we used a lag length of 12 months. To identify the most suitable ARIMA model the inspection of the correlograms of autocorrelation (ACF) and partial autocorrelation (PACF) is crucial (e.g. Hoff 1983; Pankratz 1983). The ACF showed that all lags were positively autocorrelated, although correlation decreased at higher order lags. This pattern is typical of series that are not stationary, which is a prerequisite for ARIMA. Thus, the series was differenced to obtain a stationary one. According to ACF and PACF, a first order differencing (d[1]) removed autocorrelation at all lags (lags 1 and 2 remained only marginally significant and negative). The ACF also displayed a sharp cut-off at lag 2, suggesting that two moving average terms (q[1], q[2]) would be appropriate. Thus, the model suggested was an ARIMA [0,1,2]. Finally, we also included a constant. When a time series is differenced once and there are no autoregressive terms, the constant represents the mean of the differenced series (i.e. the linear trend slope of the undifferenced series). A number of alternative models (not included here) were also tested, but the proposed one minimized the sum of squared residuals compared to others.

In order to relate population trends to environmental factors (namely, rainfall) we conducted two different analyses. First, we used distributed lags analysis (e.g. Maddala 1977) to regress monthly estimations of rainfall in the study area on monthly bird censuses. Distributed lags analysis allows the examination of relationships between variables that involve some delay. Thus, we tested the time-lagged correlation between the number of birds recorded and rainfall in previous months. We assumed that the autumn–spring rainfall (period that accounts for most of the annual rainfall) could be related to annual bird abundance and to productivity in the following breeding season (e.g. Johnson 1983; Rendón et al. 1991). Autumn rain in the study area starts to fall usually in October, while first breeding attempts are detected in February, thus the lag length used was 4 months. All the 15 years could not be used in this analysis, because monthly rainfall data were only available from October 1990. However, in order to test if any patterns found could be consistent over the whole study period, we used a linear regression model with inter-annual differences in bird abundance as the dependent variable and annual rainfall as the independent regressor. Missing datum for 1997 was interpolated, hence sample size was $n = 16$. However, this is still a relatively small sample size (see Herrera 1998), thus the statistical significance was assessed using randomization resampling methods (e.g. Crowley 1992). It is necessary to note that the latter analysis includes an implicit delay similar to the one tested with the distributed lags analysis, because annual rainfall data do not refer to the calendar year, but to the agricultural year (that begins in October). Hence, disparities resulting from such disregarded are considerably reduced.

A similar approach was used to test the relationship between annual productivity and rainfall. However, as chicks were recorded only during the breeding season, the use of a distributed lag analysis was disregarded, and only the regression model was applied. The total number of chicks observed per year (as a measure of annual productivity) was the dependent variable and the annual rainfall the independent regressor. Again, missing datum for 1997 was interpolated and statistical significance assessed by randomization.

Finally, we used Mann–Whitney tests to compare breeding success between established and new areas in central and southern Spain.

Results

Current distribution and breeding range in the Iberian peninsula

Following the decline during the first half of the 20th century (Sánchez-Lafuente et al. 1992 and references therein), the Iberian population of purple swamphen has considerably expanded its range (Figures 1A, B) and numbers since the last estimations (600–900 pairs, Sánchez-Lafuente et al. 1992; 3000–3500 pairs, Tucker and Heath 1994). Current Spanish population may be between 3500–4500 pairs (Viedma and Giménez 1999). The species breeds in wetlands of southern (Andalucia), eastern (Valencia, Catalonia, Balearic Islands) and central Spain (Castilla-La Mancha, Madrid) (Figure 1B).

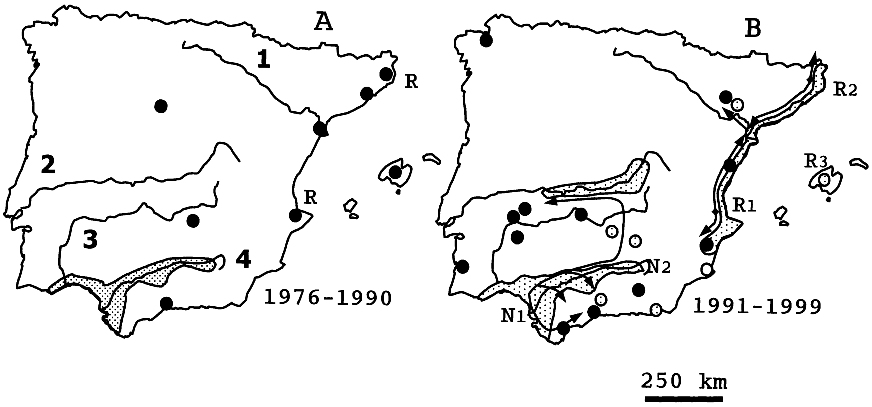

Figure 1. Purple swamphen distribution in the Iberian Peninsula. (A) Map 1976–1990 (from Sánchez-Lafuente et al. 1992) shown as a reference. Rivers indicated as 1 – Ebro, 2 – Tagus, 3 – Guadiana, 4 – Guadalquivir (B) Updated information for 1991–1999. Dotted areas = current breeding range. Empty circles = probable reproduction. Filled circles = regular observations. Reintroduction areas indicated as R1 – Albufera Natural Park, Valencia; R2 – Aigüamolls de l'Empordá Natural Park, Girona; R3 – s'Albufera de Mallorca Natural Park, Balearic Islands. Other areas indicated as N1 – Doñana National Park; N2 – Alto Guadalquivir Natural Park. Arrows indicate the likely routes followed by birds when expanding.

In southern Spain, apart from the well-known populations along the Guadalquivir River, numerous observations have been recorded along the Mediterranean coast, although breeding has not been confirmed in all cases. In southern Portugal, the small population in the Algarve has apparently expanded (but see Tucker and Heath 1994) from the first observations by Vicente and Bugalho (1974; 2 birds) to those by Ramos (1989; 5 birds), and the current 20–30 birds (N. Lecoq, pers. comm.). In central Spain, the species is becoming common in artificial wetlands on the Tagus River (Figure 1B). Birds breed from 1992 in several reservoirs in Toledo (López de Carrión and Menor 1996 and Appendix), while they are relatively abundant in several flooded gravel pits in Madrid, where breeding was first documented in 1995 (Appendix). However, only two wetlands on the Guadiana River (halfway between Guadalquivir and Tagus) are known to have small breeding populations (M. López, pers. comm. and Appendix; Figure 1B). In eastern Spain, the former distribution range (Figure 1A) has expanded from the reintroduction areas on the Mediterranean coast (Albufera Natural Park, Valencia, R1 in Figure 1B; Aigüamolls de l'Empordá Natural Park, Girona, R2 in Figure 1B). Inland, breeding has been documented in 1994 on a tributary to the Ebro River (Huesca in Appendix). Also, isolated records have been made in areas that might be colonized in the future: Extremadura in western Spain (see Appendix) and the southern Atlantic coast of Portugal (N. Lecoq, pers. comm.). Finally, observations have been eventually recorded at localities far from its current range (e.g. Galicia, northwestern Spain; Figure 1B).

Bird density and breeding success in well-established vs. new populations

In 1988, when the first reintroduction program started, bird density ranged from 0.41 birds/ha in Alto Guadalquivir to 3–6 birds/ha in favourable habitats in Doñana (Sanchez-Lafuente et al. 1992; Tucker and Heath 1994; respectively; data calculated from nest densities; summary in Table 1). Currently, maximum density in Doñana does not seem to have varied substantially (M. Máñez, pers. comm.), whereas density has considerably increased in Alto Guadalquivir (Table 1). Regarding new areas, we found that current density is similar to that found in Alto Guadalquivir in 1988 (some years after its colonization). Furthermore, in some recently colonized areas (e.g. wetlands around Albufera in Valencia), density is exceptionally high and comparable to that found in favourable areas in Doñana (Table 1).

The number of chicks/pair estimated for Alto Guadalquivir (mean ± SE = 1.96 ± 0.12) and several new areas in Central and Southern Spain (mean ± SE = 2.10 ± 0.31) does not differ (Mann–Whitney: $U = 357$, $P = 0.20$, $n_{\text{Alto Guadalquivir}} = 114$, $n_{\text{New areas}} = 19$) (see also data in Table 1 for other distribution areas), suggesting that breeding success does not seem to be lower in newly colonized areas, or areas close to the boundary of the species' range, compared to established populations.

Table 1. Bird densities (birds/ha) and breeding success (chicks/pair) in different localities where the species occurs, or has been reintroduced. Densities indicated in early, mid (just before reintroduction programs) and current stages over the period of the expansion process. (1) Source area for the recovery process (2) Colonized naturally by 1980–1982. (3) Colonized naturally over the 1990's. (4) Colonized following reintroduction programs.

Locality	Density 1983	Density 1988	Current density	Current breeding success	Source
Doñana National Park (N1, Figure 1B) (1)	?	3–6	?	Ca. 2	Tucker and Heath 1994; M. Máñez, pers. comm.
Alto Guadalquivir Natural Park (N2, Figure 1B) (2)	0.05	0.41	1.15	1.96 ± 0.12 mean ± SE n = 180 chicks contacted	Sánchez-Lafuente et al. 1992; present study
Wetlands in central Spain (Figure 1B) (3)	0	0	?	2.08 ± 0.30 mean ± SE n = 37 chicks contacted	Appendix
Wetlands around Albufera Natural Park (R1, Figure 1)	0	0	Up to 4	?	J. A. Gómez, pers. comm.
Marjal del Moro (southwards R1, Figure 1) (4)	0	0	0.30	Ca. 2	M. Giménez, pers. comm.
s'Albufera Natural Park (R3, Figure 1) (4)	0	0	0.33	>1.5	J. Muntaner, pers. comm.; Mayol and Vicens 1995

Environmental factors and population trends: the effect of rainfall

Population trend in Alto Guadalquivir is presented in Figure 2. According to the ARIMA model, a significant increase has occurred in the study population over the 13 years considered (Table 2A). The model also predicts that such increase may continue for a short-term.

The analysis carried out to relate population fluctuations and rainfall over a period of 8 years, indicated that the variation in bird number is positively related to precipitation in all lags considered (Table 2B; mean annual rainfall mean $\pm$ SD $= 471.53 \pm 134.73$ mm; $n = 16$; minimum: 273 mm in 1993; maximum: 741 mm in 1996). The regression analysis over the 16 years confirmed such relationship, suggesting that inter-annual variation in bird abundance is related to rainfall ($r = 0.59$, $n = 16$, $P = 0.011$ assessed by randomization with 5000 repetitions). Finally, a significant relationship was also found between annual rainfall and annual productivity (Figure 3) ($r = 0.65$, $n = 16$, $P = 0.010$ assessed by randomization with 5000 repetitions), suggesting that rainfall may also affect birds' ability to breed.

The outcome of the reintroduction programs

Three reintroduction programs were started in Spain between 1988 and 1991, in protected areas where the species occurred before 1900 (Sánchez-Lafuente et al. 1992).

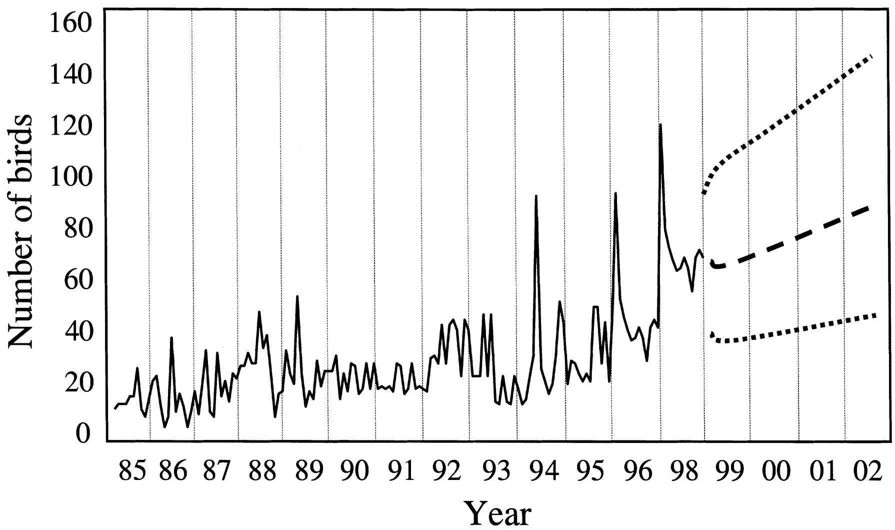

Figure 2. Trend of the purple swamphen population in Alto Guadalquivir Natural Park (N2 in Figure 1B) over a period of 13 years (1985–1998, 1997 not included). An ARIMA model fitted to the data indicates a significant increase over the study period (see Table 2A) and predicts future increases. The solid line is the original series; the dashed line is the predicted trend; dotted lines are the 95% confidence interval for the trend.

Table 2. (A) Parameters of the ARIMA model fitted to the data to detect trends in the purple swamphen population at Alto Guadalquvir. Data correspond to 13 years of monthly censuses. See Methods for further information on the model selection, and Figure 2 for a graphic presentation of the time series analysed and forecasted. (B) Results of the distributed lags analysis and relationship between number of birds recorded and rainfall in lagged intervals from October 1990. See Methods for further information.

(A) ARIMA [0,1,2] with constant; $n = 156$; MS Residual = 0.258

Parameter	Estimate	SE	*t*	*P*
Constant	0.014	0.006	2.40	0.02
q[1]	0.532	0.087	6.08	<0.0001
q[2]	0.331	0.093	3.54	<0.001

(B) Distributed lags analysis; $n = 83$, $R^2 = 0.71$

	df	MS	*F*	*P*
Regress.	5	142.06	40.08	<0.0001
Residual	78	3.54		

Lag	Coefficient	SE	*t*	*P*
Current	0.011	0.003	3.14	0.003
1	0.011	0.003	3.26	0.002
2	0.010	0.003	2.97	0.004
3	0.010	0.003	2.94	0.005
4	0.011	0.003	3.15	0.003

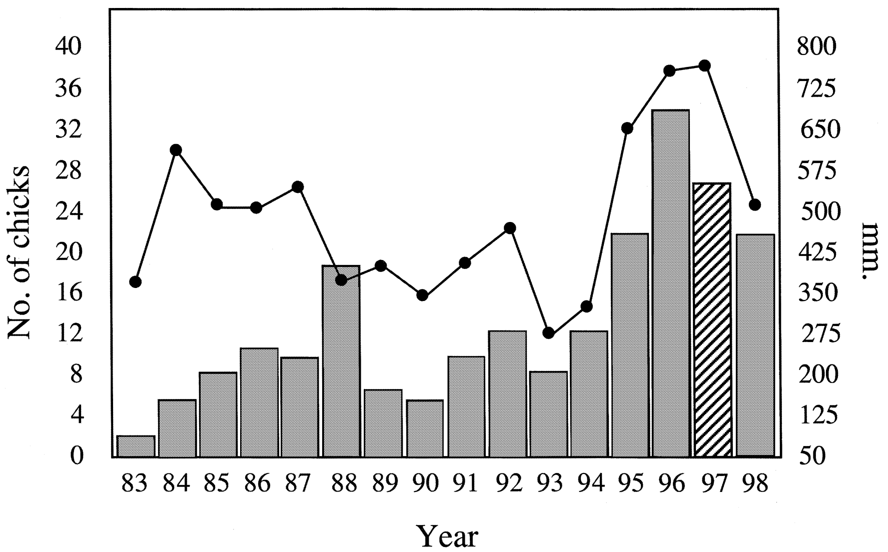

Figure 3. Plot of the total number of chicks observed per year (bars) (as a measure of annual productivity) and annual rainfall (line) in the study area over a period of 13 years. Missing datum for 1997 was interpolated. A significant relationship has been found between variables (see text).

The first one was started at Albufera de Valencia (eastern Spain, R1 in Figure 1B) in 1988. After an unsuccessful attempt to release birds from Doñana, breeding in captivity (usually in groups consisting of one male and two females) was considerably successful (J.A. Gómez, pers. comm.). Between 1989–1990, at least 20 birds escaped and were supposed to have started breeding as early as 1991 (M. Giménez, pers. comm.). However, most birds (>300; M. Giménez, pers. comm.) have been released from 1993 and currently the species occurs in almost every wetland around the reintroduction locality, even in high densities (Table 3). Another program was started in 1989 at Aigüamolls de l'Empordá (Girona, R2 in Figure 1B), releasing birds from Doñana in 1990 and 1991 (Table 3; Heredia 1992; S. Romero, pers. comm.). Breeding was first detected in 1992 (J. Sargatal, pers. comm.). Currently, birds have successfully occupied habitats around the reintroduction area. A third program was started at Albufera de Mallorca (Balearic Islands, R3 in Figure 1B), by releasing adults and yearlings from Doñana in 1991 (Table 3). Breeding was first detected in 1992 (Mayol and Vicens 1995). Current population (Table 3) is increasing, and birds can also be observed in three other wetlands on Mallorca island (J. Muntaner, pers. comm.).

Discussion

The results presented in this study indicate that the purple swamphen has recovered, in the last 20 years, from its endangered status in the Iberian peninsula. Currently, the expansion of the species is favored by natural and human-mediated factors, although it is still considered vulnerable in Spain (Blanco and González 1992) and threatened in Europe (De Juana 1998).

The recovery and expansion processes and the colonization routes

At least two colonization routes may be suggested to explain the current range in the Iberian peninsula. First, from the southernmost populations in Spain (N1, Figure 1B) birds would have expanded along the Guadalquivir river, and by 1982, the mainstream and some tributaries had been completely colonized. From the northernmost populations on this river, the species would have reached the Tagus basin northwards. The Guadiana River may have not been fully colonized because of its environmental degradation (C. Villanueva, pers. comm.; López de Carrión and Menor 1996). Also from southern Spain, birds would have expanded along the south-eastern Mediterranean coast. Second, from the reintroduction areas in eastern Spain, birds seem to have colonized both near and distant (>300 km) wetlands along the Mediterranean coast, reaching south-eastern France, where the species currently breeds (e.g. De Juana 1998).

Table 3. Summary of reintroduction programs in three Natural Parks in Spain. Situation refers to Figure 1B. Birds refer to the number of birds released since the program was started. Density/number refers to maximum density or number of birds observed in areas around the reintroduction localities. Dispersion ability reports on birds from the reintroduction areas observed elsewhere. All birds released were wearing PVC rings to allow identification.

Locality	Situation	Started	Method	Birds	Density/ number	Dispersion ability	Source
Albufera (Valencia)	R1	1988	Captive-rearing, then released. Also directly released.	>300	Ca. 4 birds/ha	Northwards (>180 km) Southwards (>140 km)	J.A. Gómez (pers. comm.)
Aigüamolls de l'Empordá (Girona)	R2	1989	Directly released in 2 stages. No captive-rearing.	38 + 28 (66)	?	Northwards (>250 km) Southwards (>300 km)	S. Romero (pers. comm.); Heredia (1992)
s'Albufera (Mallorca, Balearic Islands)	R3	1991	Directly released. No captive-rearing.	29	>200 pairs 0.33 birds/ha	Observed in several wetlands in Mallorca (>10 km)	J. Muntaner (pers. comm.); M. Máñez (pers. comm.); Heredia (1992)

Natural and human-mediated factors related to the recovery and expansion processes

A number of factors may be suggested as major reasons involved in the expansion process. First, an effective protection (the species is protected in Spain since 1973, and the majority of wetlands where it occurs are currently protected) and availability of suitable habitats. Interestingly, many of the habitats considered ‘suitable’ are artificial wetlands that developed appropriate conditions (e.g. reservoirs after siltation, when growth of emergent vegetation is favored; Torres and Raya 1982; Sánchez-Lafuente et al. 1992). Artificial wetlands have become usual breeding habitats not only in Spain, but also in other parts of the species’ range (e.g. Australia and New Zealand; Taylor 1996).

Second, intra- and inter-annual cycles of wetlands in Southern Spain. During dry periods, many wetlands (e.g. marshes, endorheic lagoons) may desiccate all year round or from late spring onwards, because of the climatic conditions and their shallowness. As a consequence, the ‘mosaic’ of flooded areas suitable for breeding is considerably reduced and many waterfowl species have to move to other areas to breed (e.g. Amat 1984). It has been suggested that environmental changes associated to these cycles would favour the productivity of habitats and species (e.g. Nudds 1983). Thus, the turnover in cycles of dry and wet years may have favored pulses of expansion and productivity, indicating a relationship between rainfall and demographic parameters (see Figure 3), supported in this study. The role of rainfall and intra- and inter-annual cycles to explain recovery processes, local abundance and breeding success has also been contemplated for other waterfowl species (e.g. Greater Flamingo *Phoenicopterus ruber*; Johnson 1983; Rendón et al. 1991; White-headed Duck *Oxyura leucocephala*; Amat and Raya 1989; Matamala et al. 1994). Consequently, although our model for Purple swamphen in Alto Guadalquivir predicts a sustained and positive population growth, the role of rainfall as a key factor affecting bird abundance and breeding success suggests that any forecasts predicting population trends for any species must be interpreted with caution if relevant environmental factors are not taken into consideration.

Third, the success of the different reintroduction programs (similar programs for closely related species have also been successful elsewhere, e.g. Maxwell and Jamieson 1997), with reintroduction areas acting as dispersion focuses. However, this role is not fully known. According to J.A. Gómez (pers. comm.), birds observed along the Spanish eastern Mediterranean coast may mostly come from Valencia and Girona (R1 and R2, Figure 1B). Nevertheless, other authors consider it to be unlikely that all these birds come from the reintroduced populations (see Del Moral 1997), suggesting that coastal areas may have been partially colonized following the natural expansion process. Would the purple swamphen have been able to colonize its current range without reintroduction programs? Considering that it has been able to colonize the Guadalquivir basin in about 10 years, and the southern Mediterranean coast in no more than 15, we believe it is likely that it would have been able to reach eastern Spain on its own (see also Grussu 1999 for the Sardinian population).

Finally, it is the species' own ability and adaptability to colonise new habitats. When factors such as protection and reasonable habitat continuity were fulfilled, birds have proven the ability to disperse long distances. Available data suggest that high densities may be a prerequisite to trigger dispersal. We found that densities were higher in areas acting as dispersal focuses (both traditional and new), than in others close to the boundary of the dispersal routes (Table 1, Figure 1B). Habitat limitation or saturation may enhance long-distance dispersal of individuals unable to establish their own territories (Hunter 1987). As in other species (e.g. Bonham and Robertson 1975; Schönfeld 1989; Valera et al. 1993), juveniles may play an important role acting as long-distance colonists (e.g. the birds observed in Galicia and Badajoz were juveniles; see Figure 1B and Appendix). Breeding success may also be a particularly useful measure of the species' ability to colonize new areas. Our data indicate that birds are able to breed very shortly after new areas are colonized and with a success comparable to that found in established areas (but see Bunin et al. 1997; Jamieson and Ryan 1998 for *Porphyrio mantelli*). Consequently, populations in new areas may be growing at similar rates to those found in established areas, hence eventually becoming new dispersal focuses. However, further research is needed to clarify how the expansion process took place, and the role played by habitat saturation, juvenile dispersal and breeding success as mechanisms of such process. Monitoring of marked birds released at the different reintroduction areas may play an important role to elucidate these subjects.

Future conservation

Unlike other closely related species (e.g. the flightless Takahe *Porphyrio mantelli*), which are still undergoing a drastic decline (Bunin and Jamieson 1995; Clout and Craig 1995), the purple swamphens have shown a high plasticity to adapt themselves to human-managed environments, and have responded successfully to protection and reintroduction measures. However, new risks have arisen in Spain, namely the use of pesticides (Del Moral 1997) and disturbance by fishermen catching Red swamp crawfish (*Procambarus clarkii*) (e.g. more than 800 birds, mostly chicks, were found dead inside funnel traps in 1989; Asensio 1991; Blanco and González 1992). Also, some irrigation policies are promoting the construction of new reservoirs covering the basins occupied by (hence, destroying) older ones. These new reservoirs will not have suitable conditions for a number of waterfowl species, including the purple swamphen; thus, the expansion process may be considerably slowed. Finally, studies on various aspects of the biology of nominal subspecies *porphyrio* are still scarce in Europe (but see Sánchez-Lafuente 1993; Sánchez-Lafuente et al. 1998; Grussu 1999). We believe that an efficient conservation requires of such studies, because our lack of knowledge implies that we may have been passive witnesses of a process we cannot fully understand, hence limiting our ability to manage populations if new conservation problems eventually arise.

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Appendix

Records published in *Ardeola* (Journal of the Spanish Ornithological Society) from which Figure 1B was drawn. All data correspond to newly colonized areas, ordered by locality and year of sighting. Reference indicates the journal volume and year of publication. Breeding indicates the occurrence of chicks as a cue to assess breeding.

Locality	Author(s)	Reference	Year of sighting	Breeding
A Coruña (north-western Atlantic coast)	Rabuñal	37, 1990	1990	No
Almería (south-eastern Mediterranean coast)	Nevado et al.	40, 1993	1993	No
	Paracuellos	41, 1994	1994	No
	Paracuellos	44, 1997	1997	No
Badajoz (central-western)	Hernández	41, 1994	1994	No
	Traverso	46, 1999	1999	No
Barcelona (north-eastern Mediterranean coast)	Chacón et al.	37, 1990	1990	No
	Chacón et al.	41, 1994	1994	No
Cáceres (central-western)	Prieta	44, 1997	1997	No
Ciudad real (central)	Gayo	45, 1998	1998	Yes
Huesca (north-eastern)	Chacón et al.	41, 1994	1994	Yes
	Gracia and Grijalbo	43, 1996	1996	No
Madrid (central)	Del Moral and Molina	38, 1991	1991	No
	Gómez	41, 1994	1994	No
	Barcála	42, 1995	1995	Yes

Appendix Continued.

Locality	Author(s)	Reference	Year of sighting	Breeding
	Del Moral	42, 1995	1995	Yes
	Vega et al.	43, 1996	1996	No
	Marchamalo and Mesonero	44, 1997	1997	No
	Fernández and Fuentes	44, 1997	1997	Yes
Málaga (southern Mediterranean coast)	Mariscal	40, 1993	1993	No
	Alba and Mariscal	41, 1994	1994	No
	Gayo	42, 1995	1995	No
	Mariscal et al.	46, 1999	1998	Yes
Tarragona (north-eastern Mediterranean coast)	Cabello	43, 1996	1996	Yes
Toledo (central)	Oliveros and Villalobos	40, 1993	1993	No
	López and Otero	40, 1993	1993	No
	Acha et al.	40, 1993	1993	Yes
	Sunyer and Manteiga	40, 1993	1993	Yes
	Grijalbo et al.	40, 1993	1993	Yes
	Gayo	41, 1994	1994	No
	De La Cruz	41, 1994	1994	No
	Blanco	41, 1994	1994	Yes
	Molina and Velasco	42, 1995	1995	No
	Pérez	42, 1995	1995	Yes
	De La Cruz et al.	42, 1995	1995	Yes
	Barcála	43, 1996	1996	Yes
	Fernández	43, 1996	1996	Yes
	Eaton	44, 1997	1997	No
	Llanos and Zorrilla	44, 1997	1997	Yes

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