

**Factors affecting the distribution of a waterbird community: the role of habitat configuration
and bird abundance**

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Abstract.- The effects of the environmental and species' characteristics were analyzed on the richness and distribution of the dabbling and diving waterbirds in a wetland complex with 26 ponds (0.1-88.6 ha) in southeast Spain. The study gains importance given the ecological value of these environments which are being lost on a world scale through human action. Various morphological, geographical, hydrochemical, vegetal and temporal parameters of the ponds (11 in total), as well as determined characteristics of the species, were sampled with the object to identify those variables with the capacity to predict the effects provoked by the habitat configuration. The function of the size and the isolation, as variables related to the habitat patchness, as well as the development of the emergent vegetation of the wetlands were discriminated as forecasters of their number of species. The avian abundance had an important role in the capacity of the birds to occupy ponds (sampling hypothesis). The differences in the abundance of the distinct species probably favored their orderly loss in the wetland complex at the same rate as the ponds diminished in size ("nested" pattern). The obtained results imply the need for the conservation or restoration of the greatest number of wetlands, paying special attention to the biggest, with peripheral vegetal coverage around large open waters in complexes of more than one pond, to preserve the greatest number of species against the important regression of wetlands which is actually occurring worldwide and is a cause of biodiversity detriment.

Key words.- Conservation, environmental factors, habitat patchness, "nested" pattern, sampling hypothesis, Spain, waterbirds, wetland configuration

Running head.- Waterbirds and wetland configuration

Wetlands have one of the highest biodiversity and biological productivity in the world (for example, Whittaker and Likens 1973; Gibbs 1993; Casado and Montes 1995), and various globally threatened avian species depend on them (Green 1996). Nevertheless, wetlands are a patched habitat immersed in surrounding terrestrial landscape, where organisms seem to be affected by the natural insularity of the environment (Brown and Dinsmore 1986; Knutson *et al.* 1999; Rey Benayas *et al.* 1999; Naugle *et al.* 1999; Wettstein and Schmid 1999; Verboom *et al.* 2001). This characteristic of wetlands is being accentuated by human action on a worldwide basis, with a higher fragmentation and loss of area, which negatively affects waterbirds (Owen and Black 1990; Finlayson *et al.* 1992; van Vessem *et al.* 1997). Furthermore, management rules for wetlands involve the creation or restoration of deteriorated or lost systems, offering new landscape designs. Consequently, it is necessary to integrate spatial configuration with species characteristics in the analysis of the factors determining avian distribution in wetlands (see for example, Finlayson *et al.* 1992; Montes *et al.* 1995; Verboom *et al.* 2001; Parsons *et al.* 2002).

In this work, waterbird distribution is analyzed in a wetland complex with the object to identify the consequences provoked by the habitat configuration in their colonization by the avifauna. For this purpose, two processes are studied: (I) The importance of different environmental variables as predictors of species richness in relation to habitat configuration. We predict that small and isolated ponds will have lower number of species than large and clumped ponds (Sillén and Solbreck 1977; Brown and Dinsmore 1986; Craig and Beal 1992). (II) The effect of waterbird abundance on their ability to colonize ponds. We predict that the number of ponds occupied by the species will correlate positively with the avian abundance of each ones (sampling hypothesis; Andrén 1994a). In this instance and when pond area is progressively reduced, the pattern of species loss will be orderly in function to the abundance of each species (“nested” pattern; Atmar and Paterson, 1993).

STUDY AREA

The study was carried out in a wetland complex of 26 ponds within a 16 km radius in the Baja Alpujarra (Southeast Iberian littoral, Almería, Spain; 36°48'N, 2°42'W), where other similar wetlands were found at least 50 km away. The ponds were in a flat area (0-50 m a.s.l.) covered principally by a matrix of greenhouses. The few uncultivated spaces were normally colonized by open shrub vegetation of semiarid habitats (Mota *et al.* 1996). For marsh dependent species, these wetlands were true islands. They typically had open, permanent, deep and slightly salty water normally surrounded by a ring of emergent vegetation (see Table 1; Ortega *et al.* 2000). When present, emergent vegetation was mainly composed of helophytes (principally *Phragmites australis* with a 66% coverage) and phreatophyte bushes (predominately *Tamarix* sp. with a 16%). Submerged vegetation, when present, was represented principally by *Potamogeton pectinatus*, *Ruppia* sp. and *Najas marina*. Other common plants were *Cladophora* sp., *Cladium mariscus*, *Typha dominguensis*, *Arundo donax*, *Juncus maritimus* and *Inula crithmoides* (Cirujano *et al.* 1992; Gómez Mercado and Paracuellos 1995-96; Giménez *et al.* 2003).

MATERIAL AND METHODS

To identify those environmental characteristics with a predictive capacity on the number of present waterbird species, in each independent pond in the wetland complex (at least 20 m distant from the nearest pond) a group of independent and not reiterative variables were sampled (11 in total; Table 1). The area (open water plus emergent vegetation surface), perimeter length, isolation degree (distance to the nearest pond), and percentage and width of shore occupied by emergent vegetation were estimated. An index of perimetral complexity was calculated for each pond taking into account the edge length divided by the circumference of a circle of equivalent area ($2 \sqrt{\pi \times \text{area}}$); Ryding and Rast 1992). The average height of emergent vegetation was visually estimated

during the spring of 1998 in marsh plant patches ≥ 5 ha within circles of 25 m radius randomly chosen (4 to 20 per patch). In smaller patches, a unique and global estimation of vegetal height was made. In the summer of 1998, the maximum cover of water surface occupied by submerged vegetation was estimated. Maximum water depth (calculated as the average value of various records of depths measured about the center of the pond) and hydrochemical variables (minimum salinity and minimum concentration of the total phosphorus) were sampled during February 1998. Another variable also estimated was the age of the different ponds as zones with depth > 0.5 m and fresh or brackish water, as characteristic which affect to avian richness in some wetlands (for example, VanRees-Siewert and Dinsmore 1996).

During the winter of 1997-1998 (December-February) and the spring-summer period of 1998 (May-September) direct censuses of waterbirds were carried out in the wetland complex at points along the edges of the ponds (Bibby *et al.* 2000). Between two and eight counts were made per pond for each period, from which the highest census of adult + subadult individuals for each species was taken into account in the winter and spring-summer. Attention was only paid to the dabbling and diving birds (Podicipediformes, Anseriformes and Rallidae), except for the Water Rail (*Rallus aquaticus*) and Purple Gallinule (*Porphyrio porphyrio*) because these were hidden in the vegetation and impossible to count.

The following avian characteristics were taken into account for each period: (i) the number of species in each pond, (ii) the species density (average value of the number of individuals ha^{-1} in wetlands >10 ha, as the largest areas where the insularity had to have less effect), and (iii) the number of ponds occupied by each species. As well, for the waterbirds present in both study periods we calculated: (iv) the interseasonal persistence of each species in the different wetlands (proportion of ponds occupied in both winter and spring-summer by each species), and (v) the average interseasonal density of each species (average value between the winter and spring-summer densities).

A forward stepwise multiple regression test (F to include = 4.00, F to exclude = 3.99) was employed for each period, using winter and spring-summer number of species as dependent variables and the characteristics of the ponds with simple significant relationship with the number of species on the ponds as independent variables.

The computer program “Nestedness Temperature Calculator” (Atmar and Patterson 1996) was used to estimate the degree of hierarchy in the species loss pattern at the same time that the ponds were ordered from the higher to the lesser number of avian species. With this algorithm, the deviation of an observed matrix from one which is perfectly nested is estimated. According to this, it could be found if the loss pattern in the ponds was determined by random or, on the contrary, followed a process where n species occupying a pond was also present in another with $n + 1$ (“nested” pattern). The program produces random assortments of species within ponds, constrained to match the observed overall frequency of species and their relative number within the ponds. It was used to generate 1,000 wetland complexes and to calculate a distance-based measure, the matrix temperature index, related to the degree of order of loss of their species. A matrix temperature index of 0° reflects a perfect “nested” pattern of extinction in a wetland complex, on the contrary being of 100° in a pattern absent of all order. If the matrix temperature index obtained in our wetland complex lay within the range of variation of the modeled results, the “nested” hypothesis of species distribution would be rejected.

The Pearson’s Correlation Coefficient (r) was used for the simple relationship analyses with the variables. When the data presented a non-normal distribution, these were logarithmically or trigonometrically transformed. The statistical methods can be consulted in Jobson (1992), Atmar and Patterson (1993) and Sokal and Rohlf (1994).

RESULTS

Only six environmental variables of the wetland complex (2 morphological, 1 isolation and 3 vegetal characteristics) were significantly correlated with number of species (Table 1). They were entered in forward stepwise multiple regression tests for the winter and spring-summer periods (Table 2). In winter, number of species was best predicted by pond area and isolation degree (distance to the nearest pond). In the spring-summer period, pond area and average height of emergent vegetation best predicted number of species (Table 2). Once the area, isolation and average height of emergent vegetation effects were controlled in the models, no other environmental variables had *post hoc* significant partial correlation with number of species in either period. Pond area was the characteristic that best predicted number of avian species in the two study periods (Table 2).

The density of a given species in large ponds (>10 ha) was directly related to the number of wetlands occupied by that species in either period (Figure 1). Species interseasonal persistence in ponds, from the winter to the spring-summer period, was also positively related to their average interseasonal density (Figure 2).

Species distribution among wetlands was nested, where n species occupying a pond was usually present in another with $n + 1$ (winter period: matrix fulfillment = 37.9%, matrix temperature of study wetland complex = 5.33° , average matrix temperature of simulations \pm SD = $58.23^\circ \pm 5.87^\circ$, $P < 0.00001$; spring-summer period: matrix fulfillment = 37.00%, matrix temperature of study wetland complex = 5.55° , average matrix temperature of simulations \pm SD = $55.33^\circ \pm 6.31^\circ$, $P < 0.00001$; $N = 1,000$). For each species, occupied ponds were usually larger than unoccupied ones (Table 3).

DISCUSSION

Our results confirm the importance of habitat size in explaining avian richness within the wetland complex analyzed, which is consistent with results of other studies in a variety of environments (Sillén and Solbreck 1977; Brown and Dinsmore 1986; Opdam 1991; Andrén 1994a; Turner 1996; Tellería and Santos 2001). Because habitat heterogeneity usually increases with pond area, it might explain part of the results (Shafer 1990; Craig and Beal 1992; Elmberg *et al.* 1994).

The importance of isolation (distance to the nearest wetland), as a variable affecting species richness, has also been shown in other aquatic and terrestrial habitats (Brown and Dinsmore 1986; Craig and Beal 1992; Andrén 1994a; Rosenberg *et al.* 1997; Tellería and Santos 2001). The relation between number of species and this parameter was significant in winter, when greater movement by waterbirds between ponds normally occurs (Craig and Beal 1992). Emergent vegetation was more important as a factor in the spring-summer period, when birds usually breed among the helophytes and are less mobile (Owen and Black 1990).

The results corroborate the role that abundance plays as a good predictor of the ability of species to occupy ponds in a given wetland complex. In this sense, less abundant species were, less colonizing capacity they had for occupying the distinct zones, appearing only in few ponds, usually the larger ones (sampling hypothesis; Andrén 1994a; Lawton 1996; Tellería and Santos 2001).

The differences in waterbird abundance had to contribute to the discriminated loss of species in the wetland complex from large to small ponds (“nested” pattern), probably reaching critical thresholds for area-dependent birds in the smaller ones (Atmar and Patterson 1993; Andrén 1994b).

Lastly, the inability of the most scarce species to occupy ponds on a long term basis (less persistent) could be due to the fact that they had populations composed by few individuals and, therefore, were very dependent on environmental fluctuations in the zone or on processes purely by

random for their apparition/extinction in the wetlands (Savard *et al.* 1994; Suter 1994; Tellería and Santos 2001).

CONSERVATIONAL IMPLICATIONS

The present study shows that the effect of isolation, development of the peripheral emergent vegetation and, mainly, wetland size on the dabbling and diving waterbird richness implies the conservation or restoration of the greatest number of ponds, paying special attention to the more clumped and larger ones with emergent vegetation around large open waters (Shafer 1990; Finlayson *et al.* 1992). However, some authors have argued that determined assemblages of small wetlands can maintain the same or more avian richness than one of an equivalent surface area to the total of the little ones (Brown and Dinsmore 1986; Craig and Beal 1992). Nevertheless, results obtained in our study indicate that this is not always the case (no groups of reduced ponds had the same or more species than any individual large one; see Table 3). These results were likely due in part according to the “nested” pattern, from the exclusive colonization of the large ponds by the scarcer waterbirds; and in part to the level of similarity in habitat heterogeneity between large and small ponds. In our study, some habitats seemed be absent from small ponds, which might explain why several of these ponds will not produce the diversity found within large ones. Management prescription that would increase the habitat heterogeneity between small wetlands would contribute to reducing these differences (Owen and Black 1990; Finlayson *et al.* 1992; Montes *et al.* 1995; Parsons *et al.* 2002). Of course, this implies that some of the small ponds must be large enough to meet the minimum requirement of some of the larger species.

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Table 1. Statistical relationships (r) between the pond characteristics and number of waterbird species during the winter and spring-summer periods. Various analyses were based on logarithmically (with the variables 1, 4, 5, 6, 8, 9) or trigonometrically (with the variable 10) transformed data. Level of significance: n.s., non-significant, * P < 0.05, ** P < 0.01, * P < 0.001. N = 26. The mean and SD values are also indicated for each pond characteristic.**

Parameters	Mean	SD	Winter period		Spring-summer period	
			r	P	r	P
Morphological characteristics:						
1. Area (ha)	10.5	22.2	0.88	***	0.82	***
2. Perimetric complexity [$2\sqrt{(\pi \times \text{area})}$]	154.09	37.78	-0.00	n.s.	0.05	n.s.
3. Maximum depth (m)	1.78	0.75	0.63	**	0.61	**
Isolation characteristics:						
4. Distance to the nearest wetland (m)	433	1,212	-0.52	**	-0.46	*
Hydrochemical characteristics:						
5. Minimum water salinity (g l ⁻¹)	8.73	9.01	0.26	n.s.	0.37	n.s.
6. Total phosphorus in water (mg l ⁻¹)	0.07	0.06	-0.22	n.s.	-0.14	n.s.
Vegetal characteristics:						
7. Shore coverage by emergent vegetation (%)	48	37	0.47	*	0.45	*
8. Height of emergent vegetation (m)	3.16	1.73	0.42	*	0.55	**
9. Width of emergent vegetation (m)	5.59	7.64	0.62	***	0.71	***
10. Coverage of water surface by submerged vegetation (%)	13	24	-0.10	n.s.	-0.07	n.s.
Temporal characteristics:						
11. Age of the pond (years)	69.92	132.77	0.04	n.s.	0.11	n.s.

Table 2. Resulting models of the forward stepwise multiple regression test, for the winter and spring-summer periods, using number of waterbird species as dependent variables, and the pond characteristics significantly correlated with the number of species in each season (Table 1) as independent variables. Analyses based on logarithmically transformed data of the variables 1, 4, 8, 9 in the Table 1. Level of significance: * P < 0.05, * P < 0.001. N = 26.**

Parameters included in the model	r ²	F _{2,23}	Coefficient	SE	Partial r ²	P
Winter period						
Model	0.83	54.5				***
Constant			7.22	1.09		***
Area			3.13	0.37	0.78	***
Distance to the nearest wetland			-1.26	0.50	0.05	*
Spring-summer period						
Model	0.74	32				***
Constant			1.89	0.79		*
Area			2.64	0.43	0.67	***
Height of emergent vegetation			3.28	1.34	0.08	*

Table 3. Matrix of distribution of waterbird species in the wetland complex during winter and spring-summer periods. Ponds are ordered by number of species and species by their appearance in the ponds during both periods (indicated by an “X”), only during winter (indicated by a “+”), and only during spring-summer (indicated by an “o”). Also, the area and the number of waterbird species are indicated for each pond in both periods; as well as the average density in the large ponds and the number of occupied ponds for each species in both periods. # large ponds (>10 ha).

	Area (ha)	Number of species in winter	Number of species in spring-summer	Little Grebe <i>Tachybaptus ruficollis</i>	Mallard <i>Anas platyrhynchos</i>	Coot <i>Fulica atra</i>	Moorhen <i>Gallinula chloropus</i>	White-headed Duck <i>Oxyura leucocephala</i>	Pochard <i>Aythya ferina</i>	Black-necked Grebe <i>Podiceps nigricollis</i>	Northern Shoveler <i>Anas clypeata</i>	Teal <i>Anas crecca</i>	Red-crested Pochard <i>Netta rufina</i>	Tufted Duck <i>Aythya fuligula</i>	Marbled Teal <i>Marmaronetta angustirostris</i>	Great crested Grebe <i>Podiceps cristatus</i>	Pintail <i>Anas acuta</i>
#	31.7	12	10	X	X	X	X	X	X	X	+	+	o	X		X	+
#	88.6	12	8	X	X	X	X	X	X	X	+	+		+		+	+
#	14.9	12	11	X	X	X	X	X	X	X	X	+	X	X		X	+
#	59.5	9	7	X	X	X	X	X	X	+	+	+			o		
#	49.7	10	9	X	X	X	X	X	X	X	X	+			X		
	2.9	8	7	X	X	X	X	X	X	+			o	+			
	9.1	6	8	X	X	X	X	X	X	o					o		
	4.7	6	7	X	X	X	X	X	X				o				
	0.8	6	1	X	+	+		+	+	+							
	1	5	5	X	X	X	X	X									
	0.6	5	4	X	+	X	X	X									
	2	4	2	+	+	X	X										
	1.6	4	0	+	+	+	+										
	1.5	4	4	X	X	X	X										
	0.8	3	4	o	X	X	X										
	0.6	4	3	+	X	X	X										
	0.2	4	3	X	X	X	+										
	0.2	4	2	X	+	X	+										
	0.1	3	3	o	X	X	+										
	1.2	3	2	+	X	X											
	0.5	3	3	X		X	X										
	0.4	3	1	+	+	X											
	0.5	2	2			X	X										
	0.2	2	2	X	X												
	0.2	2	2	X	X												
	0.4	1	1	X													
Average density in winter (individuals ha ⁻¹)				0.85	0.57	2.41	0.42	2.67	1.52	0.47	4.09	0.26	0.09	0.53	0	0.36	0.01
Average density in spring-summer (individuals ha ⁻¹)				0.79	0.58	5.06	0.36	3.14	0.93	0.16	0.06	0	0.12	0.02	0.03	0.2	0
Number of occupied ponds in winter				23	23	23	20	11	9	7	5	5	1	4	1	3	2
Number of occupied ponds in spring-summer				20	17	21	16	10	8	5	3	0	4	2	3	2	0

Captions of Figures

Figure 1. Statistical relationships between the average density in the large ponds (Individuals ha^{-1}) and the number of ponds occupied by the distinct waterbird species during the winter period ($r = 0.71$, $P < 0.01$) and the spring-summer period ($r = 0.81$, $P < 0.01$). Each point represents a different species. X and Y axes in log scale.

Figure 2. Statistical relationship between the average interseasonal density in the large ponds (Individuals ha^{-1}) and the interseasonal persistence of waterbird species in the wetland complex (Persistence) ($r = 0.81$, $P < 0.01$). Each point represents a different species. X axis in log scale.

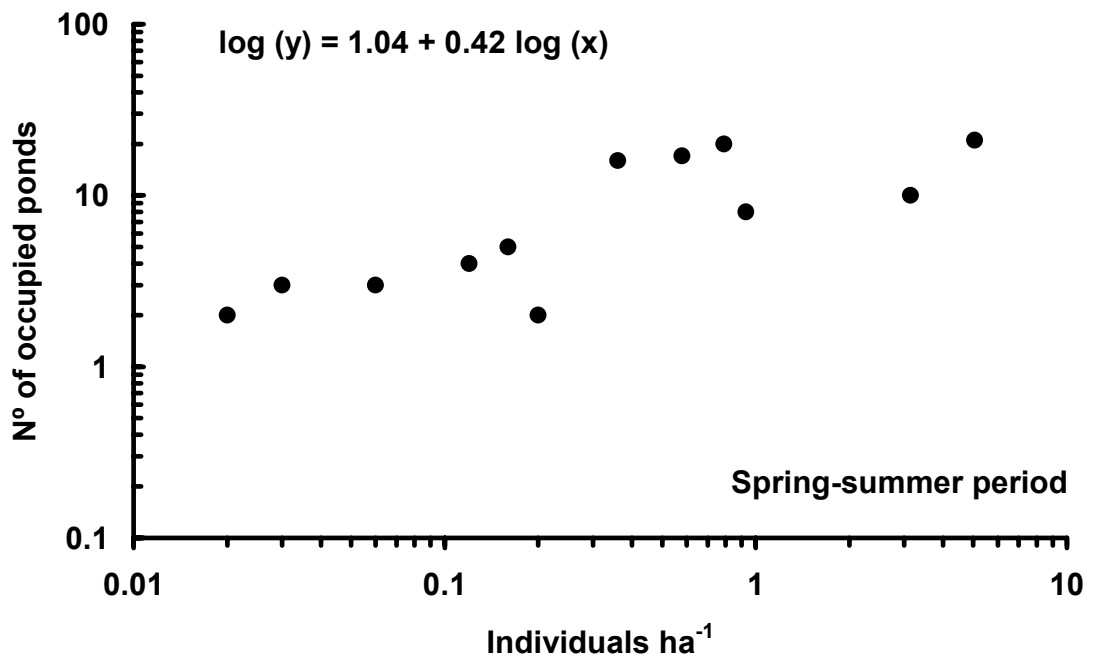
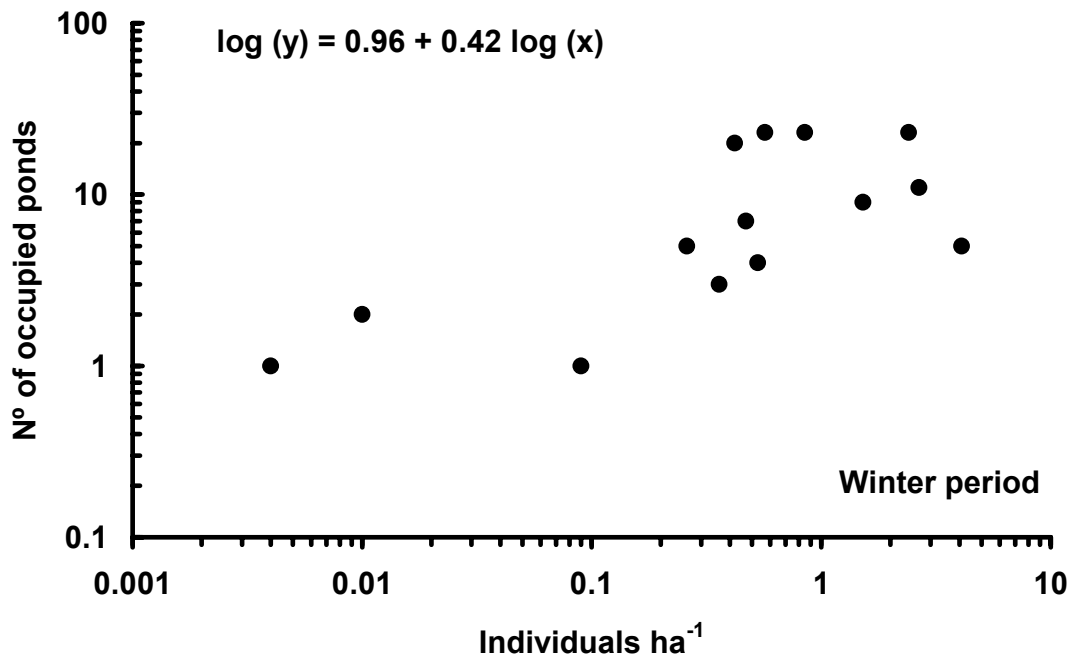


Fig. 1. Paracuellos and Tellería

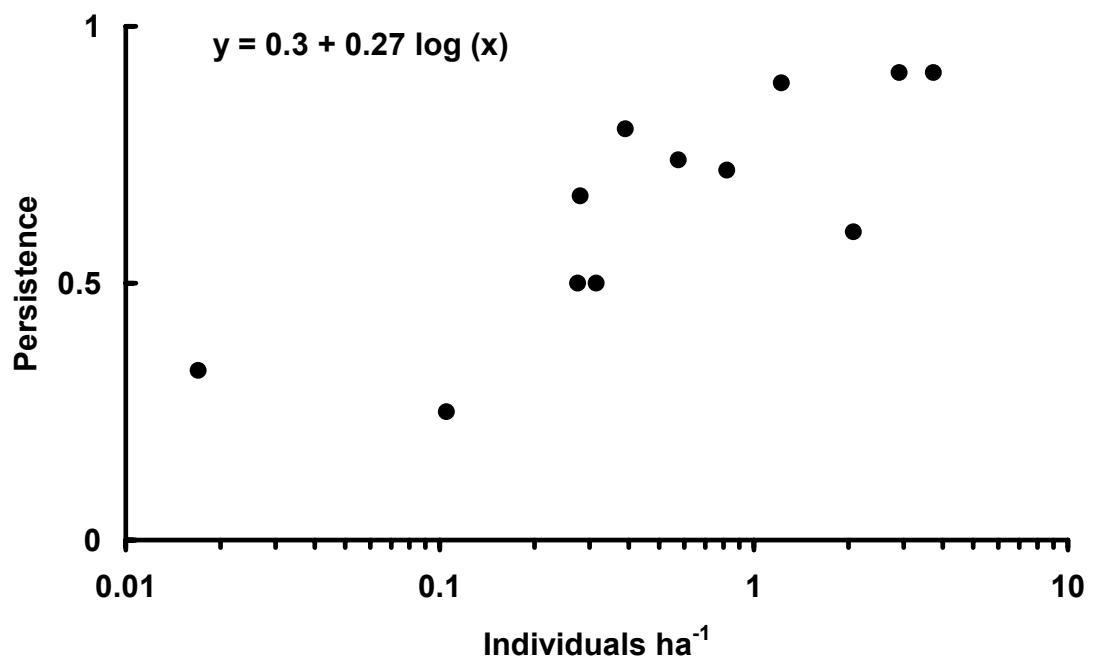


Fig. 2. Paracuellos and Tellería