Bird Study
Publication details, including instructions for authors and subscription information:
http://www.tandfonline.com/loi/tbis20

Hatching success in Avocet Recurvirostra avosetta and Black-winged Stilt Himantopus himantopus: Capsule Daily survival rate of nests was influenced by laying date and nesting period (laying versus incubation) in both species and by colony size in Black-winged Stilts.

José Javier Cuervo
Published online: 29 Mar 2010.

To cite this article: José Javier Cuervo (2005) Hatching success in Avocet Recurvirostra avosetta and Black-winged Stilt Himantopus himantopus: Capsule Daily survival rate of nests was influenced by laying date and nesting period (laying versus incubation) in both species and by colony size in Black-winged Stilts., Bird Study, 52:2, 166-172, DOI: 10.1080/00063650509461387

To link to this article: http://dx.doi.org/10.1080/00063650509461387

Bird Study (2005) **52,** 166–172

Hatching success in Avocet *Recurvirostra avosetta* and Black-winged Stilt *Himantopus himantopus*

JOSÉ JAVIER CUERVO
Estación Experimental de Zonas Áridas, Consejo Superior de Investigaciones Científicas, Calle General Segura 1, E-04001 Almería, Spain

Capsule Daily survival rate of nests was influenced by laying date and nesting period (laying versus incubation) in both species and by colony size in Black-winged Stilts.
Aims To investigate the effect of clutch size, colony size, reproductive phenology and nesting period on hatching success of Avocets and Black-winged Stilts.
Methods The study was undertaken at two localities in southwestern Spain (Doñana and Odiel Natural Parks) during 1990 and 1991 breeding seasons. The Mayfield method was used to estimate hatching success.
Results Both species bred colonially and some colonies included nests of both species. Neither year, locality, species or clutch size had a significant effect on hatching success. Daily survival rate was lower for late nests than for early and intermediate, and lower during egg-laying than during incubation in both species. Hatching success of Black-winged Stilt nests was lower in large colonies (>50 nests) than in medium-sized ones (11–50 nests).
Conclusion Late clutches within a colony (clutches with the least hatching success) might be replacements or belong to late breeders, but adults were not individually marked, precluding clarification. The results suggest a high probability of clutch predation and/or desertion in early stages of the nesting period, especially shortly after laying the first egg. The fact that hatching success in large colonies was lower than in medium-sized ones, but only for Black-winged Stilts (not for Avocets), might help to explain the difference in coloniality of the two species.

Avocets *Recurvirostra avosetta* and Black-winged Stilts *Himantopus himantopus* are the two species of recurvirostrids that breed in the western Palearctic (Cramp & Simmons 1983). The reproductive biology of Avocets has been extensively studied in Germany in recent years (Hötker 1998, 2000, Hötker & Segebade 2000). However, the reproductive biology of Black-winged Stilts is poorly known, although some studies have been carried out in Italy (Tinarelli 1990, 1992) and Spain (Castro 1993, Arroyo 2000, Cuervo 2003, 2004). Studies of hatching success in the Spanish populations of the two species have focused mainly on the effect of habitat type (Arroyo 2000) and nest location or characteristics (Arroyo 2000, Cuervo 2004). However, the study of other factors which might affect hatching success or daily survival rate of nests has either been neglected or different patterns reported. Here, the effects of clutch size, colony size, reproductive phenology and nesting period (laying, incubation) on hatching success and daily survival rate of nests are investigated in the two species. The study of Black-winged Stilts is especially important owing to the dearth of information for this species, but the study of Avocets is also important because previous studies either have been undertaken in other countries, probably under different ecological conditions (e.g. Hötker 2000), or results have been inconsistent (Arroyo 2000).

Email: jcuervo@eeza.csic.es

METHODS

Study areas

The study was carried out during the 1990 and 1991 breeding seasons (April–June) in two wetlands in southwestern Spain, the Doñana and Odiel marshes, located approximately 70 km apart. Avocet and Black-

winged Stilt nests were surveyed for two years in Veta la Palma (36°57′N, 6°14′W), Doñana Natural Park, Isla Mayor, Seville. However, La Herradura (37°14′N, 7°00′W), Odiel Natural Park, Huelva, was surveyed only in 1991, and the Black-winged Stilt was the only recurvirostrid species breeding there. The study area in Doñana Natural Park was a former dry marsh recently flooded for shrimping, consisting of large (*c.* 100 ha) shallow (*c.* 1 m) brackish ponds. Avocets and Black-winged Stilts nested on man-made dykes, small islands, and pond shores. Vegetation on emerged land was patches of typical dry marsh vegetation, mainly scattered glasswort (*Arthrocnemum* spp.) up to 50 cm high. For a description of ecological and climatic characteristics of the area see García Novo *et al.* (1977). The study area in Odiel Natural Park was a brackish marsh, profoundly altered by humans, made up of dykes, canals and shallow, formerly tidal ponds. Black-winged Stilts nested on small islands and dykes. Vegetation was scarce and typically halophile (adapted to soils with very high concentration of salt). For detailed information on climate, vegetation and ecological conditions see Rubio & Figueroa (1983) and Rubio (1985).

Data collection

Breeding areas were surveyed every 1–5 days in search of recurvirostrid nests, and content of all known nests determined. Due to the conspicuousness of adults, scarce vegetation, and limited suitable nesting locations, almost all the nests in the study area were found. Every nest was identified by means of a small numbered peg stuck into the ground, about 50 cm from the nest. Colony disturbance always lasted for less than one hour, and extreme temperature periods (early morning, noon) were avoided. No predators were observed to have taken advantage of researcher-induced disturbance to depredate on eggs or chicks. Groups of nests more than 100 m apart were considered different colonies, because that was the maximum distance birds chased potential aerial predators. Thus, any nest within 100 m of a colony might benefit from anti-predator behaviour of members of the colony. Every nest was classified as an early (first 25%), intermediate (middle 50%) or late (last 25%) nest within its colony. Since colony size might have some influence on hatching success, all colonies were classified into three groups by number of nests of the two species: small (2–10 nests), medium-sized (11–50 nests), and large colonies (>50 nests).

A nest was considered successful when at least one egg hatched. However, nest fate is often difficult to determine, because adult recurvirostrids remove eggshells immediately after hatching (Sordahl 1994) and chicks leave the nest permanently within one or two days, or even within a few hours if they are disturbed (Hamilton 1975, Adret 1984). It is also possible that predators carry away the eggs leaving no evidence of predation (Green *et al.* 1987). A nest was deemed successful if (i) a recently hatched chick was found in the nest or nearby, (ii) at least one egg showed evidence of imminent hatching (cracked or drilled eggshell), (iii) date of egg disappearance matched expected hatching date (when egg age was known) and no sign of predation was found. A nest was considered to have failed if (i) eggs were partially or totally submerged, (ii) eggshell or remains of egg content were found, (iii) the nest had been deserted (cold eggs), (iv) egg disappearance was prior to expected hatching date (when egg age was known). The fate of all other nests was considered unknown. Only nests with known fate were used to assess hatching success.

Nesting periods

Daily survival rate was calculated for three different periods: (i) between laying of first and second egg, (ii) between laying of second and last egg, and (iii) between laying of last egg and hatching of first egg. Time between laying of two consecutive eggs was assessed including only nests found when one egg had been laid, revised every two days at most, and surviving until clutch completion. Length of the second period (between laying of second and last egg) was calculated separately for each species, taking into account the number of nests with different clutch sizes and the time between laying of two consecutive eggs in that particular species. The length of the third period was assessed including only nests found during egg-laying, with at least one hatched egg, and revised every three days at most.

Statistical analysis

Hatching success was assessed by the Mayfield method (Mayfield 1961, 1975, Klett & Johnson 1982). However, hatching success estimated with the standard method (percentage of nests with at least one egg hatching) is also shown to facilitate comparison with other studies. Calculation of the variance of the Mayfield estimator was necessary to compare the daily

mortality rate between different colonies, localities or years.[a] Once daily survival rate is assessed, it is possible to estimate mean reproductive success for Avocet and Black-winged Stilt nests, simply by raising daily survival rate to the power of the number of days. If partial egg loss in successful nests (nests with at least one egg hatching) is considered, the egg survival rate, i.e. proportion of eggs that survived until hatching age, can be estimated. All statistical tests were two-tailed and the significance level was 0.05.

RESULTS

A total of 276 Avocet and 274 Black-winged Stilt nests were found and surveyed, in 13 colonies and three solitary Black-winged Stilt nests. Six colonies were formed exclusively of Black-winged Stilts, four colonies were mixed-species with Black-winged Stilt predominance, and three were mixed-species colonies with Avocet predominance. Percentages of nests with different clutch sizes were 3% (2 eggs), 13% (3 eggs), 83% (4 eggs), and 1% (5 eggs) for Avocets and 2% (2 eggs), 19% (3 eggs), and 79% (4 eggs) for Black-winged Stilts.

Nest fate and phenology

Nest fate was unknown for 117 (42%) Avocet and 51 (19%) Black-winged Stilt nests and these nests were therefore not included in subsequent analyses. All other nests either succeeded or failed due to a known cause (Fig. 1). Only 59% of Black-winged Stilt nests with known fate succeeded in hatching at least one egg, while the percentage of successful nests was 64% in Avocets. Hatching success was lower in late nests (Fig. 2), except the smallest samples, where the trend was not significant (Avocets in 1990, and Black-winged Stilts in Doñana 1991; see Fig. 2 caption).

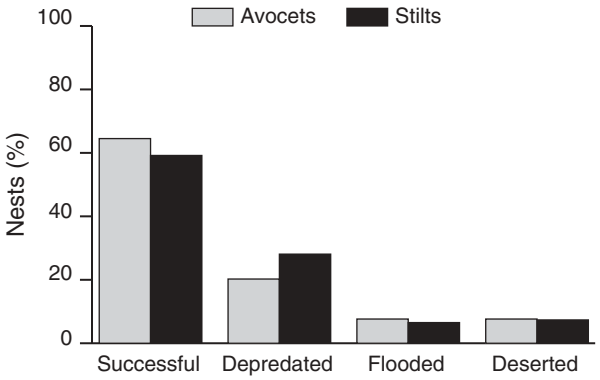

Figure 1. Percentage of Avocet (n = 159) and Black-winged Stilt (n = 223) nests that were successful, depredated, flooded or deserted. Percentage of successful nests (G-test, G_{adj} = 0.8, df = 1, ns) or causes of reproductive failure (G = 3.0, df = 2, ns) did not differ significantly between species.

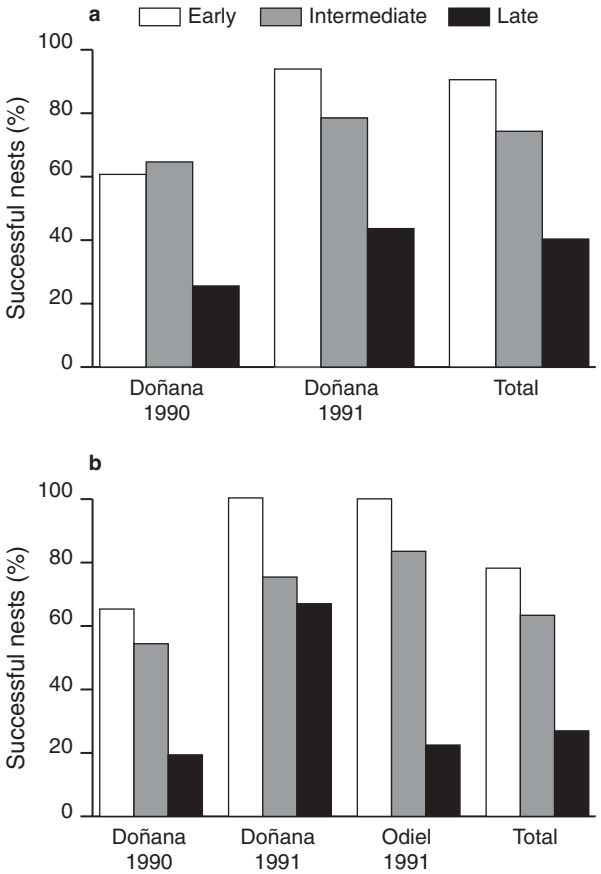

Figure 2. Percentage of successful nests (at least one egg hatched) in Avocets (a) and Black-winged Stilts (b) considering laying date (early, intermediate, or late) of each clutch within its colony. Hatching success and laying dates were significantly related for Black-winged Stilts in Doñana 1990, Black-winged Stilts in Odiel 1991, and Avocets in 1991 (G-test, in all three cases 31 < n < 114 nests, G > 12.8, df = 2, P < 0.01), and also for all Avocets (n = 138 nests, G = 30.6, df = 2, P < 0.001) and all Black-winged Stilts (n = 146 nests, G = 23.9, df = 2, P < 0.001). The relationship was not significant in the two cases with the smallest samples (Avocets in 1990: n = 24 nests, G = 3.1, df = 2, ns; Black-winged Stilts in Doñana 1991: n = 22 nests, G = 2.5, df = 2, ns).

Nest survival and colony size

Daily Avocet and Black-winged Stilt nest survival rates were estimated for the two years and both localities (Table 1). No significant differences between years for Avocet or Black-winged Stilt nests were found, nor were differences between localities for Black-winged Stilt nests significant (in all three tests, z < 1.6, ns). In the later analyses daily survival rates are pooled from different years and localities for each species. Daily

Table 1. Daily survival rate for Avocet and Black-winged Stilt nests in different years and localities.

		n	Nest-days	Failed nests	Daily survival rate (se)	Hatching success (Mayfield method)	Hatching success (standard method)
Avocets	1990	42	542.5	18	0.967 (0.008)	0.428	0.571
	1991	121	1605.0	39	0.976 (0.004)	0.541	0.678
	Total	163	2162.5	57	0.974 (0.003)	0.514	0.650
Black-winged Stilts	Doñana 1990	178	2376.5	74	0.969 (0.004)	0.454	0.584
	Doñana 1991	19	232.0	11	0.953 (0.014)	0.299	0.421
	Odiel 1991	36	440.5	9	0.980 (0.007)	0.602	0.750
	Total	233	3049.0	94	0.969 (0.003)	0.454	0.597

Daily survival rate was estimated for the period between laying of the first egg and first hatching: 25.3 days for Avocets and 25.1 days for Black-winged Stilts (see the text).

Table 2. Daily survival rate for Avocet and Black-winged Stilt nests in small (2–10 nests), medium-sized (11–50 nests) and large (>50 nests) colonies.

	Colony size	*n*	Nest-days	Failed nests	Daily survival rate (se)	Hatching success (Mayfield method)	Hatching success (standard method)
Avocets	Medium-sized	28	344.0	12	0.965 (0.010)	0.406	0.571
	Large	135	1843.5	45	0.976 (0.004)	0.541	0.667
Black-winged Stilts	Small	23	269.5	9	0.967 (0.011)	0.431	0.609
	Medium-sized	80	1265.5	27	0.979 (0.004)	0.587	0.663
	Large	130	1514.0	58	0.962 (0.005)	0.378	0.554

Three solitary Black-winged Stilt nests were pooled with nests in small colonies. Daily survival rate was estimated for the period between laying of the first egg and first hatching: 25.3 days for Avocets and 25.1 days for Black-winged Stilts (see the text).

survival rate was not significantly different in monospecific (Black-winged Stilt) colonies, mixed-species colonies with Black-winged Stilt predominance, or mixed-species colonies with Avocet predominance for either species (in all four tests, $z < 1.6$, ns). Avocets only nested in medium-sized and large colonies, and daily survival rates did not differ between these two types of colony ($z = 1.0$, ns; Table 2). Daily survival rate of Black-winged Stilt nests did not differ significantly between small colonies or solitary nests and medium-sized ($z = 1.0$, ns) or large colonies ($z = 0.4$, ns). However, survival was higher in medium-sized colonies compared to large ones ($z = 2.7$, $P < 0.01$; Table 2).

Nest survival and nesting period

Time between laying of two consecutive eggs was 1.4 days ($n = 8$, se = ±0.1) for Avocets, and 1.2 days ($n = 25$, se = ±0.1) for Black-winged Stilts, and this was considered the duration of the period between laying of first and second egg. Length of the second period (between laying of second and last egg) was 2.4 days for Avocets and 2.1 days for Black-winged Stilts. The third period (between laying of last egg and hatching of first egg) lasted 21.5 days for Avocets ($n = 10$, se = ±0.5) and 21.8 days for Black-winged Stilts ($n = 39$, se = ±0.2). Between-species difference in duration of the third period was not significant (Student's *t*-test; $t = -0.68$, df = 47, ns).

Daily survival rate in the three periods mentioned is shown in Table 3. Survival was lower in the period with only one egg in the nest than in the other two periods for both species (in all four tests $z > 3.45$, $P < 0.001$). In Black-winged Stilts, daily survival rate was lower in the second period (rest of egg-laying) than in the period with complete clutch ($z = 2.44$, $P = 0.015$), but survival difference between these two periods in Avocets did not reach statistical significance ($z = 1.93$, ns). Daily survival rate in the period with complete clutch was compared between clutches with three and four eggs, and the difference was not significant for either species (in the two tests, $z < 1.14$, ns). Comparisons were not made with two- and five-egg clutches owing to the scarcity of such nests.

Egg survival

Nesting success (proportion of nests with at least one egg hatching) for Avocets was: $0.711^{1.4} \times 0.951^{2.4} \times 0.982^{21.5} = 0.372$; and for Black-winged Stilts: $0.641^{1.2}$

Table 3. Daily survival rate for Avocet and Black-winged Stilt nests in three different periods: one egg (between laying of first and second egg), rest of egg-laying (between laying of second and last egg), and complete clutch (between laying of last egg and hatching of first egg).

	Period	*n*	Nest-days	Failed nests	Daily survival rate (se)
Avocets	One egg	35	45.0	13	0.711 (0.068)
	Rest of egg-laying	47	183.5	9	0.951 (0.016)
	Complete clutch	144	1959.0	35	0.982 (0.003)
Black-winged Stilts	One egg	68	97.5	35	0.641 (0.049)
	Rest of egg-laying	83	146.0	10	0.932 (0.021)
	Complete clutch	184	2803.5	48	0.983 (0.002)

See text for period duration.

$\times 0.932^{2.1} \times 0.983^{21.8} = 0.348$. Daily survival rate of Avocet eggs was 0.998, which means 0.951 hatching success for the whole period with eggs in the nest. Daily survival rate of Black-winged Stilt eggs was 0.999 and hatching success 0.975. Only 336 out of 376 eggs (89%) in successful Avocet nests reaching hatching age eventually hatched. Only 469 out of 497 eggs (94%) in successful Black-winged Stilt nests reaching hatching age eventually hatched. If the probability of nest survival is multiplied by probability of egg survival in successful nests and this value is multiplied by hatching probability of eggs reaching hatching age, hatching probability of just-laid eggs is obtained. This is $0.372 \times 0.951 \times 0.894 = 0.316$ for Avocets and $0.348 \times 0.975 \times 0.944 = 0.320$ for Black-winged Stilts.

DISCUSSION

Daily survival rate of nests was not significantly different between species, years, localities, or between three-egg and four-egg clutches. The only two factors that seemed to affect hatching success to any degree were laying date and colony size. In general, hatching success was the highest in early nests and lowest in late nests (Fig. 2). However, hatching success did not differ significantly among early, intermediate and late nests in the smallest samples (Avocets in 1990, Black-winged Stilts in Doñana 1991). The negative relationship between laying date and hatching success is widespread among avian species (for a review in seabirds see Moreno 1998) and different hypotheses (age and experience, food availability, predation risk, etc.) have been proposed to explain it (Moreno 1998). Determining the specific factors responsible for poor hatching success in late Avocet and Black-winged Stilt nests was beyond the aims of this study.

The other factor affecting hatching success was colony size. Daily nest survival rate was higher in medium-sized, than in large colonies for Black-winged Stilts, but not for Avocets. Hötker (2000) has previously reported for Avocets breeding in northern Germany that colony size (once nest density had been controlled) did not significantly affect hatching success. Arroyo (2000) found a similar result in southern Spain for Avocets. There is little information on the effect of colony size on hatching success in Black-winged Stilts. Arroyo (2000) found no significant relationships between the two variables, except in one year, when the relationship was significant and positive, that is, the larger the colony size the better hatching success. This result does not agree with the findings of this study, and should be accepted with caution, since it was found in only one year, sample size was rather small and the relationship was very weak (Arroyo 2000, p. 195).

Coloniality has both advantages and disadvantages, and their combination determines the degree of coloniality and characteristics of the colony (for a review see Brown & Brown 2001). Why was hatching success of Black-winged Stilts lower in large than in medium-sized colonies? One important advantage of coloniality in recurvirostrids is defence against aerial predators, but this function is probably achieved in medium-size colonies, and does not improve in larger colonies (Hötker 2000). Moreover, rats *Rattus* spp. caused almost all egg predation in this study (most nests with depredated clutches contained eggshell fragments with rat teeth marks), and coloniality is not efficient against terrestrial predators. On the other hand, breeding in large colonies might entail some costs. With increasing numbers of individuals in the colony, agonistic interactions might also increase, especially owing to nest-site competition and nest defence. Recurvirostrids are not highly territorial, but they defend a small area around their nests (Cramp & Simmons 1983). Excessive aggression might lead to inappropriate nest attendance and even to nest desertion.

In this study, Avocets bred only in medium-sized and large colonies, while Black-winged Stilts bred in small ones also, thus showing more breeding flexibility and less coloniality. Moreover, previous studies have shown that Avocets are more gregarious than Black-winged Stilts when breeding, with smaller inter-nest distances within the colony (Cuervo 2004). The difference in coloniality of the two species may be because breeding in large colonies is detrimental for Black-winged Stilts (hatching success of this species in large colonies was lower than in medium-sized ones), but not for Avocets.

Daily survival rate of nests was lower during egg-laying than during incubation for both species, and was especially low immediately after laying of the first egg. If a nest site is prone to flooding (e.g. located on windward shores) or easily accessible to predators (e.g. close to rat dens), egg mortality will probably occur soon after laying, even on the first day if the nest site is especially unsuitable. On the other hand, it is also probable that birds can abandon their nests more easily in the case of disturbances (e.g. fights with breeding neighbours) when only one or a few eggs have been laid. As the clutch is completed and incubation progresses, clutch value increases and adults would be more reluctant to desert nests (Clutton-Brock 1991, p. 170). Reviews of hatching success in different European countries have been published both for Avocets (Arroyo 2000, Hötker & Sebegade 2000) and for Black-winged Stilts (Arroyo 2000). It is important to point out that hatching success varies enormously by year and locality, ranging from almost complete breeding failure to 88% success (see reviews). Hatching success in this study is clearly within published ranges and is not very different from values observed for the two species in many other studies.

To summarize, in this study, only laying date and colony size had a significant effect on hatching success of Avocets and Black-winged Stilts. Late nests showed the lowest daily survival rate in the two species. Black-winged Stilts had less hatching success in large colonies than in medium-sized ones, which could help explain the different degree of coloniality of the two species. Daily survival rate of nests during egg-laying was significantly lower than in the incubation period, suggesting higher probability of clutch predation and/or desertion in early nesting stages.

ACKNOWLEDGEMENTS

I thank F. Alvarez and E. Aguilera for supervising this study and D. Chamberlain, H. Hötker and J. O'Halloran for their constructive criticism on a previous version of the manuscript. Arrocerías Herba S. A. and Agencia de Medio Ambiente de Huelva kindly allowed research and provided accommodation in Doñana and Odiel Natural Parks, respectively. The study was supported by a grant from the Spanish Ministry of Education and Science.

ENDNOTE

a. According to Johnson (1979): variance = (exposure – losses) × losses/exposure^3. Standard error (se) was the square root of the variance. A z-value (area under the normal curve) shows whether differences in daily survival rate are statistically significant (Johnson & Shaffer 1990): $z = |s_1 - s_2|/(v_1 + v_2)$. In this formula, s is daily survival rate and v is the variance.

REFERENCES

Adret, P. 1984. Une étude des relations spatiales entre jeunes avocettes sur leurs lieux d'elevage. *Revue d'Ecologie (La Terre et la Vie)* **39**: 193–208.

Arroyo, G.M. 2000. Influencia de las transformaciones humanas de hábitats costeros supralitorales sobre la ecología de la reproducción de la cigüeñuela *Himantopus himantopus* y la avoceta *Recurvirostra avosetta* (Aves: Recurvirostridae) en la Bahía de Cádiz: aplicación a la gestión de espacios naturales protegidos. PhD Thesis, University of Cádiz, Puerto Real, Spain.

Brown, C.R. & Brown, M.B. 2001. Avian coloniality: progress and problems. In Nolan, V. & Thompson, C.F. (eds) *Current Ornithology*, Vol. 16: 1–82. Plenum, New York.

Castro, H. 1993. *Las salinas de Cabo de Gata. Ecología y dinámica anual de las poblaciones de aves en las salinas de Cabo de Gata (Almería)*. Instituto de Estudios Almerienses, Almería, Spain.

Clutton-Brock, T.H. 1991. *The Evolution of Parental Care*. Princeton University Press, Princeton, New Jersey.

Cramp, S. & Simmons, K. (eds) 1983. *The Birds of the Western Palearctic*, Vol. 3: 36–62. Oxford University Press, Oxford.

Cuervo, J.J. 2003. Parental roles and mating system in the black-winged stilt. *Can. J. Zool.* **81**: 947–953.

Cuervo, J.J. 2004. Nest-site selection and characteristics in a mixed-species colony of Avocets *Recurvirostra avosetta* and Black-winged Stilts *Himantopus himantopus*. *Bird Study* **51**: 20–24.

García Novo, F., Merino Ortega, J., Ramírez Díaz, L., Rodenas Larios, M., Sancho Royo, F., Torres Martínez, A., González Bernáldez, F., Díaz Pineda, F., Allier, C., Bresset, V. & Lacoste, A. 1977. *Doñana. Prospección e inventario de ecosistemas*. ICONA, Monografía no. 18. Ministerio de Agricultura, Madrid, Spain.

Green, R.E., Hawell, J. & Johnson, T.H. 1987. Identification of predators of wader eggs from egg remains. *Bird Study* **34**: 87–91.

Hamilton, R.B. 1975. Comparative behavior of the American avocet and the black-necked stilt (Recurvirostridae). *Ornithological Monographs* **17**.

Hötker, H. 1998. Intraspecific variation in length of incubation period in avocets *Recurvirostra avosetta*. *Ardea* **86**: 33–41.

Hötker, H. 2000. Intraspecific variation in size and density of Avocet colonies: effects of nest-distances on hatching and breeding success. *J. Avian Biol.* **31**: 387–398.

Hötker, H. & Sebegade, A. 2000. Effects of predation and weather

on the breeding success of avocets *Recurvirostra avosetta*. *Bird Study* **47**: 91–101.

Johnson, D.H. 1979. Estimating nest success: the Mayfield method and an alternative. *Auk* **96**: 651–661.

Johnson, D.H. & Shaffer, T.L. 1990. Estimating nest success: when Mayfield wins. *Auk* **107**: 595–600.

Klett, A.T. & Johnson, D.H. 1982. Variability in nest survival rates and implications to nesting studies. *Auk* **99**: 77–87.

Mayfield, H.F. 1961. Nesting success calculated from exposure. *Wilson Bull.* **73**: 255–261.

Mayfield, H.F. 1975. Suggestions for calculating nest success. *Wilson Bull.* **87**: 456–466.

Moreno, J. 1998. The determination of seasonal declines in breeding success in seabirds. *Etología* **6**: 17–31.

Rubio, J.C. 1985. Descripción ecológica del Paraje Natural de las Marismas del Odiel. PhD Thesis, University of Seville, Seville, Spain.

Rubio, J.C. & Figueroa, M.E. 1983. Medio físico, vegetación y evolución de las marismas de los ríos Odiel y Tinto (Huelva). *Estud. Territor.* **9**: 59–86.

Sordahl, T.A. 1994. Eggshell removal behavior of American avocets and black-necked stilts. *J. Field Ornithol.* **65**: 461–465.

Tinarelli, R. 1990. Risultati dell'indagine nazionale sul cavaliere d'Italia *Himantopus himantopus* (Linnaeus, 1758). *Ric. Biol. Selvaggina* **87**: 1–102.

Tinarelli, R. 1992. Habitat preference and breeding performance of the black-winged stilt *Himantopus himantopus* in Italy. *Wader Study Group Bull.* **65**: 58–62.

(MS received 25 September 2003; revised MS accepted 26 May 2004)