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Nest-site selection and characteristics in a mixed-species colony of Avocets *Recurvirostra avosetta* and Black-winged Stilts *Himantopus himantopus*

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Capsule Causes of breeding failure determined optimal nest location, Black-winged Stilts being better adapted than Avocets to nest close to water.
Aims To compare nest size and location between the two species and to test whether there were inter-species differences that might suggest specific nesting adaptations, and to investigate possible correlates between hatching success and nest location.
Methods Nest-site selection, characteristics and hatching success were studied during 1989 in a large mixed-species colony located in southern Spain.
Results Black-winged Stilt nests differed in composition and size depending on distance to water (nests touching the water were larger and included mud), but Avocet nests did not. Avocets nests were more aggregated and central within the colony than those of Black-winged Stilts. Causes of breeding failure were flooding and rat predation. Successful or unsuccessful Black-winged Stilt nests did not differ significantly in characteristics or location. Successful Avocet nests were further from water than flooded nests and further from dry land than depredated ones. Distance to the centre of the colony did not affect hatching success.
Conclusion Black-winged Stilts were better adapted than Avocets to nest near water, due to their greater plasticity in nest-building behaviour. Causes of breeding failure determined optimal nest location.

Nest-site selection in birds refers to the choice of a particular location for nesting from all possible sites (Burger 1985). The exact location of a nest may have important consequences for breeding success, for example influencing predation risk (Regehr *et al*. 1998) or probability of flooding (Lauro & Burger 1989). Consequently, birds carefully choose nest-sites in order to maximize their possibilities of a successfully breeding outcome. Nest-site selection has been studied in many bird species, both solitary (Burger 1987) and colonial breeders (for example seabirds; Buckley & Buckley 1980). When choosing nest-sites, birds must consider the proximity of feeding areas, shelter and protection or camouflage against predators. In the case of colonial birds, they must add social factors, strongly influenced by the relative position of the nest within the colony and distance to neighbouring nests. Different factors can produce different or opposite selection pressures (Spear & Anderson 1989, Burger & Gochfeld 1990), and nest-site selection becomes a compromise depending on what factors most strongly determine nesting success in each circumstance.

Nest-site selection and nest characteristics in Avocets *Recurvirostra avosetta* and Black-winged Stilts *Himantopus himantopus* were investigated in a large mixed-species colony. The aim was to compare nest size and nest location between the two species and to test whether there are inter-species differences that might suggest specific nesting adaptations. A second aim was to investigate possible correlates between hatching success and nest location. In relation to hatching success and causes of breeding failure, three predictions were made: (i) flooded nests are closer to water than successful ones, (ii) depredated nests are further from the centre of the colony than successful ones, and (iii) depredated nests are closer to dry land than successful ones if predation is mainly due to terrestrial predators.

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METHODS

The study took place in spring/summer 1989 in Veta la Palma (36°57′N, 6°14′W), Doñana Natural Park, Isla Mayor, Seville, southwestern Spain. The area was a former dry marsh recently flooded for a shrimp *Palaemonetes varians* fishery. A mixed colony of Avocets and Black-winged Stilts was located on narrow man-made dykes attached to a small island in the middle of a brackish pond of *c*. 100 ha (Fig. 1). Water depth averaged 0.75 m and minimum distance between the island (or the colony) and mainland was 100 m. Vegetation on the dykes was patches of typical dry marsh vegetation, mainly scattered glasswort *Arthrocnemum* spp. up to 50 cm high and Graminae.

During the incubation period (May and June) the colony was surveyed every 10 days. Due to conspicuousness of recurvirostrid nests on poorly vegetated ground and their distribution along narrow strips of land, I am confident that all nests were found. Each nest was marked with a numbered plastic tag. During each visit, for each nest I recorded the number of eggs, the species and any evidence of hatching success (chicks emerging from eggs, newborn chicks) or failure (submerged eggs, large eggshell fragments, yolk remains). A nesting attempt was considered successful when at least one chick hatched. If nests were found empty and with no evidence of hatching success or failure their fate was deemed 'unknown'.

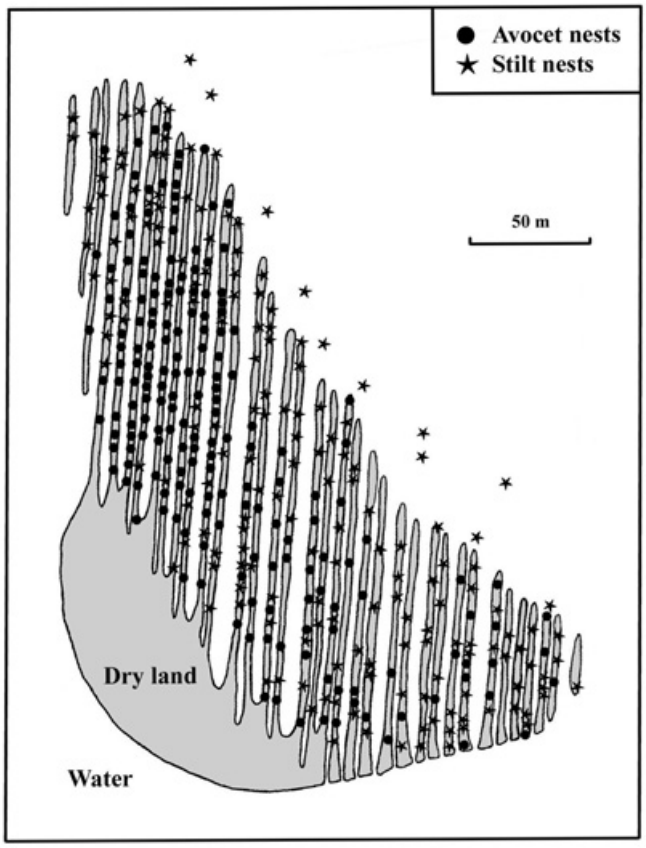

Figure 1. The mixed colony of Avocets and Black-winged Stilts studied.

In July, once all clutches had either hatched or failed and all birds had left the colony, for each nest I measured (to nearest 1 cm) its height (from ground level) and (maximum external) diameter, shortest distance to water, distance to closest vegetation (under which a small chick could hide) and distance to closest nest. All distances were measured from the external rim of the nest. The location of each nest was mapped to calculate distance to the island and to the geometric centre of the colony. To map the nests I measured distances from each nest to several points of reference using two rangefinders (ranges 0.5–30 m and 45–1500 m). Nests of the two species were relatively mixed and did not cluster in subcolonies (Fig. 1). I also calculated distance to the geometric centre of the colony formed exclusively by conspecific nests, i.e. the distance from each Avocet nest to the centre of Avocet nests and the distance from each Black-winged Stilt nest to the centre of Black-winged Stilt nests. Not all nests could be measured due to loss and this explains the inconsistency in sample sizes among different variables.

Non-parametric statistical tests (Wilcoxon–Mann–Whitney test and Spearman's rank-order correlation) (Siegel & Castellan 1988) are used throughout. Distances to closest nest and to the centre of the colony were calculated only for simultaneously active nests at the time of maximum occupation. All tests are two-tailed and the significance level is 0.05.

RESULTS

The total number of nests in the colony was 375 (192 Avocet and 183 Stilt nests). The maximum number of simultaneously active nests was 318 (154 Avocet and 164 Stilt nests). Nests were composed of small fragments of vegetation, mainly *Arthrocnemum* and Graminae. Nest materials included mud in many Stilt nests, mainly in those very close to or touching water: 38 out of 58 Stilt nests touching water contained mud, but all Stilt nests more than 8 cm from water (n = 32) lacked mud. Mud was mixed with fragments of vegetation shaping solid nest walls. Mud was not used in any Avocet nest.

Black-winged Stilt nests were significantly higher and narrower and were placed closer to water and

further from the island than Avocet nests (Table 1). Distance to closest vegetation was not significantly different between nests of the two species. Nest dimensions were significantly correlated to distance to water in Black-winged Stilts (height, $r_s = -0.33$, $n = 100$, $P < 0.01$; diameter, $r_s = -0.20$, $n = 105$, $P < 0.05$) but not in Avocets (height, $r_s = -0.14$, $n = 122$, ns; diameter, $r_s = -0.02$, $n = 138$, ns). However, when those nests touching water were excluded, relationships for Black-winged Stilt nests were no longer significant (height, $r_s = -0.07$, $n = 44$, ns; diameter, $r_s = 0.01$, $n = 47$, ns). Avocet nests touching water did not differ significantly from those that were not, either in height or diameter. Black-winged Stilt nests touching water were higher and wider than those that were not (Table 2).

Black-winged Stilt nests were more scattered than those of Avocet (Table 1). Moreover, Stilt nests were also more peripheral, with larger distances to the centre of the colony (Table 1). Qualitatively similar results were obtained considering distances to the nearest conspecific nest and to the centre of the colony formed exclusively by conspecific nests (Table 1).

Twenty-one Avocet clutches successfully hatched, 38 were flooded and 14 suffered predation. Nine Black-winged Stilt clutches hatched, 15 were flooded and five were destroyed by predators. All nests with depredated clutches contained eggshell fragments with rat *Rattus* spp. teeth marks. Successful Avocet clutches were located further from water than flooded clutches and further from dry land (i.e. the island) than depredated ones (Table 3). However, distance to the centre of the colony did not differ significantly between successful and depredated clutches (Table 3). For Stilts, location of successful clutches did not differ significantly from flooded or depredated ones either in distance to water, to dry land or to the centre of the colony.

DISCUSSION

Nest-site selection and nest characteristics of Avocets and Black-winged Stilts were studied in a large mixed colony. Inter-species comparisons within the same colony appeared to be most appropriate, because other sources of variability (different colonies subject to different predation pressures, different years with different climatological conditions, etc.) could be controlled. The first important difference between the two species was that Avocets exclusively made nests from fragments of vegetation, never using mud in their construction, while many Black-winged Stilt nests,

Table 1. Mean (± se) values for nest size and nest location in two recurvirostrid species nesting in a mixed colony. Results from between-species comparisons are shown.

Parameter	Avocet	*n*	Black-winged Stilt	*n*	*Z*	*P*
Diameter (cm)	22.4 (0.3)	138	21.0 (0.3)	105	–4.0	< 0.001
Height (cm)	2.0 (0.1)	122	3.2 (0.2)	100	5.6	< 0.001
Distance to						
Water (cm)	28.7 (1.9)	161	6.2 (1.0)	156	–9.9	< 0.001
Vegetation (cm)	22.1 (2.9)	153	27.6 (3.8)	151	0.9	ns
Dry land (m)	54.6 (2.3)	192	72.2 (2.6)	183	36.2	< 0.001
Closest nest (m)	4.9 (0.1)	154	6.2 (0.2)	164	4.5	< 0.001
Closest conspecific nest (m)	7.2 (0.3)	154	8.2 (0.3)	164	4.0	< 0.001
Colony centre (m)	64.8 (2.6)	154	84.2 (3.0)	164	4.6	< 0.001
Centre of colony formed exclusively by conspecific nests (m)	61.1 (3.0)	154	83.0 (3.0)	164	5.1	< 0.001

Table 2. Mean (± se) height and diameter of recurvirostrid nests touching water (distance to water = 0) and not touching (> 0), and results from mean comparisons.

	Distance to water = 0	*n*	Distance to water > 0	*n*	*Z*	*P*
Avocet						
Height (cm)	2.4 ± 0.3	17	1.9 ± 0.1	105	1.2	ns
Diameter (cm)	23.1 ± 0.8	18	22.3 ± 0.3	120	1.0	ns
Black-winged Stilt						
Height (cm)	3.7 ± 0.2	56	2.6 ± 0.2	44	3.1	< 0.01
Diameter (cm)	21.6 ± 0.4	58	20.2 ± 0.4	47	2.1	< 0.04

Table 3. Mean (± se) distance to water, to dry land and to the centre of the colony of Avocet nests with successful, flooded and depredated clutches, and results from mean comparisons.

					Successful vs. flooded				Successful vs. depredated	
Distance to	Successful	*n*	Flooded	*n*	*Z*	*P*	Depredated	*n*	*Z*	*P*
Water (cm)	30.0 ± 3.3)	20	11.0 ± 4.1)	22	–3.6	< 0.001	30.4 ± 7.5)	11	0.1	ns
Dry land (m)	56.3 ± 6.0)	21	71.1 ± 4.7)	38	1.8	ns	38.8 (9.0)	14	–2.2	< 0.04
Colony centre (m)	71.4 ± 7.7)	21	73.0 ± 5.5)	38	0.3	ns	59.0 (5.6)	14	–0.8	ns

mainly nests close to water, combined mud and vegetation. Mud is very important for protecting nests close to water.

Black-winged Stilt nests were higher and narrower than those of Avocet and, interestingly, Black-winged Stilt nests touching water were higher (and wider) than those of conspecifics some centimetres away from water. Black-winged Stilts thus considered nest location in relation to water when adding material to the nest. This behavioural plasticity to build different nests in different locations seems to be an adaptive mechanism. Black-winged Stilts build large nests when the site is close to water, so preventing flooding, but small nests when the site is further away, so that they can save energy/time in nest building and maybe reduce nest conspicuousness (and hence predation risk; Cresswell 1997). In contrast, dimensions of Avocet nests did not depend on their distance to water, showing that this species apparently does not have the capacity to modify nest size in relation to flooding risk. This suggests that Black-winged Stilts are better adapted than Avocets to nest close to water, because they have developed mechanisms to minimize reproductive failure from flooding. The relationship between distance to water and nest size in Black-winged Stilts had been already previously reported (Casini 1986, Tinarelli 1990), but this study allows an appropriate inter-species comparison, never undertaken before.

Inter-nest distance was slightly larger than the minimum mean values found in the literature both for Black-winged Stilts (Goutner 1989, Tinarelli 1990) and Avocets (Goutner 1985, Casini 1986), although much larger than in some extremely dense Avocet colonies described by Hötker (2000). Here Avocet nests were significantly closer to a conspecific nest and to the geometric centre of the colony than Black-winged Stilt ones, revealing a higher degree of gregariousness.

The fate of clutches was only determined for a small number of nests, but I assume that nests considered as successful, flooded or depredated are unbiased samples of successful, flooded or depredated nests. This makes it possible to compare nest-site characteristics among the three types of nest. For Avocets, some of the predictions were fulfilled: flooded nests were closer to water, and depredated nests closer to dry land, than successful nests. However, non-significant differences were found in distance to water, distance to the island and distance to the centre of the colony among successful, flooded and depredated Black-winged Stilt nests. This result should be considered cautiously however, because sample sizes for Black-winged Stilts were small.

The two main causes of breeding failure during the incubation period were predation by rats *Rattus* spp. and flooding. Rats live on the island and predated preferentially upon nests close to the island, which might explain why depredated nests were closer to dry land than successful nests. However, depredated nests were not further from the centre of the colony than successful ones. This result could be explained because of the ability of rats to walk along the dykes where nests were placed, reaching not only external nests close to the island but also nests located relatively central within the colony (Fig. 1). Rats can swim but they probably prefer to walk when searching for food. The characteristics of the colony and the type of predator determined the fulfilment of predictions.

In conclusion, this study suggests that Black-winged Stilts are better adapted than Avocets to nest in proximity to water. Moreover, optimal nest location will depend on nest characteristics and on the relative importance of different causes of breeding failure.

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