Mixed clutches in shorebird nests: why are they so uncommon?

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Mixed clutches, in which two females deposit their eggs in the same nest, have been recorded in many shorebird species, but their frequency of occurrence is low in comparison with that of other precocial birds (*e.g.* ducks). This paper provides new observations of mixed clutches both between and within species, for Kentish Plover *Charadrius alexandrinus*, Black-winged Stilt *Himantopus himantopus* and Avocet *Recurvirostra avosetta*. I argue that mixed clutches are relatively uncommon among shorebirds because of a limitation in the parental ability to care for very small chicks when broods are large, rather than by a limitation in the ability to incubate large clutches.

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INTRODUCTION

Facultative nest parasitism among birds may be either intra- or interspecific. Intraspecific nest parasitism has been reported in many avian species, both altricial and precocial (Yom-Tov 1980; Rohwer & Freeman 1989). Facultative interspecific nest parasitism, however, is mainly limited to precocial species, mainly belonging to the families Anatidae and Phasianidae (*e.g.* Weller 1959; Sayler 1992). In many precocial species, the chicks are not fed by their parents, thus the costs of nest parasitism should not be as high for precocial as for altricial species. Several hypotheses have been advanced to account for the occurrence of facultative nest parasitism among precocial birds, and these may be grouped into a number of categories (reviewed by Sayler 1992). One category concerns competition for nesting sites, and suggests that when the availability of nesting sites is limited, two females may be forced to lay in the same nest. Another group of hypotheses addresses the behavioural strategies adopted by parasitic nesting females; these strategies may be either alternative or conditional. Individuals adopting alternative strategies usually initiate laying in the nests of other individuals, and after laying some eggs in such nests continue laying, in some cases almost without interruption, in their own nests (Weller 1959; Clawson *et al.* 1979; Hori 1987; Sorenson 1991). Individuals adopting conditional strategies usually parasitise nests of others when there is no possibility of initiating normal nesting; therefore such individuals would be making the 'best of a bad situation' (Amat 1985; Lank *et al.* 1989; Briggs 1991; Sorenson 1991; Lyon 1993). In the case of shorebirds, it has been suggested that, when females lose their nests to predators during the laying period, they may deposit the remainder of the clutch in nests of other shorebirds (Colwell 1986). If so, such individuals would be adopting a conditional parasitic nesting strategy. In other cases, the occurrence of superclutches has been attributed to female-female pairings or polygynous matings (Scott 1974; Walters & Walters 1980; Warriner *et al.* 1986).

There are many factors affecting the rate of nest parasitism, some of which include conditions during nesting, such as the utilisation of similar nesting habitats by hosts and parasites, the ease with which nests to be potentially parasitised are found, laying synchronisation between hosts and parasites, etc. (*e.g.* Weller 1959; Sayler 1992). These conditions should be met particularly in the case of species nesting at high densities, such as colonial nesting birds (Brown 1984; Emlen & Wrege 1986; Lyon & Everding 1996).

This note reports on the occurrence of mixed clutches in the nests of Kentish Plovers *Charadrius alexandrinus*, Black-winged Stilts *Himantopus himantopus* and Avocets *Recurvirostra avosetta* in two wetlands of southern Spain. Examples of mixed clutches in the literature are reviewed to examine the reasons why mixed clutches are relatively rare among shorebirds (Charadrii), even among colonially nesting species.

METHODS

The observations were made in the marshes of the Guadalquivir (37°7' N, 6°12' W) and Fuente de Piedra lake (37°6' N, 4°45' W). Descriptions of these sites may be found in Amat (1985) and Fraga & Amat (1996).

Nests were considered to contain mixed clutches of conspecifics when (1) more than one egg appeared during a single day in the nest, (2) there were clear differences in size, background colour and/or spotting pattern between some egg(s) and the rest of the clutch (but see McRae 1997), and (3) clutch sizes were larger than the mode, *i.e.* >3 eggs for Kentish Plovers, and >4 eggs for Black-winged Stilts and Avocets. In all cases in which clutch sizes were larger than the mode, it was possible to separate two groups of eggs in the clutch, based on size, background colour and/or egg spotting pattern (usually by at least two criteria). Assignment of eggs to individual Kentish Plover females was possible when females were captured more than once at nests, since egg size characteristics (length, breadth and volume) are highly repeatable between clutches in the Kentish Plover (J. A. Amat, R. M. Fraga & G. M. Arroyo, unpubl.). In the case of Kentish Plovers, laying dates were estimated by an equation given in Fraga & Amat (1996), based on observed egg masses in relation to egg volumes, for those cases in which nests were found once the clutch was completed. In the Guadalquivir marshes, nests were visited at irregular intervals, while at Fuente de Piedra, nests were visited every 3-6 days to determine their outcome.

In the marshes of the Guadalquivir, only information on stilt clutches was gathered, whereas at Fuente de Piedra information for all three species was recorded.

RESULTS

Kentish Plover

During a study on the breeding biology of this species in 1991-1996, nine nests (1% of 883) were found containing eggs of more than one female. Three of the nests had six eggs, one had five eggs, three had four eggs, one had three eggs, and one nest had two eggs. In two of the nests with six eggs, three eggs were deposited by a second female in deserted nests that already contained three eggs; these two nests were subsequently abandoned. In the other nest with six eggs, two females laid on alternate days; the first female was captured during incubation. This female had been captured in another nest in the same nesting season, as well as in previous and subsequent breeding seasons. This last nest with six eggs was predated during incubation.

In the nest with five eggs, two females laid simultaneously, but the nest was deserted before incubation started. The outcome of the remaining five nests with mixed clutches was variable but, in all the nests, incubation started, and only a pair of adults was captured incubating at each one. Two of the nests with four eggs and the nest with three eggs were successful, a nest with four eggs was deserted during mid-incubation, and the nest with two eggs was predated. This last nest was discovered during incubation, and it could have suffered partial predation (see Fraga & Amat 1996).

Black-winged Stilt

During studies of other waterbird species, nests of this species were found with mixed clutches, either of conspecifics or of other shorebird species. In 1984, in a colony of 24 nests in the marshes of the Guadalquivir, two nests with seven eggs were found. Ten days after discovery, only one egg remained in each of these nests. The fate of these nests could not be determined, as the colony was visited at irregular intervals. No nests with a supercluch (*i.e.* >4 eggs) were recorded in 1985, when at the same site there was a colony of 24 Black-winged Stilt nests.

At Fuente de Piedra, an extra egg was deposited in a stilt nest that contained four eggs and was in mid-incubation. About five days before hatching, the parasitic egg was cracked and only three eggs hatched from the nest.

Also at Fuente de Piedra, two stilt nests were found each containing eggs of other species. One of these nests had four stilt eggs and an Avocet egg, and was deserted when found. This was the single stilt nest on an islet where there was a small colony of Avocets (four nests). About 1.5 m from the stilt nest, there was an Avocet nest with three eggs very similar to the avocet egg found in the stilt nest.

The other Black-winged Stilt nest contained two Kentish Plover eggs and four stilt eggs when discovered on 16 May; another plover egg was found about 1.5 m from the nest. On 20 May the two plover eggs were cracked, and two days later one plover egg had disappeared from the nest. On 5 June, the remaining plover egg had disappeared and two recently hatched stilt chicks were on the nest. Peeping vocalisations were heard from the other two stilt eggs and they hatched later in the day. Only the stilts were recorded incubating in this nest.

All the nests with mixed clutches in Fuente de Piedra were recorded in 1996, and represented 5% of 57 Black-winged Stilt nests found there that year.

Avocet

An Avocet nest was found with five eggs during mid-incubation. Three eggs were from one female and two from another female. The first set of eggs hatched about 48 hours before the other. This nest was found in 1996 and was located on an islet where there was a mixed colony of seven Avocet and nine stilt nests. It represented 2% of 41 Avocet nests found in Fuente de Piedra in 1996.

DISCUSSION

Some of the cases of mixed clutches in the shorebird nests that were observed could be accounted for by the competition for nesting sites hypothesis, but the ecological conditions promoting the occurrence of such competition varied between different cases. For example, superclutches of Black-winged Stilts were recorded in the marshes of the Guadalquivir in a year of low water levels (1984), but not in the subsequent year when water levels were higher. Under drier conditions, the frequency of two females laying in the same nest possibly increased due to a limitation in the availability of nesting sites (Colwell 1986).

In contrast, at Fuente de Piedra, all cases of nests with mixed clutches of both Black-winged Stilt and Avocet were recorded during a year of high water levels (1996) in which both species established nesting colonies on islets. Also at Fuente de Piedra, all but one of the cases of mixed clutches by Kentish Plovers were recorded on islets, where distances between nests were shorter than in other parts of the lake (Fraga & Amat 1996).

Some of the nests found at Fuente de Piedra containing mixed clutches could have resulted from two females simultaneously starting laying in the same scrape. This would account for the mixed Avocet clutch and most of the Kentish Plover nests with eggs of two conspecific females, as well as for the Black-winged Stilt nest containing Kentish Plover eggs, as determined by back-calculations. In the cases of intraspecific mixed clutches, the female initiating laying in the first place was probably the one which subsequently incubated the eggs. In one case (Kentish Plover) this was suggested by the laying sequence and, in the remaining cases, because it was likely that the clutches of one of the females were not completed, probably because of being prevented from doing so by birds that had completed clutches and had initiated incubation (Warriner *et al.* 1986). In the Kentish Plover, reutilisation of nest scrapes within a nesting season by different pairs may occur (Fraga & Amat 1996), and this may explain, at least in part, why two females simultaneously deposited their eggs in the same nest scrape.

The Black-winged Stilt nest containing Kentish Plover eggs could have resulted from that nest being initiated by Kentish Plovers, suggested by the fact that the Kentish Plover clutch was completed, and during the laying period a stilt initiated laying in the same site and then usurped the nest once incubation commenced. Also in Fuente de Piedra, in the nesting season of 1996, a scrape of Kentish Plovers was observed that two days after excavation was usurped by the Black-winged Stilts that had initiated laying in this site. In the few instances in which laying by two shorebird species has been recorded in the same nest, the larger species was subsequently recorded incubating the eggs (Parrinder 1969; Larson 1978; J. Figuerola, pers. comm.; this note).

In one case, a Black-winged Stilt and, in two cases, Kentish Plovers deposited eggs in nests of conspecifics containing completed clutches. The nests of Kentish Plovers were already abandoned when second females laid in them. I cannot offer any explanation for the occurrence of these last three nests.

Some authors have considered mixed clutches among shorebirds to be nest parasitism (*e.g.* Colwell 1986; Reynolds 1987; Delehanty & Oring 1993). Nevertheless, to categorise these clutches as nest parasitism may be incorrect. Firstly, most cases of mixed clutches by conspecific females reported above seem to be the result of two pairs simultaneously using the same nest during laying. Secondly, in cases of interspecific mixed clutches, including those in which eggs of shorebirds have been recorded in species other than shorebirds, mainly gulls or terns, the larger or dominant species was the incubator of eggs, even if the smaller or least dominant species was the first one to complete the clutch and initiate incubation (Parrinder 1969; Larson 1978; Radford 1985; Kuyt & Johns 1992; J. Figuerola, pers. comm.; this study). The fact that, in some cases, the second female was the one that incubated the eggs argues against a parasitic nesting strategy. Thirdly, duck eggs have been recorded in shorebird nests (Weller 1959; Hildén 1964; pers. obs.), but the ducks did not incubate the eggs, in spite of their larger body size and likely dominance over shorebirds, probably because ducks adopt true parasitic nesting strategies.

Although clutch sizes larger than the mode which are attributable to two females laying in the same nest have been recorded in many shorebird species (Cramp & Simmons 1983), the frequency of occurrence of mixed clutches among shorebirds is very low (but see Giroux 1985), contrasting with other precocial species in which facultative nest parasitism is high (i.e. >20% of nests of the host species parasitized, Joyner 1976; Clawson *et al.* 1979; Amat 1985; Sorenson 1991; Lyon & Everding 1996). Thus, in this study only 1-5% of clutches contained eggs of more than one female. Similarly, in three other sites in southern Spain, Cuervo (1993) and Castro Nogueira (1993) found that 1-8% of clutches of colonial Black-winged Stilts and Avocets were larger than the mode. This low frequency of occurrence of mixed clutches may seem surprising given that the potential for the occurrence of mixed clutches in shorebirds is high, especially among colonially nesting species. It has been suggested that incubation ability is one of the main factors limiting the clutch size of shorebirds (Hill 1980; Kålås & Løfaldli 1987; Székely *et al.* 1994; Yogev *et al.* 1996), and the same factor has been used to explain the occurrence of mixed clutches among shorebirds (Delehanty & Oring 1993).

Nests of shorebirds containing clutch sizes one egg larger than modal clutch sizes may be successful (Hill 1980; Castro Nogueira 1993; Székely *et al.* 1994; Yogev *et al.* 1996; Sandercock 1997; this note), but enlarged clutches require longer incubation and their hatching success is lower than clutches of modal size (Gibson 1971; Hill 1980; Delehanty & Oring 1993; Székely *et al.* 1994; Yogev *et al.* 1996; Sandercock 1997). In addition, shorebird nests with clutch sizes two or more eggs larger than modal clutch size are rarely successful (Castro Nogueira 1993; Delehanty & Oring 1993). When the number of eggs is large, shorebirds have difficulty in covering them all (Hussell & Woodford 1965; Hill 1980; Delehanty & Oring 1993).

Lower hatching success due to inefficient incubation has also been reported for parasitised nests of other precocial bird species (Amat 1985, 1993; Lank *et al.* 1990) and, in spite of this, nest parasitism among those birds is frequent (references above). Thus, it seems that inefficient incubation may not be the main factor explaining the low occurrence of mixed clutches among shorebirds. The question still remains: if shorebird nests with mixed clutches only one egg larger than modal clutch sizes may be successful, why shorebird females do not adopt parasitic nesting tactics by laying only one egg in nests of potential hosts and then continue laying clutches of modal size in their own nests. This would be feasible given that clutch sizes of shorebirds may not be limited by egg-formation costs, as they may lay one or two eggs if the first eggs in the clutch are removed shortly after being laid (Rinkel 1940; Székely *et al.* 1994; Yogev *et al.* 1996).

The low occurrence of mixed clutches among shorebirds may therefore be related to a limitation of the parental ability to care for very small chicks, and this could be exacerbated in species in which parents feed the chicks (*e.g.*, *Burhinus, Dromas, Haematopus, Glareola*). Safriel (1975) showed that experimentally enlarged broods of Semipalmated Sandpipers *Calidris pusilla* suffered higher chick losses than normal broods. Adoption of chicks by shorebirds has been recorded in several species (*e.g.* Warriner *et al.* 1986), but the fate of adopted chicks in mixed broods has seldom been determined. When adoptions were successful (Cooper & Miller 1992; Lanctot *et al.*1995), brood amalgamation occurred when chicks were large enough to be able to reach homeothermy with little or no brooding by adults, and/or when such chicks were not as vulnerable to predators as younger chicks, or when chicks were adopted into broods with lower than the modal number of chicks. As parental care is not as critical for the survival of older chicks, this may explain why amalgamation of broods may be viable but mixed clutches may not. This bottleneck in the life-history of shorebirds could be one factor limiting their clutch sizes (Safriel 1975; Sandercock 1997). Further research, especially experimental, is needed to quantify the incidence of mixed clutches among shorebirds, as well as to determine factors affecting chick survival in enlarged broods.

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