

Parental roles and mating system in the black-winged stilt

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Abstract: The breeding behaviour of black-winged stilts (*Himantopus himantopus*) was studied in southwestern Spain. In the prelaying period males devoted more time than females to agonistic encounters, locomotion, and nest building. During egg laying, males spent more time than females at the nest, mostly building the nest and covering the eggs, while females spent more time foraging than males. During late incubation, females spent significantly more time at the nest than males. These results suggest very similar parental investment by the sexes. During part of the female's fertile period, males stayed at the nest while females were foraging, which precluded efficient mate guarding. However, females were reluctant to engage in extra-pair copulations, being always very aggressive towards conspecifics except for their mates. Even in two cases of extra-pair copulation, the first described for this species, the female continuously attacked the intrusive male and did not cooperate in copulation. Male parental care seems to be essential for reproductive success and females are probably faithful in order to assure male parental investment. The need for parental care from both males and females would maintain social, and perhaps also genetic, monogamy in this species.

Résumé : Le comportement reproducteur a été étudié chez l'échasse blanche (*Himantopus himantopus*) dans le sud-ouest de l'Espagne. Avant la ponte, les mâles consacrent plus de temps que les femelles à des rencontres agonistiques, à la locomotion et à la construction du nid. Au cours de la période de la ponte, les mâles passent plus de temps au nid que les femelles, surtout pour la construction du nid et la couvaison, tandis que les femelles passent plus de temps que les mâles à chercher la nourriture. Vers la fin de l'incubation, les femelles passent significativement plus de temps au nid que les mâles. Ces observations montrent que les investissements parentaux sont très semblables chez les deux sexes. Au cours d'une partie de la période de fertilité des femelles, les mâles restent au nid alors que les femelles vont à la recherche de nourriture; ils ne peuvent donc pas surveiller leur partenaire de façon efficace. Cependant, les femelles sont toujours très réticentes à s'accoupler avec des mâles autres que leur partenaire et elles sont toujours très agressives vis-à-vis des autres oiseaux de leur espèce, à l'exception de leur partenaire. Même dans les deux cas d'accouplement avec un mâle étranger, un phénomène signalé pour la première fois chez cette espèce, la femelle a attaqué tout le temps le mâle importun et n'a pas collaboré à l'accouplement. Les soins prodigués par le parent mâle semblent essentiels au succès reproductif et la fidélité de la femelle sert probablement à garantir l'investissement parental du mâle. La nécessité des soins parentaux combinés des mâles et des femelles doit pouvoir maintenir la monogamie sociale et peut-être aussi la monogamie génétique chez cette espèce.

[Traduit par la Rédaction]

Introduction

According to Clutton-Brock (1991), parental care in its broadest sense is "any form of parental behaviour that appears likely to increase the fitness of a parent's offspring", including not only the care of eggs and young but also egg production. On the other hand, parental investment can be defined as "the extent to which parental care of individual offspring reduces the parent's residual reproductive value" (Clutton-Brock 1991). Parental care does not include efforts to acquire a mate, but parental care and mating efforts may be considered together as the whole reproductive effort (Low 1978).

Most avian species (ca. 90%) are socially monogamous (Lack 1968; Møller 1986). Biparental care is common in monogamous species, and monogamy has often been explained by the need for male parental care in order for offspring production to succeed (Lack 1968; Emlen and Oring 1977; Wittenberger and Tilson 1980). Comparing male and female parental investment is difficult because a common "currency" for different types of investment is necessary. According to Trivers (1972), the currency of all forms of parental investment is its cost in terms of the parent's ability to invest in other offspring. One approach is to calculate the time-energy budget, i.e., to estimate the energy spent in performing different behaviours and in gamete production (for an example see Brunton 1988).

Social monogamy is common in birds, but extra-pair copulations are frequent in many socially monogamous species, leading to instances of extra-pair paternity (Birkhead and Møller 1996; Birkhead 1998). In fact, genetic monogamy is quite uncommon in birds, although interspecific variation in the percentage of offspring fathered by extra-pair males is enormous (Møller 1998; Petrie and Kempnaers 1998). Differ-

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ent factors related to this variation have recently been investigated: male parental care, coloniality, breeding synchrony, genetic variability, etc. (reviews in Birkhead and Møller 1992; Birkhead 1998; Petrie and Kempenaers 1998). Males might be expected to search actively for extra-pair copulations because it would be a relatively inexpensive way of increasing reproductive success. For the same reason males would be expected to assure paternity of their own broods by, for example, mate guarding or frequent intra-pair copulations (Birkhead and Møller 1992).

Black-winged stilts (*Himantopus himantopus*) are large waders (ca. 200 g) with a long bill, neck, and legs. Their preferred habitats are marshes, lagoons, and estuaries, where they feed predominantly on small water invertebrates (Cramp and Simmons 1983). The general breeding biology of European populations has been studied in Italy (Casini 1986; Tinarelli 1990, 1992) and Spain (Castro 1993; Cuervo 1993; Arroyo 2000). However, their reproductive behaviour has been poorly investigated (but see Goriup 1982; Cuervo 1993). Black-winged stilts are socially monogamous and breed in open habitats, colonially or semicolonally, although solitary nests are not rare. Nests are placed on the ground, usually close to water, and both sexes incubate the eggs (three to five per clutch) and protect the young. Chicks leave the nest soon after hatching and feed on their own.

The aim of this study was to investigate differences in parental care and other breeding-related behaviours between males and females in the black-winged stilt, a species in which the sexes have previously been assumed to share most parental duties. Male and female parental investment will be discussed in order to understand the social monogamy characteristic of this species.

Materials and methods

This study was carried out in spring 1990 in Veta la Palma (36°57'N, 6°14'W), Doñana Natural Park, Seville province, southwestern Spain. The area was a former dry marsh recently flooded for shrimp-fishery purposes. A small colony of black-winged stilts (13 breeding pairs) was located on narrow man-made dykes attached to a small island in the middle of a brackish pond covering ca. 100 ha. Water depth averaged 1 m and the minimum distance between the island and the mainland was 100 m. Vegetation on the dykes consisted of patches of typical dry-marsh vegetation, mainly scattered glasswort (*Arthrocnemum* spp.) up to 50 cm high. On the island itself vegetation was more varied, with a few prickly pears (*Opuntia ficus-indica*) and abundant Gramminae.

Black-winged stilts were observed with binoculars (8 × 30) and a telescope (15–45×) from a blind located on the island 3 m above ground level. Stilt behaviour was recorded in two different ways: scan sampling for behaviour on the nest and focal-individual sampling for behaviour outside the nest (Altmann 1974). Every method supplies different and supplementary information and is most appropriate in different circumstances. For example, scan sampling is very useful for determining birds' activities in the nest, because nests are easy to find at any particular moment. However, individuals far from the nest can be hard to find, so we used focal sampling. Nests were observed from the beginning of May, when

early breeders began egg laying, until mid-June, when all eggs had hatched. All nests containing at least one egg were observed every 15 min and for males and females I recorded whether they were (i) absent (>4 m from the nest), (ii) present (<4 m from the nest) but not incubating, or (iii) incubating. The nesting period was divided into four subperiods for each breeding pair: egg laying, early incubation (first week after clutch completion), mid-incubation (second week after clutch completion), and late incubation (from the end of mid-incubation until hatching of the first egg, a period of approximately 1 week). Each nest was scanned at least 20 times (corresponding to 5 h of observation) in every subperiod. The total duration of scan sampling was 158 h. Information for the egg-laying period was not available for two nests. All observations were carried out during daylight (0600–1900 GMT). To check for the possible influence of time of day on birds' behaviour on the nest I divided day length into 5 periods: 0600–0900, 0901–1130, 1131–1400, 1401–1630, and 1631–1900.

To determine stilt behaviour >4 m from the nest I chose one non-incubating individual randomly and followed it continuously for as long as possible up to 10 min or until it began to incubate. The total duration of all focal-individual observations was 45 h. Birds were individually identified and the time spent in different activities (foraging, resting, preening, vigilance, nest building, locomotion, aggression, and chick brooding) was recorded. I considered any upright posture with extended neck, or head turning while watching the sky for potential avian predators, to be vigilance. Nest building included scraping the ground and collecting nest material (for detailed information concerning nest-building behaviour in recurvirostrids see Makkink 1936; Gibson 1971; Hamilton 1975; Cuervo 1993). Both flying and walking with no obvious purpose were considered locomotion. Aggressive encounters were both intra- and inter-specific: against predators (black kite (*Milvus migrans*), red kite (*Milvus milvus*), lesser black-backed gull (*Larus fuscus*)) or against other species (Kentish plover (*Charadrius alexandrinus*), pied avocet (*Recurvirostra avosetta*), redshank (*Tringa totanus*), ruff (*Philomachus pugnax*)). All focal sampling was assigned to four reproductive periods: prelaying, laying, incubation, and chick rearing. Obviously, chick-brooding behaviour was observed only during chick rearing. Focal sampling began in early April (all observations made in April corresponded to the prelaying period) and finished in mid-June. Only sampling periods more than 3 min long were considered. All observations of the same individual during the same period were pooled. Some individuals observed during the prelaying period never bred in the controlled area, and this explains why the sample size for females during the prelaying period is larger than that for total breeding pairs. Birds both on and outside the nest were observed from the same blind, so I recorded bird behaviour only in the colony area. In all observation sessions I paid special attention to copulations, always following the birds involved and determining whether they were a stable pair.

In this study, adult stilts were not captured, consequently it was not possible to mark birds individually with colour rings or any other device. All identifications of individual birds relied on the distinct coloration of the head and neck

feathers. The head and neck plumage is predominantly white, usually with some dark feathers on the crown, nape, and (or) hindneck that vary enormously in extent, location, and degree of darkness (Goriup 1982; Cramp and Simmons 1983; Xeira 1987). The male's head pattern is particularly variable, ranging from a completely white head and neck to a black hindneck, nape, and crown down to the eye. In the female, the dark feathers on the head and neck are very often greyish, but show substantial variation. Since the number of breeding pairs was not large, it was relatively easy to identify all individuals exclusively from the coloration pattern on the head and neck, but in a few cases when doubt arose (mainly due to a long distance between bird and observer), the observations were not included in the analyses. Sex identification was easy because during the breeding period the lower mantle, scapulars, tertials, and tertial covers are glossy black in males but sepia brown in females (Cramp and Simmons 1983).

I used non-parametric tests for statistical analyses because the sample size was rather small and most variables did not follow a normal distribution even after transformation. Wilcoxon's paired-sample test was used to compare male and female activity on the nest, using a paired comparison of males and females from the same nest. Both the standard procedure and the normal approximation (Zar 1984, pp. 153–156) gave qualitatively identical results, and only results from normal approximations are shown. A Mann–Whitney test was used to compare male and female behaviour outside the nest. Tests for two independent samples were used in this case because I did not collect data for both members in all pairs. Observed individuals were chosen at random and, hence, individuals that spent less time within the colony were not observed, while other individuals were observed many times. Paired comparisons would be most appropriate, but the sample size was excessively reduced when only pairs with information for both members were considered. All tests were two-tailed and the significance level was 0.05.

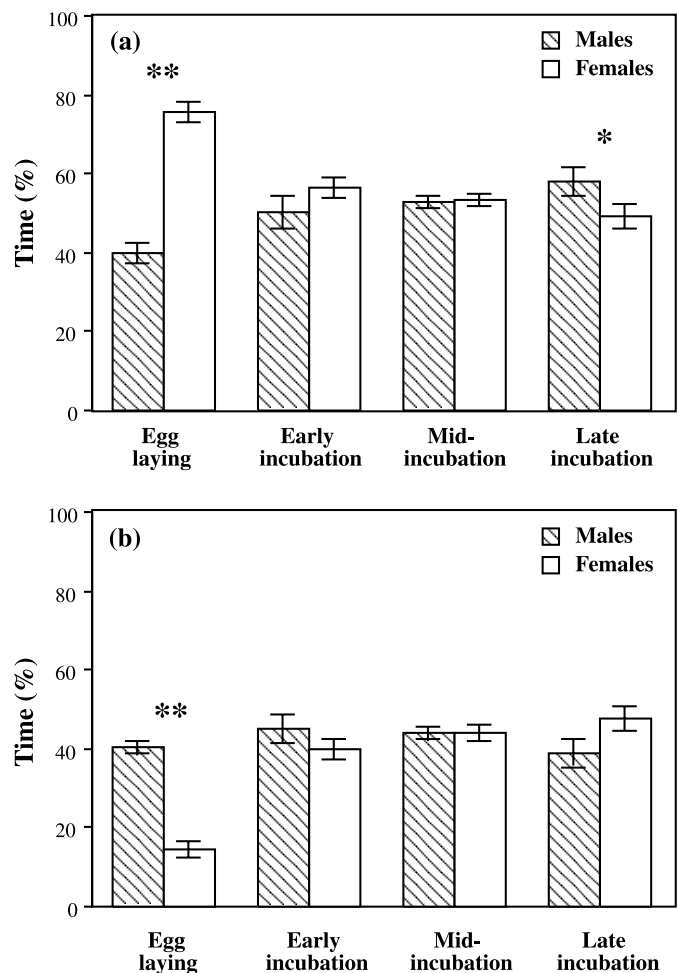
Results

Sex differences in nesting behaviour

Scan sampling of behaviour on the nest

Male and female behaviour on the nest was markedly different during egg laying. The percentage of time spent incubating was significantly larger in males, while the percentage of time spent absent from the nest or close by was significantly larger in females (Wilcoxon's paired-sample test, in the two cases, $N_{\text{males}} = N_{\text{females}} = 11$, $Z = -2.9$, $P = 0.0033$) (Fig. 1). Sex differences were no longer significant during early and mid-incubation (in the four analyses, $N_{\text{males}} = N_{\text{females}} = 13$, $-0.04 \geq Z \geq -1.3$, $P > 0.10$). During late incubation, sex differences in incubation were not significant ($N_{\text{males}} = N_{\text{females}} = 13$, $Z = -1.8$, $P > 0.07$) but the percentage of time spent absent from the nest was significantly larger in males ($N_{\text{males}} = N_{\text{females}} = 13$, $Z = -2.1$, $P = 0.039$) (Fig. 1). Time of the day did not have a significant influence on the percentage of time spent incubating or absent from the nest for either sex (Kruskal–Wallis test, in the four tests, $N = 13$, $df = 4$, $H \leq 7.0$, $P \geq 0.14$).

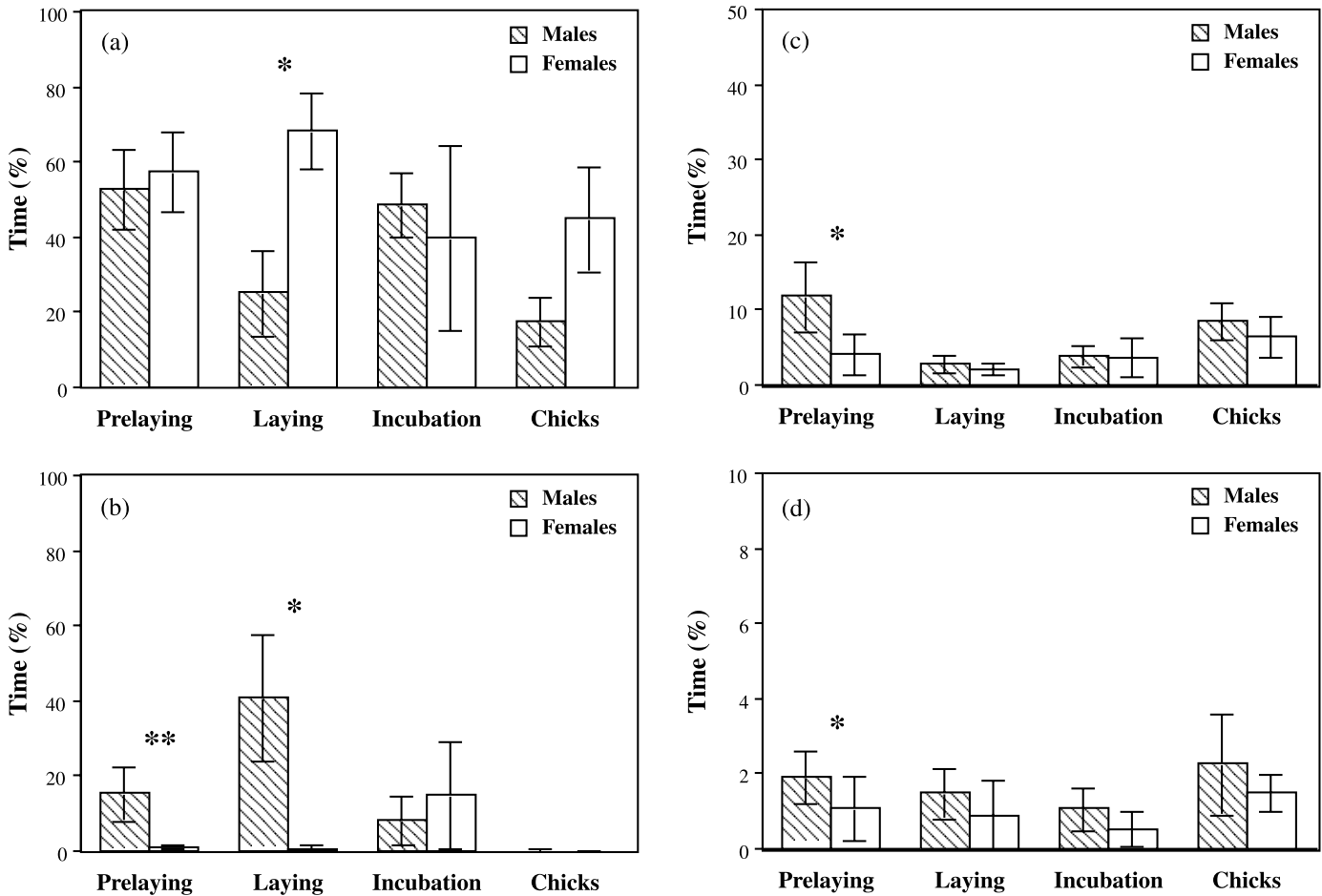
Fig. 1. Percentages of time (mean \pm SE) that male and female black-winged stilts (*Himantopus himantopus*) spent absent from the nest (>4 m away) (a) and incubating (b) during four nesting periods: egg laying, early incubation, mid-incubation, and late incubation. During the rest of the time birds were present (<4 m from the nest) but not incubating. $N = 11$ breeding pairs for egg laying and $N = 13$ for the other periods. After paired comparisons between males and females of the same pair: *, $P < 0.05$; **, $P < 0.001$.



Focal-individual sampling of behaviour outside the nest

Males and females differed significantly in the percentage of time they dedicated to different activities while away from the nest (Fig. 2). During prelaying, males spent more time than females building the nest (Mann–Whitney test, $N_{\text{males}} = 10$, $N_{\text{females}} = 17$, $U = 143.0$, $P = 0.0017$), flying or walking ($U = 126.5$, $P = 0.034$), and involved in aggressive encounters ($U = 125.0$, $P = 0.021$) (Fig. 2). During egg laying, males spent more time building the nest ($N_{\text{males}} = 8$, $N_{\text{females}} = 6$, $U = 41.0$, $P = 0.019$) but females spent more time foraging ($U = 8.0$, $P = 0.038$). Sex differences in the percentage of time dedicated to other behaviours (resting, preening, vigilance, chick brooding) or to the previously mentioned activities during the other periods were not statistically significant.

Fig. 2. Percentages of time (mean \pm SE) that male and female black-winged stilts spent foraging (*a*), building the nest (*b*), flying and walking (locomotion) (*c*), and involved in aggressive encounters (*d*) during four nesting periods: prelaying, egg laying, incubation, and chick rearing. The rest of the time in each period was dedicated to other behaviours: resting, preening, vigilance, or chick brooding. Numbers of individuals observed were as follows: 10 males and 17 females in the prelaying period, 8 males and 6 females in the laying period, and 7 males and 6 females in the incubation and chick-rearing periods. After unpaired comparisons between males and females: *, $P < 0.05$; **, $P < 0.001$.



(in all 24 cases, $10 \geq N_{\text{males}} \geq 7$, $17 \geq N_{\text{females}} \geq 6$, $110.0 \geq U \geq 10.5$, $P > 0.10$) (Fig. 2).

Extra-pair copulations

I observed 91 copulations during 225 h of observation beginning in early April and finishing on 26 May, when all stilt pairs had completed their clutches. Two of these copulations were performed by pairs during the egg-laying period and 2 copulations involved one female during the egg-laying period and one extra-pair male. These 2 extra-pair copulations were performed by the same individuals (see below). This amounts to 89 intra-pair (97.8%) and 2 extra-pair (2.2%) copulations. Eighty-seven copulations were performed by pairs during the prelaying period. The above values do not represent the frequency of copulations because several pairs could be observed simultaneously. However, copulation frequency may be assessed using only copulations that involved individuals under focal sampling. During the prelaying period I

observed 3 copulations during 25 h of focal sampling. This amounts to a rate of 0.12 copulations per hour. No copulations were observed in 6 h of focal sampling during the laying period, 8 h during incubation, and 6 h during chick rearing.

This is the first time, to my knowledge, that extra-pair copulations in this species have been reported, and I will briefly describe these interactions. During the afternoon of 15 May a breeding female had already laid one egg and was foraging in the area surrounding the nest. Her male partner was on the nest, covering the egg. Another male approached the female and was attacked by her twice, but instead of flying or running away, he stayed close to her. The female kept still and the intruder began copulatory display, ritually self-preening on both sides of the female alternately, then jumping on her back and copulating (for detailed information on copulatory display see Goriup 1982; Cramp and Simmons 1983; Cuervo 1993). The female did not adopt a soliciting

posture but simply kept still with the neck slightly retracted. After copulation the male took hold of female's beak with his, as is usual in copulatory display in this species, but received a peck from her. Immediately the female resumed attacking and chasing the male and he flew away. The incident occurred only 35 m from the nest but the incubating male did not intervene. Half an hour later the same intrusive male came back and again was repeatedly attacked by the female. After a while the female kept still (ca. 25 m from the nest) and the male began copulatory display. This time, however, the female uttered loud alarm calls and her male partner left the nest and ejected the intruder, preventing extra-pair copulation. Immediately the female adopted the soliciting posture and the social pair copulated.

The second instance of extra-pair copulation was observed 2 days later, during the late afternoon of 17 May, when the third egg of the clutch had been laid, and involved the same three individuals. Events occurred in a similar way, with the female attacking the intrusive male repeatedly both before and after extra-pair copulation. The female did not adopt a soliciting posture but simply kept still. Her male partner was incubating 25 m from the scene and did not intervene. A few hours earlier the incubating male had aborted another attempt at extra-pair copulation by the same intruder that was taking place only 6 m from the nest. It is probable that the paired male could see the female each time she interacted with the extra-pair male, since the breeding area was flat and sparsely vegetated. In the two cases of extra-pair copulation, the female did not utter alarm calls. I am not sure if cloacal contact actually occurred in the two cases of extra-pair copulation, but the duration of mounting was about the same as in intra-pair copulations. The three individuals could be identified easily from the coloration pattern on the head and neck. The intrusive male was not breeding in the colony area and had probably not mated.

Discussion

The contribution of males and females to parental care has not been previously studied in detail in black-winged stilts. It was known that both sexes help in nest building, nest defence, incubation, and chick rearing (Cramp and Simmons 1983), but knowledge of sex differences or variation among different reproductive periods was very limited. Parental behaviour had been mostly studied in the black-necked stilt (*Himantopus mexicanus*) (Hamilton 1975; Sordahl 1980; James 1991), and was thought to be very similar in the black-winged stilt, owing to general similarities between the two species. However, this study has yielded new findings, namely striking differences in behaviour between the sexes during the prelaying and laying periods. Before egg laying began, males devoted more time than females to agonistic encounters, locomotion, and nest building. Later on, during egg laying, males spent more time at the nest site than females, mostly building the nest and covering the eggs, while females spent more time foraging than males (Figs. 1 and 2).

Egg formation is highly energy demanding, and females are forced to spend most of their time foraging when laying eggs (ca. 70% of daytime in this study). As a consequence, during this period females can stay at the nest only for short intervals of time. If any other time-consuming activity is re-

quired for egg survival during this period (e.g., protection against predators or adverse weather conditions), the male must do it. In fact, during egg laying males spent much more time at the nest site than females, devoting themselves to nest building and covering the eggs.

If protecting the nest against predators or competitors is one of the reasons why males stay at the nest during egg laying, and provided that males spend more time at the nest than females, we would expect males to be involved in aggressive encounters more frequently than females. However, although there was a general tendency for males to engage more frequently in these kind of interactions, differences between the sexes were only significant during the prelaying period, and not during egg laying as expected (Fig. 2). This might be partly explained if efficient nest protection is sometimes achieved without aggression. For example, the mere presence of an adult at the nest may deter other birds from approaching. In any case, this result should be regarded cautiously, because the sample size was rather small (8 males and 6 females during the egg-laying period; Fig. 2), consequently the test has low statistical power (effect size = 0.30, power = 0.08 (Cohen 1988)).

Although it has been predicted that female birds will have invested more energy in reproduction by the beginning of incubation, owing to anisogamy (Trivers 1972), in monogamous species males could easily balance the cost of egg production by making a larger contribution to parental care (Burger 1981). This seems to be the case in the black-winged stilt. During the prelaying and laying periods, males spent significantly more time than females building the nest, and during egg laying males spent more time covering the eggs. These results suggest similar parental investment by the sexes, even before incubation begins. As incubation was progressing, male and female activity patterns changed remarkably, with females spending an increasing amount of time incubating and the opposite for males. During late incubation, females spent a significantly larger proportion of time at the nest, and tended to incubate more than their partners (Fig. 1).

Of 91 observed copulations, only 2 (2.2%) were extra-pair ones. This is a low percentage in comparison with other socially monogamous bird species (Birkhead and Møller 1996). Molecular techniques developed during the last decades (e.g., Burke and Bruford 1987) have confirmed that extra-pair copulations frequently result in extra-pair fertilization (reviews in Birkhead 1998; Petrie and Kempenaers 1998), but in the present study genetic parentage was not investigated. The female involved in extra-pair copulations was always very aggressive towards the extra-pair male and did not collaborate at all in copulation, but simply kept momentarily still while the male mounted her. If female cooperation is crucial for cloacal contact and sperm transfer in birds, it is probable that the extra-pair copulations did not succeed. On the other hand, it is also possible that the observed extra-pair copulation rate underestimates the extra-pair fertilization rate. Many extra-pair copulations might take place in concealment, and thus difficult to observe. In this case, male black-winged stilts (and I) could not observe females' activities at all times because females spent long periods far away from the breeding colony. If extra-pair copulations took place preferentially outside the colony, the extra-pair copulation rate might be seriously underestimated. In any case, the lack

of genetic analyses of paternity in this study makes all discussion of extra-pair fertilization merely speculative.

Males of some species invest heavily in parental care, consequently a loss of paternity would be very costly in terms of fitness. As a result, paternity assurance becomes an extremely important issue in these species. Males of avian species have evolved two behavioural anticuckoldry strategies to reduce the risk of extra-pair paternity: mate guarding and frequent copulations (review in Birkhead and Møller 1992). Mate guarding consists of males closely following their mates during the fertile period, preventing them from copulating with other males. The fertile period of female black-winged stilts is not known, but they can be considered fertile during most of the egg-laying period and for a few days before egg laying begins (Birkhead and Møller 1992). During this period females spent most of their time foraging, very often far away from the colony, while males spent most of their time at the nest site (Figs. 1 and 2). Therefore, males could not efficiently guard their mate from other males during her fertile period. There might be a conflict for males between mate guarding to avoid extra-pair paternity and protecting the nest/eggs while the female is foraging. A similar conflict between mate guarding and nest guarding during the female's fertile period has been shown in penduline tits (*Remiz penduline*) (Schleicher et al. 1993). However, while male penduline tits gave preference to mate guarding, male black-winged stilts tended to stay at the nest instead of following their mate. Interestingly, this pattern of behaviour has been also found in other waders. For example, no evidence of male mate guarding has been observed in the ringed plover (*Charadrius hiaticula*), a species with an apparent lack of extra-pair paternity (Wallander et al. 2001).

The second common anticuckoldry behavioural strategy in birds is frequent copulations. When circumstances prevent males from guarding females continuously, frequent intra-pair copulations can dilute sperm from hypothetical competitors in the female's reproductive tract, enhancing the probability of intra-pair fertilization. I observed 0.12 copulations/h in stilts during the prelaying period, and no copulation was observed in 6 h of focal-individual sampling during egg laying. This information suggests that in this species the copulation rate is low, or at least not high, compared with that in other waders (ranging from 0.09 copulations/h in *Phalaropus tricolor* (Delehanty et al. 1998) to 0.60 copulations/h in *Haemotopus ostralegus* (Ens 1991)). Thus, there is no evidence that male stilts use frequent copulations as a means to assure paternity.

This study of breeding behaviour in the black-winged stilt suggests the following scenario. During part of the egg-laying period, at least between laying of the first and penultimate eggs, females are fertile. They are forced to forage most of the time, sometimes far from the nest, owing to energy requirements for egg production. Meanwhile, males must stay at the nest, protecting the nest site and eggs from competitors, predators, or adverse weather conditions. Thus, during part of the female's fertile period, male mate guarding is not possible, and the male's risk of being cuckolded is not diminished by frequent intra-pair copulations. Fertilization is completely under the female's control, but females are reluctant to engage in extra-pair copulations and behave very aggressively towards any approaching male except their mate.

The female's behaviour could be explained if the disadvantages of extra-pair copulations override possible advantages. A very important disadvantage would be the risk of male desertion if assurance of paternity was not high enough. Male parental care seems to be essential for reproductive success. I have never observed a successful breeding attempt with only one adult tending the nest, at least before egg hatching, and there is no such report in the literature. Probably females are faithful in order to assure male parental care and, hence, success in reproduction. The necessity for male and female parental care would maintain social monogamy in this species. The females' behaviour suggests that monogamy may be genetic as well as social, but the lack of paternity analyses in this study precludes any firm conclusion.

The scenario described above, with little or no extra-pair paternity and an absence of efficient male anticuckoldry strategies (mate guarding and frequent copulations), is not rare in socially monogamous waders with high paternal investment. From studies of ringed plovers (Wallander et al. 2001), purple sandpipers (*Calidris maritima*; Pierce and Lifjeld 1998), and western sandpipers (*Calidris mauri*; Blomqvist et al. 2002) it was concluded that the potential costs in terms of reduced male parental care deterred females from engaging in extra-pair copulations.

Future studies should certainly include genetic analyses of paternity to clarify how frequently extra-pair fertilization occurs in this species. It would be also advantageous to pay attention to male agonistic behaviour during the different reproductive periods, especially if attacks on other male black-winged stilts were more frequent during the female's fertile period.

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