Mate replacement and male brood adoption in Lapwings *Vanellus vanellus*

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Mate replacement and male brood adoption has been reported in a range of bird species, but does not seem to have been reported before now in waders. We present details of a case where a bigamous male Lapwing *Vanellus vanellus* died at the onset of egg laying, whereupon his territory with the two females was divided between and taken over by two neighbouring males. One of the replacement males incubated on the nest of his new mate, while the other behaved indifferently. Based on current brood adoption theory, it is suggested that the males' behaviour could arise from either (1) the chance of gaining future fitness benefits, or (2) confidence of paternity or (3) a combination of both.

INTRODUCTION

The degree of parental care by males should depend on their certainty of paternity (Trivers 1972, Westneat & Sherman 1993, Houston 1995). Yet, observations of replacing males adopting and caring for offspring apparently fathered by another male exist from at least 17 species of birds (Rohwer 1986, Meek & Robertson 1991). Parental care for the young of other males thus appears altruistic, and the adaptive value of this behaviour may not be obvious.

Rohwer (1986) discussed whether adoption is just misdirected parental care not costly enough to be selected against (maladaptive view), or a result of natural selection (adaptive view). In the latter case, replacements could gain future mating benefits by increasing their breeding experience, get access to limited resources, or increase the probability of remating with the female by demonstrating their parental ability to her. Meek & Robertson (1991) pointed out that observations of brood adoption often lack quantitative information about paternal care, and argued that it is important to distinguish between full and partial adoption based on the amount of care that is provided. Further they suggested that confidence of paternity in some cases may play a role when replacement males are providing parental care. If so, what looks like full brood adoption actually differs little from normal paternal care.

Here we report a case of mate replacement and apparent brood adoption in two male Lapwings *Vanellus vanellus* who took over the mates of a bigamous neighbour that was killed by a predator at the onset of his mates' egg-laying. Subsequent observations of the replacement males may indicate that their behaviour reflected confidence of paternity.

METHODS

We studied the breeding behaviour of Lapwings in two grass fields at Gimramyra, Sola, Southwest Norway, in spring 1998, from 20 March to 10 May, covering the period from territory establishment until late chick-rearing. We recorded pair bonds by making field sketches of the birds that showed characteristic plumage markers (Byrkjedal *et al.* 1997) and made it possible to separate all studied individuals. Territory boundaries were mapped by plotting the locations of males and their flight display routes. The main study included 32 territorial males with 46 nesting females in a total area of *c.* 20 ha. Figure 1 shows a map of the territories of the birds referred to in this paper and other birds nesting in the same field.

Observations of Lapwing behaviour were carried out daily between 08:00 and 15:30 from hides or a car at the perimeter of the fields, by watching individual birds continuously for standard periods of 20 minutes through 15–45↔ telescopes and binoculars. Nests were found during the observation bouts, or at other times by regularly searching the fields visually for incubating birds. All observations of copulations were recorded, including those seen outside the standard observation periods.

RESULTS

Male No. 30 (M30), who was mated to females Nos 22 and 27 (F22, F27), disappeared permanently from the field on 30 or 31 March 1998. Subsequently two neighbouring males, M36 and M34, each took over half the territory of M30 along with F22 and F27, respectively. Figure 2 shows the phenology of events, and the details were as follows:

M30 was unmated until 23 March, when F22 (primary female) appeared and settled on his territory. On 25 March, F27 (secondary female) was also present. M30 was seen copulating with F27 on 30 March, just a few hours before he disappeared. He was last seen in the afternoon of 30 March. Feathers of a depredated male Lapwing, that we assume was M30, were found on a field about 150 m from his territory at about 14:00 the next day. On the day M30 disappeared, the

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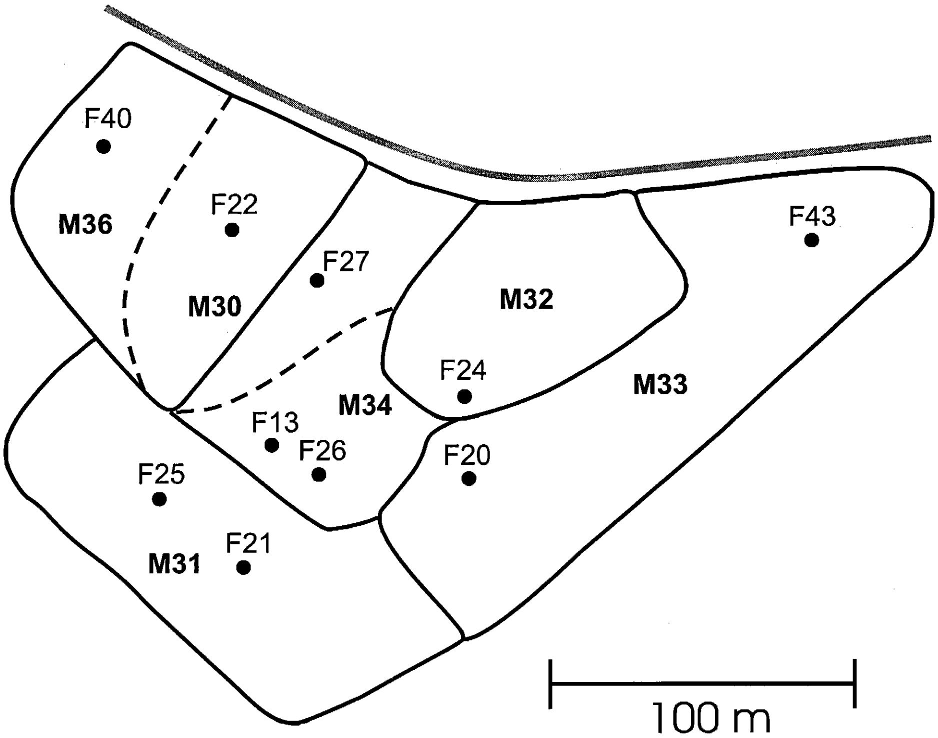

Figure 1. Map showing the Lapwing territories where mate replacement was observed and other territories on the same field. Territory borders are indicated by solid lines and the number of the defending male (M) is presented within each territory. The broken line indicates the border of the area defended by the replaced male. Nest placement is shown by solid dots and the number of the associated female (F). A road (grey-scale line) runs along one edge of the field, but otherwise it is surrounded by other farmland.

primary female (F22) had already laid one egg, while his secondary female (F27) was still in her pre-laying period.

By 31 March, the males M34 and M36, which held territories on opposite sides of M30's territory, had divided M30's territory as well as his two mates between themselves. M34, who was already mated to two females, adopted F27 as his tertiary female, while M36 took over F22 to become his secondary female.

On 3 April, the nest of F22 contained 3 eggs and, on 6 April, 4 eggs. All four eggs hatched on 2 May and all chicks were present on 10 May, when they were checked for the last time. F22 and M36 were seen copulating once, on 21 April. In comparison, we observed two copulations with his primary female during the same period (20 March–21 April). M36 took part in the incubation on the nest of F22 as well as on that of his primary female (Table 1).

On 31 March, M34 attempted to copulate with F27 twice during 20 seconds at 12:35, but she refused both times. At 12:43 the same day, another neighbour (M32) attempted to copulate with her, but also in this case she refused. He responded by pecking at her and chasing her into the air. Then M36 attacked M32, and the copulation attempt turned into a territory dispute.

The nest of F27 was found containing two eggs on 3 April, and four eggs on 6 April, suggesting that the clutch was completed on 5 April. At 11:45 and 12:00, on 5 April, M34 made three attempts to copulate with F27 during about 20 seconds, but was rejected each time. At 10:30 on 21 April, M34 flew over to F27 and tried to copulate with her, but she refused. The nest became heavily sprayed with manure on 28 April and was subsequently deserted by F27.

From the disappearance of M30 until F27 deserted the nest, no successful copulations with M34 were observed. He acted indifferently towards the eggs of F27 (Table 1), and was never seen on this nest at other times of sporadic observations. His total incubation effort was not lower than that of M36, however, as he spent 39.6% of the time incubating the clutches of his other two females.

Although he died before most of the eggs were laid, it is possible that all eggs in both clutches were fertilized by M30, because female birds are able to store sperm for several days (Birkhead & Møller 1992). The possibility, however, that some eggs had been fertilised by M34, M36 or other males cannot be discounted because no information on paternity exists from the studied nests.

DISCUSSION

As far as we are aware, this is the first report of male replacement and apparent brood adoption in any shorebird. The two male Lapwings clearly differed in the parental behaviour they exhibited towards the clutches of their new females. However, as male incubation contribution in this species ranges from 0 to 90%, with an average of about 30% (Liker & Székely 1999, own unpublished data), the two males' incubation contributions did not differ from the normal pattern. There are at least two types of potential costs incurred by caring for the offspring of other males: (1) reduced time to court other females and (2) reduced time to care for own offspring in other nests. We suggest the following three hypotheses for the behaviour of the replacement male Lapwings:

(1) Brood adoption was adaptive because of future reproductive benefits to the replacement males (Rohwer 1986). Lapwings seem to show relatively high breeding

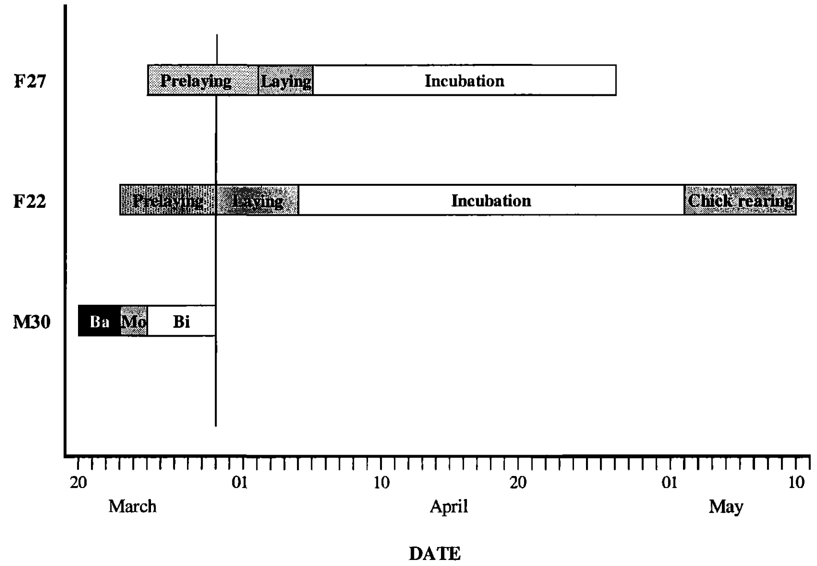

Figure 2. Phenology of male 30 and the replacement nests. Periods when M30 was a bachelor (Ba), monogamous (Mo) and bigamous (Bi) are indicated, together with prelaying, egg laying, incubation and chick rearing periods for the females. The date that male 30 disappeared is shown by a vertical line.

site fidelity, and even mate fidelity (Thompson *et al.* 1994, Parish & Coulson 1998, own unpublished data). Thus, because of a relatively high chance of meeting the female again, brood adoption could be viewed as a means of increasing the chance of re-mating in the subsequent breeding season. Possibly, it could also be a way of investing in future mating opportunities later in the same season, replacement clutches being common in Lapwings if the first nesting attempt fails (Berg *et al.* 1992, own observations). Another possible benefit of brood adoption to males is that they gain breeding experience that may increase their future reproductive success. Such a benefit should be of relatively little importance in our case, however, since the incubating male already had a mate with a nest to care for when he adopted the clutch of his dead neighbour's female.

(2) Male brood adoption was maladaptive, but occurs too rarely to be selected against (Rohwer 1986). From this view, brood adoption is misdirected care, male incubation simply being a response to any clutch found within the borders of a male's territory. However, this cannot adequately explain the differences in nest attentiveness between the two replacement males described here. Further, males do not always incubate on all nests within their territories (Liker & Székely 1999, own unpublished data), indicating that male incubation rules are more complex in Lapwings than assumed by the maladaptive hypothesis.

(3) Paternal care was contributed in relation to male confidence of paternity (Meek & Robertson 1991). The female that received help from the male was seen copulating with him after the clutch was completed, while the female who incubated alone rejected the male's copulation attempts several times. The exact fertile period of female Lapwings is not known, but is generally thought to last until the laying of the penultimate egg (Birkhead & Møller 1992). It is therefore possible that paternal care was associated with paternity certainty if the incubating male also copulated with F22 during the egg laying period. In addition, the egg laying phase of F22 seemed to last for about one day longer than normal, possibly further increasing the probability of her replacement male fertilizing the last three eggs. Moreover, he could also have fertilized the first egg that was laid just prior to replacement, because extra-pair matings have been occasionally recorded in the species (own unpublished data).

Table 1. Male attentiveness, total nest attentiveness by either parent and total observation time (hours) on nests of the replacement males.

Male	Female	Male att. (%)	Total att. (%)	Obs. time
34	27 (adopted)	0	71.4	17.2
	13 (alpha)	1.2	79.2	22.2
	26 (beta)	38.3	74.3	19.5
36	22 (adopted)	12.2	79.2	17.7
	40 (alpha)	26.2	74.1	15.5

Female solicitation of copulations may increase the chance of receiving help from a replacement male, either because she is able to deceive him into believing that he shares paternity in the offspring (Robertson 1990) or because he actually does so (Meek & Robertson 1991). If F27 had a chance of receiving male help by copulating with M34, her motives for refusing are not obvious. In fact she had more to offer than F22, because she had not laid a single egg at the time her first mate died and therefore could give the replacement a chance of fertilizing all her eggs. One possible adaptive reason for not doing so could be that her original male was of better genetic quality than the replacement.

Infanticide should be adaptive to replacement males who do not share paternity in the adopted clutch if the probability for females leaving them after nest failure is low and they instead stay and lay a new clutch sired by the new male (Rohwer 1986, Freed 1986, Robertson 1990). In waders, such behaviour is known in polyandrous female Jacanas *Jacana* sp. (Jenni 1996). Female Lapwings sometimes leave their original mate after clutch predation (Parish *et al.* 1997, own unpublished data). Therefore the risk of losing a mate may mean that indifference is a better option than infanticide for males in this species. Possibly this is the reason why M34 took no part in the incubation of F27's eggs. However, as male care also includes territory defence and chasing of potential predators (Parish & Coulson 1998, Liker & Székely 1999), the female may have gained indirectly from the male's presence even though he did not care for her eggs.

We believe that hypotheses 1 and 3, or a combination of these, are most likely to account for the behaviour that we observed in the Lapwing males. Recent papers indicate that male confidence of paternity often seems to determine whether replacement males adopt broods or reject them (Meek & Robertson 1991, Dickinson & Weathers 1999). In Western Bluebirds *Sialia mexicana*, for example, males have an "all or none" provisioning rule, where normal parental care is provided only when replacement takes place during the females' fertile period (Dickinson & Weathers 1999). As in the present study, data on paternity have often been lacking in reports of male brood adoption, making it questionable whether males actually do adopt eggs or young, or simply take care of offspring sired by themselves in extra-pair copulations or after the original male disappeared. Hence, carefully designed male removal experiments combined with paternity analyses (Kermott *et al.* 1990, Smith *et al.* 1996, Dickinson & Weathers 1999) would be very useful to discriminate between alternative hypotheses concerning male replacement behaviour in the Lapwings.

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Features of breeding biology in Pacific and American Golden-Plovers nesting on the Seward Peninsula, Alaska

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We studied site-fidelity, nesting, and the chronology of hatching in Pacific and American Golden-Plovers (*Pluvialis fulva* and *P. dominica*) from 1988 to 2000 on breeding grounds near Nome, Alaska. Banded males of both species were strongly site-faithful in subsequent seasons with 12 of 16 *fulva* and 11 of 15 *dominica* (at return rates of 77% and 80%, respectively) nesting near, and occasionally in, previous nests. The fidelity of males did not appear to be reduced by lack of breeding success, suggesting that familiarity with a territory is of primary importance. Among females, only 2 of 12 *fulva* and 1 of 11 *dominica* (at return rates of 25% and 15%, respectively) were seen in subsequent seasons. Each of the *fulva* females was present for three consecutive seasons including the season when captured; one mated with the same partner for two seasons, the other with the same male in all seasons. The single *dominica* female paired for one season with a different mate than she had when captured. We estimated that *dominica* females produced replacement clutches in 12–14 days after loss of the first clutch. Hatching began in late June and intra-clutch chronologies were similar in each species. The first indications of hatching were hairline cracks that appeared 5–50 hours before more obvious breakage (star-pip or tiny pip-hole). Most eggs progressed from the latter conditions to emergence of a chick in 10–20 hours. Intervals from the first hairline-cracked shells and the first obvious breakage of shells to four dry chicks in and around the nest were approximately 2–4 days and 1–3 days, respectively. Brood members emerged sequentially over the course of about one day, and often at least two chicks were already foraging near the nest before the last sibling had appeared.

INTRODUCTION

The Pacific Golden-Plover *Pluvialis fulva* and American Golden-Plover *P. dominica* are seasonally monogamous shorebirds with male-biased breeding ground fidelity (Greenwood 1980, Johnson *et al.* 1993, 1997a, Sviridova 2000). Males (sexes are dimorphic in breeding plumage) establish the territories, build nests, and perform most defensive behaviours (Connors *et al.* 1993, Johnson & Connors 1996, Byrkjedal & Thompson 1998). Returning to a familiar place presumably lessens intra-sexual competition among males and facilitates rapid re-occupancy in the spring (Greenwood & Harvey 1982, Flynn *et al.* 1999, Sviridova 2000). However, variation in the quality of a male's territory (related to timing of snowmelt) may reduce his attractiveness to females in certain seasons. Although some pairs probably form before arrival on breeding territories (Sauer 1962, Connors *et al.* 1993, Johnson & Connors 1996, Sviridova 2000), the response of most females to variable spring conditions appears to be site-unfaithful opportunistic pairing with males possessing suitable territories (Tomkovich & Soloviev 1994, Johnson *et al.* 1997a). A useful overview of nesting-site fidelity in male shorebirds together with additional references is provided by Flynn *et al.* (1999).

Our studies on the Seward Peninsula began in 1988, and some of the plovers we banded in earlier years survived after initial accounts of site fidelity were published (Johnson *et al.* 1993, 1997a). We continued to record their breeding activities in subsequent seasons, and also marked additional birds. General knowledge of reproductive biology in Pacific and American Golden-Plovers is reasonably good, but many details are lacking (Johnson & Connors 1996, Piersma *et al.* 1997, Byrkjedal & Thompson 1998). In this paper, we quantify fidelity more thoroughly by combining data on returning birds in all seasons up to and including 2000, and report findings on interannual spacing of nests, re-nesting, and time intervals associated with hatching.

STUDY AREAS AND METHODS

We conducted fieldwork from 1988 to 2000 at two sites on golden-plover breeding grounds north of Nome, Alaska. Most data are from the Feather River site, an area of about 550 ha near mile 37 on the Nome-Teller Road (64°51'N,

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