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Male and female incubation in Pied Wagtails *Motacilla alba*: shared costs or increased parental care?

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The incubation behaviour of Pied Wagtails *Motacilla alba* was observed at six nests of monogamously and polygynously mated males. The proportion of time spent incubating by males varied markedly with mated status: polygynous males incubated less in total, in briefer sessions, or not at all. Polygynous females incubated for a greater proportion of the day than monogamous females. For assisted females, sessions preceding nest-relief by the male were shorter than sessions ending when the female left the nest unattended. When relieved by the male, females took longer recesses than in the male's absence; monogamous females lengthened their recesses more than the assisted polygynous female. Females lengthened their incubation sessions immediately after a recess during which the male incubated; the duration of female sessions following male-attended recesses correlated with recess length. The length of female sessions after a recess when the eggs were unattended did not vary with mated status or correlate with the preceding recess duration. Daily nest attendance was not correlated with temperature or rainfall for either sex. As a result of these varying incubation schedules, limited male incubation produced an increase in the proportion of the day the eggs were covered, whereas more extensive male incubation at monogamous nests produced both a greater increase in egg coverage and some reduction in the female's workload: male incubation in the Pied Wagtail thus primarily provides additional parental care.

1. Introduction

Incubation is potentially a time of energetic stress for the incubating bird (Yom-Tov & Hilborn 1981); considerable energy may be required for incubation (Haftorn & Reinertsen 1985, Williams 1993), and as the time available for foraging is severely curtailed by nest attendance, even a moderate energy expenditure may entail a deficit in the bird's energy budget (Mertens 1977, Drent et al. 1985, Williams & Dwinnel 1990, Hinsley & Ferns 1994). Incubation can therefore be a critical period, especially if environmental conditions are poor (Mertens 1987). In many socially monogamous non-passerines both birds incubate, apparently sharing these costs. In many passerines, however, including those which have been studied in greatest detail, the female alone incubates; the male's role during incubation can instead be that of providing the female with food (Skutch 1957) either on the nest or during the female's breaks from incubation (recesses) (Skutch 1962).

Incubation schedules in female-only incubating passerines are typically alternations between incubation sessions lasting less than an hour and recesses lasting only a few minutes (Kendeigh 1952); the female is on the nest at night and for 60–80% of the daytime (Skutch 1962), the eggs being uncovered for the remainder. In other avian orders, where the male takes an equal share in incubation, nest relief usually occurs at regular intervals and the eggs are rarely left uncovered. However, under adverse environmental conditions longer foraging absences by one bird may force its partner to undertake longer sessions, possibly resulting in the incubating parent leaving the nest before the return of its partner (Chaurand & Weimerskirch 1994) or nest desertion (Cézilly 1993).

In contrast, studies of incubation in passerines where the male incubates as well as the female have shown that the male usually undertakes a smaller proportion of daytime incubation than the female, which also incubates continuously at night (Walraff 1953, Leinonen 1973, Drent et al. 1985, Pinxten et al. 1994, Smith et al. 1995, Kleindorfer et al. 1995). The male does not always regularly alternate with the female, and the female leaves the nest unattended at intervals during the day. The eggs may thus be left uncovered for a considerable proportion of the day (5–40%), and total incubation can therefore apparently differ little between the female-only and shared incubation passerines. This raises the question of the relative importance of male incubation in these passerines — does it represent increased parental care of the eggs, or is it a mechanism for reducing the energetic stress on the female of her major share of egg-care?

In wagtails the male incubates and does not feed the female (Kendeigh 1952, Dittberner & Dittberner 1984, Ölschlegel 1985), incubation conforms to the pattern described above: Pied/White Wagtail *Motacilla alba* females are on the nest overnight and incubation is shared unequally between the female and the male during the daytime (Schweinsteiger 1938, Löhrl 1957, Leinonen 1973, Nakamura et al. 1984, Ölschlegel 1985), males have been reported to incubate for 17.2, 24 and 6% of the time (Löhrl 1957, Leinonen 1973, Nakamura et al. 1984). As the females sometimes took daytime recesses in the absence of the male, the eggs were uncovered for 14.7–35.2% of the day (Löhrl 1957, Leinonen 1973). However, male participation in incubation can be even more variable than these studies suggest, with general accounts of the female alone incubating at some nests (Niethammer 1937, Simms 1992). This variability permits a closer examination of the role of the male in incubation, and its effect on female incubation behaviour.

In this study, six nests were intensively observed during the breeding cycle. The male incubated at four of these, but, although present, did not assist the female in incubation at the other two. These latter nests were those of secondary females of polygynous males; intense conflict with the primary female apparently contributed to the subsequent failure of one of these nests (Fitzpatrick 1994). This paper analyses the scheduling of incubation sessions and recesses by the males and by females with and without male assistance, and assesses the impact of the male's role: does male wagtail incubation reduce female costs by allowing her more free time, and/or does male incubation improve parental care by increasing the proportion of daytime hours the eggs are warmed?

2. Methods

The six nests observed were all in the same enclosed courtyard on the Jordanstown campus of the University of Ulster. Observations were made from inside the building, at a distance of less than 15 m, using 7 × 50 Zeiss binoculars, for continuous periods of time which varied, but were as long as possible (see Table 1 for details). The times of all arrivals to and departures from the nest were noted to the nearest second and used to calculate the durations of the incubation sessions and recesses. Although not ringed, the wagtails were individually distinguishable by plumage characteristics (Fitzpatrick 1994). The males in 1991–1993 had brownish coverts, indicating second-year birds (Svensson 1992), while the coverts of the 1990 male were black: four different males were therefore studied. The female present in 1991 closely resembled the 1990 female in plumage, and, while prospecting for a site for the first 1991 nest, entered the site of the 1990 nest using exactly the same mode of approach. It was thus probably the same female. Likewise, the female of 1993 resembled that of 1992 in plumage, and chose the same nestsite (both plumage and nestsite differing from those of the female of 1990/1), and was thus possibly the same individual. Although the presence of the same females in different years reduces the independence of the data, both females were observed at a monogamous and at an non-assisted polygynous nest, providing balanced comparisons.

The polygyny of the males involved in the 1991 and 1992 nests was established from observations of male courtship of two different females within the courtyard; in 1992 there was intense female-female aggression (see Fitzpatrick 1994 for details). Courtship of the other female during the early incubation period of the 1991 second brood was followed by a 5-day period of 'mate guarding' of the second female by the male. The male incubated at the nest in the courtyard before and after, but not during, this period; there was no interaction between the females. In the years when the males were considered monogamous, no other females were seen in the courtyard or interacting with the male.

The overall share of daytime incubation was assessed by the percent of total observation time each bird was at the nest each day. The durations of sessions and recesses for each incubating bird at each nest were analysed according to type of nest relief:

a) sessions which ended at the arrival of the mate to take over (relieved sessions) vs. sessions which ended with the incubator leaving the nest in the absence of the mate (unrelieved sessions)
b) recesses during which the mate was/was not incubating (attended vs unattended recesses, attended recesses follow nest relief).

Daily average values for each type of session and recess were calculated for each observation day at all nests.

1, 2 factor and repeated measures ANOVAs were used to analyze the daily percentage of time spent incubating and durations of sessions and recesses of both types according to mating status — monogamous (N = 3 nests), assisted polygynous (N = 1 nest) and non-assisted polygynous (N = 2 nests). The data were checked for normality and transformed if necessary. These analyses assume independent data; however, several values from the same individuals can be used without producing erroneous conclusions from the tests if either the within-individual variance is greater than the between-individual variance, or the number of data points (N) from each individual is equal (Leger & Didrichsons 1994). For sessions, but not recesses, female within-individual variance was greater than between-individual variance. In order to produce equal N, five daily averages for each nest were entered into the analyses (when more than five daily averages were available, exclusions were made at random). For the assisted polygynous nest, five days on which male incubation was observed were included. ANOVAs including individual identity as a factor were used as an additional check for bias related to individual differences.

Daily maximum and minimum temperatures and rainfall were measured. Stepwise multiple regression was used to assess the impact of these weather variables on overall nest attendance by males and females.

3. Results

3.1. Share of incubation

The females spent a much greater proportion of the daytime hours incubating than did the males, even

Table 1. Details of the nests studied and the hours of observation during incubation. ID identifies the parent wagtails; fem, female; polygynous +M, the male incubated; polygynous –M, the male did not incubate. The 1992 nest failed during the nestling stage and female 2 disappeared at the expected time of hatching of the 1993b nest.

year	ID		observations		mated status	outcome
	fem	male	total h	mean duration		
1990	1	1	24.75	2.15	monogamous	fledged 3
1991a	1	2	56.03	6.23	polygynous –M	fledged 3
1991b	1	2	64.06	6.14	polygynous +M	fledged 4
1992	2	3	29.32	1.83	polygynous –M	failed
1993a	2	4	27.74	2.31	monogamous	fledged 5
1993b	2	4	25.55	1.70	monogamous	failed

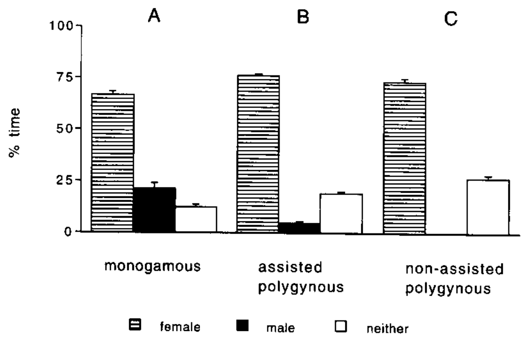

Fig. 1. Proportion of observed daytime hours spent in incubation by each sex, and time eggs uncovered. A, at monogamous nests (N = 3); B, at an assisted polygynous nest (N = 1),. and C, at non-assisted polygynous nests (N = 2). 5 daily averages included from each nest, means and standard errors shown.

at monogamous nests (Fig. 1). The proportion of time spent incubating varied significantly with mated status for both females and males (ANOVA, female: $F_{2,27} = 7.45$, $P = 0.0026$; male: $F_{2,27} = 26.48$, $P = 0.0001$). Polygynous females with and without male assistance incubated for respectively 76.3% and 73.4% of the day, more than monogamous females (66.5%) (Fisher PLSD, $P < 0.01$), but there were no overall individual differences between the two females $F_{1,28} = 1.06$, $P = 0.3115$. Male incubation significantly reduced the proportion of time the eggs were left unattended ($F_{2,27} = 28.95$, $P < 0.0001$), from 26.6% with no male incubation to 19.1% at the assisted polygynous nest and to 12.2% at the monogamous nests (Fig. 1).

3.2. Female incubation

Female incubation sessions averaged about 25 minutes in length (Fig. 2), but were variable. Unrelieved sessions tended to vary with mated status (Fig. 2A) $F_{2,27} = 2.65$, $P = 0.089$, being longer in monogamous than non-assisted polygynous females (Fisher PLSD, $P < 0.05$). Relieved sessions did not differ between individual females at monogamous nests ($F_{1,12} = 0.07$, $P = 0.794$), and did not differ between the assisted polygynous and monogamous nests ($F_{1,17} = 0.99$, $P = 0.3338$) (Fig. 2B). Relieved sessions were shorter than unrelieved sessions (repeated measure, $F_{1,17} = 5.04$, $P = 0.0383$), with neither mated status nor individual identity having

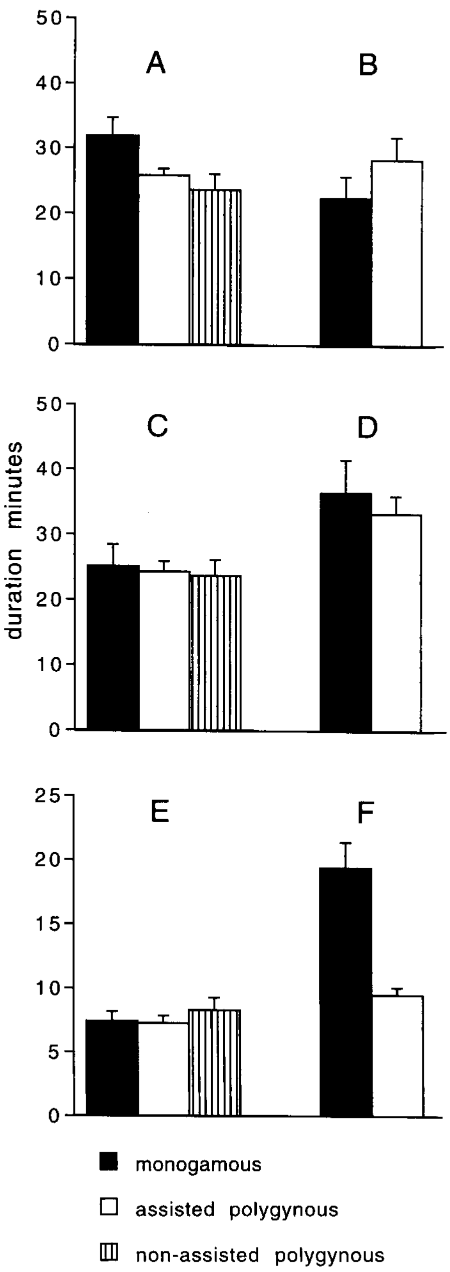

Fig. 2. Mean durations of incubation sessions and recesses of females with differing mated status. A, unrelieved sessions; B, sessions before relief by the male; C, sessions following unattended recesses; D, sessions following male-attended recesses; E, female recesses when eggs unattended; F, female attended recesses, i.e. when male incubating eggs. 5 daily averages included from each nest of a mated status, means and standard errors shown. Monogamous, 3 nests; assisted polygynous, 1 nest; non-assisted polygynous, 2 nests. Note change of scale in E and F.

an effect ($F_{1,17} = 0.001$, $P = 0.9763$ and $F_{1,17} = 0.08$, $P = 0.7872$ respectively).

Sessions following recesses when the nest was unattended were similar in all nests (Fig. 2C), and did not differ with mated status ($F_{2,26} = 0.07$, $P = 0.9332$). However, sessions following recesses when the male was on the nest (Fig. 2D) were longer than those following unattended recesses (repeated measure $F_{1,17} = 5.06$, $P = 0.381$), with no significant effect of either mated status or individual identity ($F_{1,17} = 0.19$, $P = 0.6727$ and $F_{1,17} = 2.98$, $P = 0.1027$ respectively; at monogamous nests the effect of female identity was reduced $F_{1,12} = 2.30$, $P = 0.1556$). The daily average duration of sessions following attended recesses correlated strongly with the average duration of attended recesses ($r = 0.63$, $F_{1,18} = 11.61$, $P = 0.0031$), but the average duration of sessions following unattended recesses only tended to correlate with the average duration of unattended recesses ($r = 0.31$, $F_{1,27} = 2.95$, $P = 0.0973$).

The duration of unattended recesses did not differ according to mated status ($F_{2,26} = 0.37$, $P = 0.6939$) (Fig. 2E), but the duration of attended recesses did vary with mated status ($F_{1,18} = 7.73$, $P = 0.0124$), with the assisted polygynous female having shorter attended recesses (Fig. 2F). Attended recesses were longer than unattended recesses (repeated measure $F_{1,17} = 31.87$, $P = 0.0001$). Both females responded similarly at monogamous nests ($F_{1,12} = 1.81$, $P = 0.2034$). Females thus stayed away for longer when the male was on the nest, but the assisted polygynous female returned more quickly to the nest than the monogamous females.

Daily female nest attendance did not correlate significantly with temperature or rainfall (stepwise multiple regression, all nests, all $F < 0.31$; monogamous nests only, all $F < 2.6$, $P > 0.1$).

3.3. Male incubation

At monogamous nests the average length of male sessions was nearly 20 minutes (Fig. 3A) and there was no difference between the two monogamous males in session duration ($F_{1,13} = 0.98$, $P = 0.341$). Monogamous males always waited for the female to return before leaving the nest (27/27 sessions). On most occasions when a monogamous male arrived to take his turn, the female was still on the nest; on only 3/30 sessions, all during the first week of incubation, did he arrive after the female had already left. In contrast, when the male incubated at a polygynous nest until relieved by the female, the duration of his sessions was significantly briefer ($F_{1,18} = 21.30$, $P = 0.0002$) (Fig. 3A). The polygynous male frequently left the nest before the female returned (6/17 sessions) and arrived after the female had left (7/19 sessions). These differences between monogamous and polygynous males are significant (Fisher exact test, $P = 0.03$ for early departures, and $P = 0.0018$ for late arrivals). The polygynous male's relieved sessions did not differ in duration from his unrelieved sessions ($t_7 = 0.77$, $P = 0.4669$) (Fig. 3A).

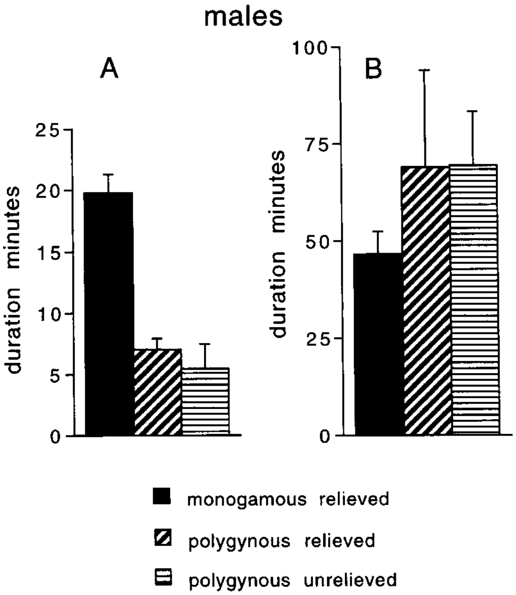

Fig. 3. Mean durations of incubation sessions and recesses of monogamous and assisting polygynous males with differing patterns of nest relief. A, sessions; B, recesses following relieved and unrelieved sessions. Monogamous males (black bars) always incubated until relief by the female; the assisting polygynous male sometimes incubated until relief (oblique hatched bars), but sometimes left the nest before the female returned (unrelieved sessions, horizontal hatched bars). 5 daily averages included from each nest; monogamous, 3 nests; polygynous, 1 nest. Means and standard errors shown.

The recesses taken by males after relief by the female did not differ with mated status ($F_{1,15} = 1.54$, $P = 0.2338$) (Fig. 3B) or with male identity ($F_{2,14} = 1.01$, $P = 0.3888$). For monogamous males, average recess duration correlated with the average duration of the preceding session ($r = 0.58$, $F_{1,10} = 5.17$, $P = 0.0462$).

Male daily nest attendance did not correlate significantly with temperature or rainfall (stepwise multiple regression, all nests, all $F < 3.05$; monogamous nests only, all $F < 1.6$, $P > 0.1$).

4. Discussion

With such a small sample of nests, these analyses, and any general conclusions drawn from the results, assume that the few individuals studied are representative of at least the local population. The similarity in incubation behaviour between same-sex individuals with the same mated status supports local generality. The population of Pied Wagtails in Ireland is largely isolated from other populations: the wagtails migrate short distances or not at all, remaining within the island, and British-ringed Pied Wagtails have not yet been recovered in Ireland (Davis 1966, Dougall 1991). Population-specific variation in behaviour is thus possible, but comparison with other studies indicates that the Pied Wagtails observed here incubated in a manner representative of their species when they were monogamous. Incubation scheduling has been studied in other subspecies of *Motacilla alba* in Finland (Leinonen 1973, 8 pairs at 8 nests), in Germany (Löhrl 1957, 1 pair, 1 nest) and in Japan (Nakamura et al 1984, 1 pair, 2 nests), in all cases at monogamous nests with assisting males. Mean session and recess durations reported for females and males are similar to those found at monogamous nests in this study; also, where changes in female scheduling with male nest relief and attended recesses were noted (Nakamura et al. 1984), the results were similar to those presented in greater detail here. What evidence there is thus supports the possibility that the present results may be general, in spite of the small sample size. As only four species of male-incubating passerines have been the subject of detailed, large-scale studies of incubation (Drent et al. 1985, Smith & Montgomerie 1992, Pinxten et al. 1994, Kleindorfer et al. 1995, Smith et al. 1995), even limited data on other species may be of general interest.

Although very few individuals were studied here, both females were observed at two levels of male assistance with different mated status, and shown to have altered behaviour; both females adjusted their behaviour similarly. Because the female involved was also recorded at a monogamous and a non-assisted polygynous nest, the different incubation pattern found at the single nest involving an assisted polygynous female can be interpreted as due to these circumstances. Further studies are obviously needed to confirm the generality of these changes in individual behaviour.

When non-assisted, the female Pied Wagtails studied here had incubation behaviour comparable to that of other small passerines in which only the female incubates: short recesses averaging 6–10 min and sessions usually at least twice as long (e.g. Haftorn 1978, 1981, Haftorn & Ytreberg 1988). When not relieved by the male, assisted female wagtails also showed this pattern of incubation. This pattern of scheduling is considered to be controlled by an endogenous rhythm linked to the cooling rate of the eggs during recesses (Haftorn & Reinertsen 1990); the incubator returns before the eggs have cooled below about 25° (Haftorn 1988). Although avian eggs are usually tolerant of short exposure to temperatures as low as 16° (Webb 1987), rewarming eggs from such a low temperature is energetically very expensive (Jones 1989).

When monogamous female Pied Wagtails were relieved by their mate, they took much longer recesses, averaging 15–25 min. As the monogamous males in this study reliably remained at the nest, the returning females were saved the cost of rewarming the eggs and had the benefit of a longer break. A relieved female similarly lengthened her recesses in Japan (Nakamura et al. 1984), and in the data presented by Löhrl (1957), although in both cases the male did not always stay until the female's return. While reliable male incubation provides the female with longer recesses without high egg-rewarming costs, to obtain these benefits the female must tailor her recesses to the session length tolerated by her mate, as seemed to be occurring here in the assisted polygynous female. The individual flexibility in female incubation behaviour shown here is necessary for coordination between mates with variable incubation schedules to be possible. The correlations between female session length and the length of the preceding male-attended recess on the one hand, and between male session length and recess length on the other, may indicate an underlying dynamic process allowing flexibility in the pattern of bisexual incubation schedules whilst maintaining coordination.

The sessions subsequent to an attended recess were significantly longer, even in the assisted polygynous female whose attended recesses were not greatly lengthened. The female studied by Nakamura et al (1984) also lengthened her sessions after an attended recess. Females therefore immediately expended some or all of the benefits gained from attended recesses on parental care. With a lesser degree of male incubation, egg coverage was increased by 7.5% of the day at the assisted polygynous nest, whereas the effect of the more intensive male incubation at monogamous nests was to both increase the proportion of the day the eggs received incubation by 14.4%, and to enable the female to spend a further 9.8% of the day off the nest. Male incubation thus seemed to be of greater direct benefit to the eggs than to the female Pied Wagtail, but the distribution of these benefits was influenced by female incubation behaviour.

Similarly, male incubation in Starlings, *Sturnus vulgaris*, increased the proportion of time the eggs were covered in male-assisted compared to non-assisted nests (Walraff 1953, Pinxten et al. 1994, Smith et al. 1995) and the females' nest attendance was also reduced. Food availability influenced female recess duration and hence the incubation share of the male in regularly alternating pairs (Drent et al. 1985). In two species of *Acrocephalus* warblers, too, female foraging breaks were longer after male nest relief (Kleindorfer et al. 1995), and the females also incubated for longer sessions after lengthy recesses. However, there were subtle differences in the adjustments of their sessions by the females of the two species: *A. scirpaceus* maximized the male contribution to incubation by reducing the female proportion as male incubation increased, but *A. melanopogon* maintained the female proportion of incubation by also increasing female incubation as male incubation increased (Kleindorfer et al. 1995).

The lack of any significant correlation in this study between Pied Wagtail incubation by either sex and temperature or rainfall is somewhat surprising, but was not due to lack of environmental variability: daily maxima for temperature varied between 8.5° and 24.3° on the days studied, and daily rainfall varied between 0 and 15.2 mm. It thus appears, from this small sample of nests, that the incubation routine of Pied Wagtails is not tightly linked to the weather on a day-by-day basis. Other studies, utilizing more frequent recording of environmental factors, have found temperature and/or rainfall to influence male passerine incubation behaviour (Drent et al. 1985, Smith & Montgomerie 1992, Kleindorfer et al. 1995), as well as female incubation (e.g. von Haartman 1956, Haftorn 1978, 1981). It is possible that environmental influences on within-day incubation scheduling differ from those on between-day scheduling in Pied Wagtails, if other costs to male incubators, such as lost mating opportunities, vary on a between-day timespan.

There are costs to both males and the nest associated with increasing total nest attendance by male incubation: the lesser effectiveness of male incubation may increase the total incubation period (Kleindorfer et al. 1995), adding to the risk of nest predation. For the male, time spent incubating might conflict more than incubation feeding with other fitness-enhancing activities such as territory defence or attracting more females; territorial conflict probably reduced male incubation at one White Wagtail nest (Nakamura et al. 1984), and although mating opportunities did not seem to influence male Barn Swallow *Hirundo rustica* incubation (Smith & Montgomerie 1992), they did lead to reduced incubation by male Starlings (Smith 1995). The greatly reduced incubation by polygynous male Pied Wagtails described here may indicate that secondary mate attraction and/or guarding does conflict with incubation in this species. The results of this limited study thus support the view of male and female incubation behaviour as a dynamic decision-making process (Kleindorfer et al. 1995).

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Selostus: **Haudonnan jakaminen sukupuolten kesken västäräkillä**

Västäräkillä samoin kuin monilla muilla varpuslintulajeilla, joilla koiras osallistuu hautomiseen, naaras vastaa suurimmasta osasta munien lämmittämiseen vaadittavasta ajasta. Koiraan haudonnan merkitys on vähentää haudonnan naaraalle aiheuttamia kustannuksia (engl. shared costs) tarjoamalla aikaa ruokailuun ym. toimintoihin ja/tai tarjota kehittyville jälkeläisille paremmat olosuhteet lisääntyneen lämmittämisen muodossa (parental care). Kirjoittaja tutki Pohjois-Irlannissa koiraan roolia haudonnassa ja sen merkitystä seuraamalla sukupuolten ajankäyttöä kuudella västäräkin pesällä, joista osa kuului monogamisille, osa polygynisille pareille. Koiraiden haudonta-aika vaihteli pariutumistavan mukaan: polygyniset koiraat hautoivat kokonaisuudessaan vähemmän kuin monogamiset, lyhyempiä jaksoja kerrallaan tai eivät ollenkaan. Monogamiset koiraat hautoivat keskimäärin 22% havainnointiajasta, polygyniset 0–6%. Polygynisten koiraiden puolisot käyttivät suuremman osan päivästä hautomiseen kuin monogamiset naaraat (74–77% vs. 66%). Koiraan tarjoaman haudonta-avun merkitys oli ensisijaisesti tarjota lisälämmitystä kehittyville poikasille. Koiraan haudonta lyhensi osuutta ajasta, jonka munat olivat ilman lämmitystä, 27%:sta (polygyniset parit, joilla koiras ei hautonut ollenkaan) 12%:iin (monogamiset parit). Monogamisilla pareilla koiraan haudonta myös jossain määrin vähensi naaraan työtaakkaa. Kirjoittaja päättelee, että koiraan haudonta västäräkillä on lisäpanostusta jälkeläisten hoitoon, ei niinkään haudonnan aiheuttamien kustannusten jakamista puolisoiden kesken.

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