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Female yellowhammers (*Emberiza citrinella*) prefer yellower males: a laboratory experiment

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Abstract The importance of male plumage coloration as a signal of male dominance and a cue for female choice in the monogamous yellowhammer, *Emberiza citrinella*, was tested in two sets of experiments in an indoor aviary. Dominance was tested by introducing two individuals, with no previous experience of each other, in an aviary with food and water. Aggression occurred more often between two males than between a male and a female and more frequently between pairs of males including at least one old male than between two young males. Dominance was not related to male colour in trials between males of the same age class, but it was in trials between an old and a young male, often differing in colour. Thus, age may be a more important determinant of dominance than colour. Female preference for more colourful males was tested by allowing hormone-induced females to choose between a more and a less colourful dummy male. Females spent more time in front of more colourful than drabber males and also more often perched beside colourful males than duller individuals. Although male colour cannot be ruled out as a dominance signal, the results suggest that male colour is primarily used as a signal in mate choice. Female choice may hence be responsible for maintenance of bright plumage in the male yellowhammer.

Key words Sexual selection · Male coloration · Female choice · Male-male competition · *Emberiza citrinella*

Introduction

Sexual selection consists of two major components, intra- and inter-sexual selection, as first pointed out by

Darwin (1871). The current strong interest in sexual selection is emphasised by the extensive theoretical work as well as a large number of empirical studies (reviews in Bradbury and Andersson 1987; Andersson 1994; Møller 1994). Male dominance has been found to be related to degree of ornamentation in a number of birds (e.g. Rohwer 1975; Studd and Robertson 1985; Watt 1986a; Møller 1987; Evans and Hatchwell 1991). In comparison, evidence for female preference for male traits, upon which several hypotheses rely, is less common. While several observational studies have indicated a female preference for exaggerated male traits, experimental evidence has been obtained only in a small number of cases (e.g. Andersson 1982; Bischoff et al. 1985; Møller 1988a; Milinski and Bakker 1990; Hill 1991).

Apart from structural traits, plumage coloration has been assumed to function as a sexually selected character in a variety of avian species (Darwin 1871; Hamilton and Zuk 1982) although empirical data are still scarce. Two main groups of pigment compounds are responsible for avian plumage coloration (Volker 1938; Fox and Vevers 1960), viz melanins and carotenoids. Whereas melanins can be synthesised in situ, carotenoid pigments, producing red, yellow and orange, are obtained through the diet (Goodwin 1950; Brush 1978; Kodric-Brown 1989; Hill 1992). In birds, male plumage signals are commonly expressed as contrasting dark or brightly coloured badges (Rohwer 1975; Møller 1987; Hill 1991, 1993a; Sundberg 1992, 1994a) and the variation in terms of badge size and colour intensity may be of importance in sexual selection.

Although sexual signals are probably heritable they may also be influenced by environmental components (Møller 1994). Size and intensity of many brightly coloured patches depend upon amount of pigments ingested (Brush 1978; Kodric-Brown 1989; Hill 1992, 1993a) and may be good indicators of the ability of individuals to acquire resources. Coloration thus may

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function as an honest condition-dependent trait (Milinski and Bakker 1990; Hill 1990, 1991; Johnstone and Norris 1993), on which females may base their mate choice.

The yellowhammer (*Emberiza citrinella*) is a medium-sized, socially monogamous bunting with sex and age related differences in size and brightness of patches of yellow colour (Sundberg 1992, 1994a, 1995; Sundberg and Larsson 1994). It is a short-distance migrant or resident, commonly flocking during winter. Males establish territories early in spring and pair formation may occur in winter flocks. Males defend their territory from intruders, but both sexes spend considerable time feeding outside their territory (Hansen 1984; Sundberg 1992, 1994b). Females build the nest and incubate the eggs (3–5) single-handedly, but males contribute approximately 40% of all feeding bouts (Packhurst and Lack 1946; Yom-Tov 1992; Sundberg and Larsson 1994).

If male colour is related to qualities which to some degree affect female fitness, for example through paternal care, or reflects indirect genetic benefits, females can be expected to choose mates on the basis of their coloration. Coloration may also signal dominance and status among males. Here I report on a series of experiments designed to disentangle the effects of intra- and inter-sexual selection on the size of coloured badges in the yellowhammer. The experiments were performed in indoor aviaries using wild-caught birds. First, I investigated whether fighting ability, as a measure of dominance, was related to male coloration. I did this by introducing two individuals with no previous experience of each other in an aviary and scoring dominance based on the outcome of aggression over a food source. Second, I examined female choice by introducing an estradiol-implanted female into a cage and allowing her to choose between one more and one less colourful male dummy.

Methods

The experimental birds were caught in three different areas outside Uppsala (59° 50' N, 17° 45' E) during late winter and early spring 1991–1993, at winter feeding sites. Birds were sexed, aged as young or old (Svensson 1984; Sundberg 1992), measured (see Sundberg 1992, 1995; Sundberg and Larsson 1994, for methods of measurement) and repeatedly re-measured during captivity. They were kept in three separate aviaries (minimum 2 m × 2.4 m × 2.4 m) until used in experiments. In both experiments I used the same aviary (Fig. 1; 1.8 m × 1.8 m × 1.8 m). In addition, 16 birds used in the competition experiment were caught in 1993 at two sites around Konnevesi research station (62° 37' N, 26° 20' E), central Finland, where birds were kept and handled under similar conditions.

I determined male badge size, hereafter colour, from the absolute size of areas of yellow on (1) the crown, (2) chin, (3) eyebrow (supercilium), and (4) throat. In addition, since the crown feathers often are partly covered by dark feather edges, the (5) yellow cover on the crown was estimated to the nearest 5%. Based on the individuals used in the study a relative measure of colour was produced using a principal component analysis (PCA) (SAS 1985) of variables 1–5. These variables were highly positively intercorrelated and

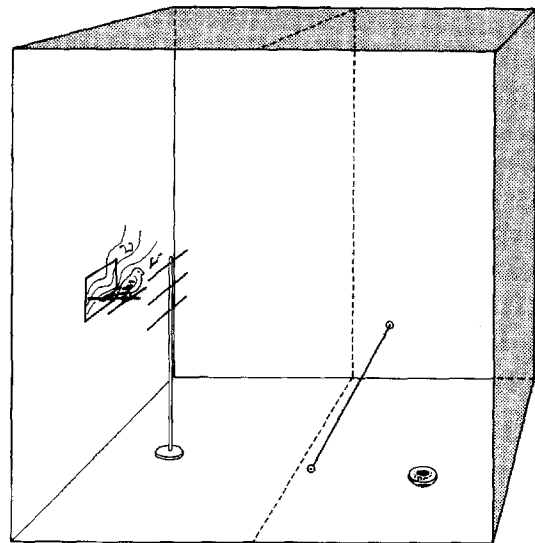


Fig. 1 Experimental aviary used in competition and female choice experiments. In the competition experiment the set-up consisted of a bowl of seeds and water, placed on the floor on the right-hand side. In the centre of the aviary a perch was placed from the front to the back whereas the left side was free of objects. In the female choice experiment two opposing and identical sides were set up (only left side shown). On each side a dummy male was attached to the wall of the aviary using a clipper. Behind the dummy, but out of sight, a loudspeaker was placed. In front of each male a pole was placed with three levels of perches, allowing females to sit in front of, just under or above the male. See text for more details

accounted for 65% of the variance of the first principal component (correlation coefficients ranged from +0.32 to +0.50). The PC1 scores were thereafter used as measures of colour where negative and positive values represent below and above average coloration, respectively (see Sundberg and Larsson 1994; Sundberg 1992, 1994a, b, 1995 for further details on methods, repeatability of measurements, and similarities to other sample sizes).

Male-male competition experiment

In addition to male-male experiments, some male-female and female-female trials were performed in order to check for differences in propensity of interacting between sex and age combinations. All trials were performed using pairs of individuals caught at different sites and kept in separate aviaries and, hence, with no previous experience of each other. Thereby, a number of confounding variables affecting dominance within flocks were eliminated.

In the experimental aviary the only perch was in the lower centre of the cage (c. 20 cm above the floor, Fig. 1, right). A bowl (10 cm diameter) with oat seeds, including a small bowl containing water (4 cm diameter), was placed on the floor in the front right quarter of the cage on which a video camera was focused. When birds were released into the cage the bowl was covered by a box which was elevated to the top of the cage at the start of each trial. Birds were acclimatised for 20 min in the aviary before a trial. During the experiment the following activities were monitored from a hide. First, as a measure of individual motivation to feed, I noted latency to start of feeding for each individual and number of seeds consumed. Trials where one or both individuals did not feed were excluded ($n = 12$). Second, I recorded the number of (1) threats in which an individual takes up a threat position, usually with lowered wings, bowing and aggressive chatters with an open beak (Andrew 1957), and (2) direct attacks in which a male attacks the opponent, sometimes resulting in physical contact. Sub-dominance

was scored when one individual (3) stopped, making no further approaches towards the seed bowl in response to a threat or an attack, or (4) retreated when facing threat or attack. Since attacks were rare (< 10%) I scored one individual as dominant by adding number of attacks plus retreats. Sub-dominance was based on number of stops and retreats. In several trials neither individual was clearly dominant since no aggression occurred, and these were discarded. In three trials the sub-dominant individual also took up a few threat positions towards the end of the trials. Dominance scoring was still clear in these cases. The length of each trial depended on the latency to start of feeding. Birds that started to feed within 5 min generally stopped eating after c. 20 min. They then moved away from the food and rested or preened. My observations ended 8–10 min after active feeding ceased. Average duration of trials was 35.3 min (SD = 5.6) and latency to start of feeding 4.6 min (S = 6.8) for the first bird followed by the other bird on average 3.0 min later (SD = 3.7). Neither latency to feeding, number of seeds consumed nor weight changes affected the outcome of the trials since neither factor was related to dominance [stepwise logistic regression (SAS 1985), $P > 0.18$ in all cases].

In captivity, birds were kept at a temperature of 5–10°C, with a natural light cycle and fed ad lib with oats, commercial finch-seed mixture, and water with soluble vitamins. Birds were kept in aviaries for on average 11 days before the first experiment, thereby allowing a period of acclimatisation to captivity. Individuals were separated from their respective flock on the day before an experiment, weighed and placed separately in cages (30 cm × 30 cm × 40 cm), provided with water only, for the night. Experiments were started between 0900 and 1200 hours the following day after an average starvation period of 17 h (SD = 3.4). Experiments were performed between early February and late March.

The birds in a trial were matched with regard to time in captivity (± 2 days). Several individuals could not be matched, since capture success depended on snow cover, and they were not used in any trial. To increase sample size, I used 40 of the 48 males in a second trial, on average 4 days after the first trial. To avoid dependency of the outcome of previous tests I re-combined males with respect to the outcome of their previous trials, such that dominants were combined with other dominants, and sub-dominants with sub-dominants. In four cases, males with unknown dominance levels were re-combined with sub-dominant males. The outcome of the first trial appeared not to affect the second trial since the 40 males used twice 50% achieved a different outcome in their second trial, and the distribution of males of different degrees of coloration being scored as dominant, sub-dominants or neither did not differ between the first and the second trials ($\chi^2 = 1.75$, $df = 4$, $P > 0.70$).

Female choice experiment

I performed the mate choice experiment between late April and early May 1993, which is the normal period of egg laying, using females caught during late winter. During captivity females were kept in aviaries (as above) with a normally increasing spring light regime. Hormone implantations were done from mid to late April, and the light cycle at the same time was increased by one hour to further increase stimulation. The hormone, β -estradiol (Sigma), was packed in 12 mm Silastic tubing (inner diameter: 1.47 mm; outer diameter: 1.97 mm) and sealed with Silastic adhesive (Dow Corning). Implants were placed subcutaneously in the pectoral region by cutting a small hole in the skin. The cut was sealed with a detergent plaster spray and sewn with two stitches in order to prevent removal of the tubes (see Alatalo et al. 1990 for a more detailed description of the procedure). An equivalent dose of hormones given to pied flycatchers (*Ficedula hypoleuca*) resulted in a degree of assimilation of hormones within the range found naturally in females in breeding condition (Silverin 1991).

As male dummies I used freeze-dried male yellowhammers obtained from a neighbouring air field. The specimens were mounted in an upright natural position with wings close to the

body, perching in the middle of a twig (c. 15 cm long). In each pair of dummy males one was designated as more and the other as less colourful. My scoring of 12 of the pairs used was in agreement with the judgement made by seven colleagues, four with much and three with little experience of birds [binomial test for each comparison: $P < 0.04$ in all cases; Fisher's combined probability test (Sokal and Rohlf 1981), $df = 14$, $n = 7$, $P < 0.01$]. In order to remove any other confounding effects of male characteristics I designated one-third of the females to choose between male decoys where I had altered the colour. Originally colourful dummies were made duller by dyeing their yellow patches with green and brown felt tip markers. Originally dull males were made more colourful by increasing the size of the coloured patches by cutting off dark crown feather edges covering the yellow crown. I also added yellow colour by dyeing the coloured patches on head, throat and belly. In successful experiments, 15 different decoys were used, 12 young and three old males. Seven of these were reused and were then re-combined with a different decoy or had their colour altered as described above.

The experimental set-up (Fig. 1, left) consisted of a pair of opposing males, attached to the wall, 70 cm above the floor. Loud speakers were attached behind each decoy. From each loud speaker I played the same yellowhammer song strophe, five strophes/min from each of them, in an alternate fashion during the experiment. The song type used in the experiment is common in the area (J. Sundberg, unpublished work) and has previously been illustrated in other studies (Hiatt and Catchpole 1982, Fig. 2a; Baker et al. 1987, Fig. 1a). In front of each dummy male (20 cm), I placed a pole with horizontal twigs for perching, attached at three different heights: at the same level as the decoy male and 12 cm below and above, respectively, thus enabling close inspection from different positions. The two males were randomly placed on each side of the cage and covered until the start of each experiment. Perch sites and loud speakers were exchanged between sides every second or third trial in order to avoid side effects.

Females used in the experiment were allowed 20 min to acclimatise before the start of a trial, which lasted 40 min. During the trials I measured the time females spent on each side and in each position as (1) floor, and (2) tree, including time at (3) bottom, (4) centre, or (5) top branch. Preference for a side, and primarily in front of a particular male, was regarded as mate preference. The total time spent by females in different positions in trees was significantly and positively correlated with the time they spent in the top and the centre of the tree, both in front of the yellow (top: $r = 0.61$, $P = 0.025$, centre: $r = 0.85$, $P < 0.001$) and the drab decoy males (top: $r = 0.82$, $P = 0.001$, centre: $r = 0.82$, $P = 0.001$). Thus, only results of total time in tree are further presented. Females occasionally sat in the exact middle on the floor and sometimes on the netted walls of the aviary, out of sight of the observer or the video camera. Such activity was excluded.

In all, 24 females were implanted. Behavioural changes, most notably vocal utterances, were already detectable after 24 h. I used six females in order to achieve a functional experimental set-up, including exclusion of male song, decoy males on the floor, and determination of optimal time for tests after implantation. Of the remaining 18 females, 7 made no choice, including 5 females on the floor not moving, 2 of which had lost their hormone tubes, and 2 females sitting motionless in one tree only. The weak response by some of the females may have been caused by lack of light stimulus since some had been kept in an aviary lacking natural light and had only been exposed to artificial light. This group of females was transferred to an aviary with additional outdoor light when implanted, whereas the majority of females were influenced by both artificial and outdoor light during the entire period in captivity. Of the 11 females used in the analysis, 8 were young with no previous experience of mate choice and the remaining 3 were old birds, with previous experience. Time between implantation and experiment varied between 3 and 8 days.

Of all birds kept indoors ($n = 161$), four died, while all survivors were released at their site of capture after the end of the experiments and after hormone tubes had been removed from females.

Table 1 Number of trials with aggressive interactions in different age combinations of yellowhammers in male-male trials used to determine dominance

Age combination	Yellow dominant	Drab dominant	No aggression	Total	Sign test <i>P</i>
Young-young	3	4	7	14	0.99
Old-old	5	4	3	12	0.99
Old-young	11	2	5	18	0.02
Total	19	10	15	44	0.14

Table 2 Number and frequency of aggressive interactions between male yellowhammers in trials with different age combinations

Age combination	Number of attacks plus threats	Attacks plus threats/trial mean (SD)	Trials with aggressive interactions (%)	<i>n</i>
Young-young	30	2.14(3.10)	50	14
Old-old	90	7.50(6.45)	75	12
Old-young	62	3.44(3.60)	72	18
Total	182	4.14(4.82)	66	44

Five males bred in the study area the following spring. Values are given as means (\pm SD) and two-tailed probabilities are used.

Results

Male-male competition

A total of 61 successful competition trials was performed, 44 of which were male-male encounters, 12 female-female encounters and five male-female encounters. Aggression occurred in 3 out of 17 (18%) of the trials in which at least one female was included but was significantly more frequently observed in male-male encounters (66%, $\chi^2 = 12.01$, $df = 1$, $P < 0.001$). Aggression was observed in 29 trials between males, but no indications of more colourful males being dominant (Table 1, sign test, $P = 0.14$). Since colour is related to age (colour score of young: -1.14 (1.24), $n = 32$; old: 1.46 (1.26), $n = 25$, $F_{1,56} = 60.9$, $P < 0.001$), this result was highly influenced by the results of trials between a young and an old male ($n = 18$) where the older and more colourful males were dominant in 11 out of 13 trials (Table 1, sign test, $P = 0.02$). Old males also had significantly longer wings than young males (paired t -test, $t = 2.95$, $P < 0.01$), but did not differ in mass ($t = 0.35$, $P = 0.73$). Trials within age classes showed no significant advantage for more colourful males (young vs. young and old vs. old males combined; more colourful male won in 8 out of 16 trials, sign test, $P > 0.99$, $n = 26$). Neither did the outcome of these trials depend on differences in size, measured as wing length, or mass (paired t -test, wing length: $t = -0.47$, $P = 0.65$, mass: $t = 0.27$, $P = 0.79$).

The number of attacks plus threats was highly positively correlated with the number of retreats ($r = 0.89$, $n = 152$, $P < 0.001$); 182 attacks and threats were counted in 29 of the 44 male-male trials at an average of 5.8 per trial (4.6), of which 169 (93%) were performed by males scored as dominants. Aggression

occurred less frequently in encounters between two young males (50%), but did not differ from that recorded in trials including two old males (73%; $\chi^2 = 2.31$, $df = 1$, $P > 0.10$, Table 2). The frequency of aggression differed between different age combinations (Kruskal-Wallis one-way ANOVA, $KW = 10.48$, $df = 2$, $P < 0.01$) and was lowest between two young males or between one old and one young male (Table 2). Aggressive encounters were most frequent in trials between two old males but did not differ significantly from the other two groups (Table 2, $P > 0.10$ in both cases). The establishment of dominance was independent of colour differences within pairs of males, since no relationship was found between frequency in aggression and difference in colour in pairs of males ($r_s = -0.05$, $n = 44$, $P > 0.70$). However, in trials between two young males a large colour difference resulted in fewer aggressive encounters (Fig. 2, $r_s = -0.59$, $n = 14$, $P = 0.03$), whereas no such relationship was found in trials between two old or one old and one young male ($P > 0.24$, in both cases).

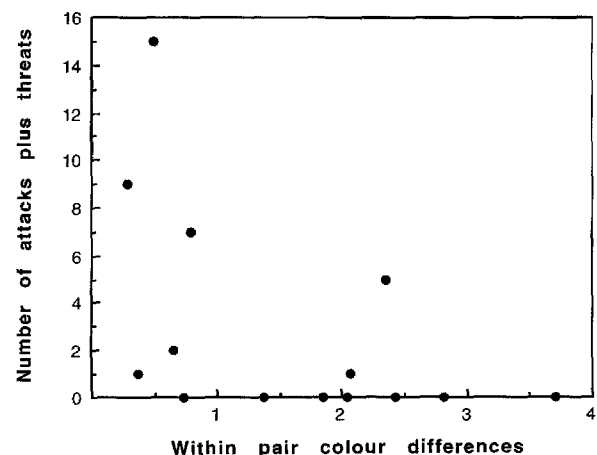


Fig. 2 The relationship between amount of aggression and differences in colour within pairs of young yellowhammer males during competition trials

Table 3 Average time [min (\pm SD)] at different sides and positions of choosing female yellowhammers in mate choice experiment

Position	Yellow male	Drab male	All trials p^a $n = 11$	Natural males p^b $n = 7$	Altered males p^b $n = 4$	Combined probability p^c
Tree	10.7 (6.3)	5.3 (2.8)	0.006	0.015	0.062	$p < 0.05$
Floor	11.4 (5.9)	9.3 (6.3)	0.41	0.31	0.88	$p > 0.50$
Total	22.1 (5.3)	14.6 (5.7)	0.034	0.055	0.31	$p < 0.10$

^aPaired *t*-test^bWilcoxon matched-pairs signed-ranks test^cFishers combined probability test**Table 4** Number of visits and time spent (s) with yellow and drab male by female yellowhammers where they visited males in mate choice experiment

Trial no.	Yellow male No. of visits	χ (SD)	Drab male No. of visits	χ (SD)
1	1	2	0	—
2	2	3 (1.4)	1	2
4	7	10.4 (10.7)	0	—
5	1	10	0	—
6	4	11.2 (6.7)	1	8
7	11	25.0 (18.7)	8	12.1 (4.1)
9	1	5	0	—
10	0	—	1	23
Mean (SD)	3.4 (3.8)	15.4 (15.5)	1.4 (2.7)	11.8 (5.9)

Female choice

Females spent significantly more time on the perch in front of the more colourful male but not on the floor on the side of the more colourful male as compared to the drab male (Table 3). These results were significant when females were given a choice between two naturally coloured males ($n = 7$), and there was a tendency in the same direction in the group of females choosing between decoy males with altered coloration ($n = 4$). Combining the probabilities (Fisher's combined probability test) of the two sub-groups also resulted in a significant preference for the more colourful male (Table 3). Moreover, in eight trials females came and sat beside the decoy male, on the perch on which the decoy was mounted, whereas the dull males were visited in four trials only (Table 4). Hence, females visited the brighter male significantly more often than the drab male (Wilcoxon matched signed rank test: $n = 8$, $P = 0.02$), but on average did not stay significantly longer at each visit (Wilcoxon signed ranks test, $n = 8$, $P = 0.08$, Table 4).

Discussion

My results indicate that male colour in the yellowhammer may play a role in inter-male relationships, but more clearly that females show a preference for more colourful decoy males. Male ornamentation in the yellowhammer, hence, appears to primarily be influenced by intra-sexual selection although the affect of inter-sexual selection cannot be ruled out.

Male plumage ornaments have earlier been found to signal dominance and status in a number of bird species (Rohwer 1975; Rohwer and Rohwer 1978; Watt 1986a, b; Møller 1987, 1988b; Evans and Hatchwell 1991), and more dominant males are likely to enjoy an advantage in resource competition. In the yellowhammer the relationship between colour and dominance was weak and might be questioned since dominance relationships were to a large extent dependent on age rather than colour. Aggressive interactions occurred significantly more often in trials between males than when females were involved, and rate of aggression varied between different male age class combinations, old males showing the highest rate. Age has commonly been found to be associated with high dominance rank (Morse 1980) and frequent interactions might thus be expected between older individuals with similar badge size as found in studies of other species (e.g. Järvi and Bakken 1984; Møller 1987). The fact that the young males of similar colour interacted more aggressively suggests that colour plays some role in signalling dominance. Alternatively, older males may signal dominance through behaviour while colour, per se, may turn out to be of less importance as an indicator of dominance. Thus, age-dependent rather than colour-related dominance appears to be the rule in yellowhammers. This was also indicated in previous studies where old males initiated more fights during the fertile period of their mates compared to young males (Sundberg 1992), and young males intruded less than expected on territories of older males (Sundberg 1994b).

Several factors may be responsible for a lack or reduced importance of a relationship between plumage and dominance. Plumage coloration is often age-related

although considerable overlap may occur between different age classes, as in the yellowhammer (approximately 40% overlap in colour between the age classes, Sundberg 1994a), making coloration a less reliable age-indicator. Other passerine species are likely to show a stronger age-related ornamentation (Jackson et al. 1988; see also Pyle et al. 1987; Svensson 1992) emphasising the necessity of distinguishing among different age-classes in behavioural studies. However, other species show delayed plumage maturation (Studd and Robertson 1985) with age-specific plumages, suggesting that different moult systems may reflect different relationships between plumage and dominance. Size, motivation, condition and previous experience are other factors likely to influence dominance hierarchies (Møller 1987), although these factors were ruled out in this experiment. Thus, plumage variation may be a reliable predictor of dominance in some species but not in others (e.g. Watt 1986a, b). Still, a lack of colour-related dominance as found in this experiment may not necessarily reflect competition for other important resources such as territories. In the yellowhammer, severe competition for food is likely to be absent outside winter. Male yellowhammers in this population also show high breeding-site fidelity between years, with more than 75% resuming their former territories if surviving (unpublished work). This will result in territory owner asymmetries, which may further reduce the importance of signals for assessment of dominance.

As indicated by visiting rate and perching time in front of more colourful males the results of the second part of this study suggest that female yellowhammers base their mate choice on male plumage. The use of standardised male decoys and song, which excludes other behavioural influence, in combination with the use of males with altered plumage coloration gives additional strength to this conclusion. Alternatively, females may have chosen particular males for reasons other than mate choice. For instance, in this experiment only one female was observed to solicit copulation (in one set-up test). However, after implantation the majority of females uttered similar sounds as may be heard in the field when females initiate copulations, suggesting that females were sexually stimulated and that the behaviour observed was a choice for mates.

Evidence for female choice based on plumage features is rare for monogamous, territorial species but is more persuasive for lekking and polygynous species (e.g. Andersson 1989; Alatalo et al. 1991). Among socially monogamous bird species experimental evidence for female preference for males with particular traits exists only for zebra finch (*Taeniopygia guttata*, Burley 1986), barn swallow (*Hirundo rustica*, Møller 1988a), house sparrow (*Passer domesticus*, Møller 1988b), and house finch (*Carpodacus mexicanus*, Hill 1991). Several field studies (reviews in Andersson 1994; Møller 1994) also imply female preference for more ornamented males.

My data for the yellowhammer support the notion that sexual selection contributes to the evolution and maintenance of sexual dimorphism in monogamous species. Variation in male reproductive success may be due to several factors (reviewed in Kirkpatrick et al. 1990; Møller 1994), including indirect benefits where more ornamented males, except for possible competitive advantages, benefit through higher survival. Male attractiveness may result in benefits in terms of acquisition of high quality females (Darwin 1871; Kirkpatrick et al. 1990; Møller 1991), capable of laying earlier and larger clutches, more frequent second clutches, all normally improving fitness. Males will further benefit from their attractiveness if this makes them preferred as extra-pair copulation (EPC) partners (Møller 1988a; Smith et al. 1991; Kempenaers et al. 1992). Females may also benefit from being choosy and using appropriate cues in their choice, if preferred males are better parents and advertise this by more or brighter coloration (Heywood 1989; Hoelzer 1989). Clearly, males in good condition have much to gain from signalling their qualities.

In the yellowhammer, colour (badge sizes) and colour intensity is highly correlated and both males and females are quite variable in both aspects (Sundberg 1994a, 1995, unpublished work). This variation makes it possible for both males and females to choose partners on the basis of their coloration (see also Jones and Hunter 1993). Pairing is to a large extent age-assortative and some evidence for colour-assortative mating exists indicating that more colourful individuals pair-up with one another (Sundberg 1994a). This colour-related pairing is not due to age-related arrival to the breeding grounds since yellowhammers are sedentary in the area (Sundberg 1994a). Furthermore, female yellowhammers have been found to choose EPC partners that are more colourful than their pair mate (J. Sundberg and A. Dixon, unpublished work) providing further evidence that females prefer yellower males. Females paired with less desirable males thus compensate for their deficiency of their pair-mate by performing extra-pair copulations with preferred males.

What do more colourful yellowhammer males signal? Coloration, composed of carotenoid pigments, is related to the amount of pigments ingested through the diet (Fox and Vevers 1960; Brush 1978; Kodric-Brown 1989; Hill 1992, 1993a, b). Colour may thus signal foraging ability during the period of moult. The yellowness of male yellowhammers may therefore signal experience as well as survival since males increase in colour until at least their 4th year (Sundberg 1994a). Colour may function as a condition-dependent trait indicating phenotypic quality. Male colour may also signal genetic qualities such as resistance to parasites since male colour has been found to be negatively correlated with haemoprotozoan intensity (Sundberg 1995).

The results of this study provide evidence that male coloration is a sexually selected character in the yellowhammer. Age, rather than colour determines dominance although age and coloration are coupled. Females, on the other hand, prefer more colourful decoy males. Male colour may signal experience used as an honest signal of male qualities preferred and maintained primarily by females.

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