

SEASONAL CHANGE IN FEMALE MATE CHOICE CRITERIA IN PENDULINE TITS (*REMIZ PENDULINUS*)

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SUMMARY.—*Seasonal change in female mate choice criteria in Penduline Tit (Remiz pendulinus).* Most studies on intersexual selection are concerned with the significance of cues females use in the mate choice process. To date, not much attention has been paid to the possibility of changes in female choice criteria throughout a breeding season, in particular where choice cues include territory characteristics. This topic was investigated in Penduline Tits (*Remiz pendulinus*). Previous studies revealed the importance of nest quality in Penduline Tit for female reproductive success and its role in female choice given benefits of improved insulation. However, one might predict that the insulation capacity of the nest is most important in the early breeding season, when the ambient temperature is expected to be low, and decreases across the breeding season. In line with this, other factors, such as male intrinsic quality (expressed in morphology or male display behaviour) could become more important later on. This study examines the importance of different mate choice cues throughout the breeding season by comparing the quality of chosen and not chosen males (considering both morphological and behavioural parameters), nest quality (considering size), and the variation in mating success among males. The results show a significant decrease in the importance of the nest with the season while male display behaviour becomes more important. Nest size does not change throughout the breeding season, and there is also a significant repeatability in nest size within successive nests of one male. Thus, the decreasing importance of nest size for female choice is not reflected in male nest building behaviour. Rather, the significant repeatability indicates that male nest building skill may have a genetic determinant.

Key words: Male quality, mate choice, nest quality, nest size repeatability, Penduline Tit, *Remiz pendulinus*.

RESUMEN.—*Cambios estacionales en los criterios de selección de la pareja por parte de la hembra en el Pájaro Moscón (Remiz pendulinus).* La mayoría de los estudios sobre selección intersexual se centran en la importancia de los criterios usados por las hembras en el proceso de selección de pareja. Sin embargo, hasta la fecha no se ha prestado mucha atención a la posibilidad de cambios en tales criterios a lo largo de la estación de cría, en particular en aquellos casos donde los criterios de selección incluyen características del territorio. Este trabajo trata sobre la variación en los criterios de elección usados por la hembra del Pájaro Moscón (*Remiz pendulinus*). Estudios anteriores han demostrado la importancia de la calidad del nido en el éxito reproductor de la hembra de esta especie y su papel en el proceso de elección realizado por la hembra como consecuencia de los beneficios relacionados con la capacidad termorreguladora del nido. Sin embargo, se podría predecir que esta capacidad aislante es más importante al comienzo de la estación de cría, cuando la temperatura ambiente suele ser baja, y disminuye a lo largo de la temporada. De acuerdo con esto, otros factores, como la calidad intrínseca del macho (expresada en términos de morfología o conducta de exhibición) podrían ser más importantes conforme la estación transcurre. Este trabajo examina la importancia de los diferentes criterios de selección de la pareja a lo largo de la estación de cría comparando la calidad de machos elegidos y machos no elegidos, en base tanto a parámetros morfológicos como conductuales, calidad del nido (expresada por su tamaño) y variación en éxito de apareamiento entre machos. Los resultados demuestran una disminución significativa en la importancia del nido a lo largo de la estación mientras que la conducta de exhibición del macho cobra importancia. Sin embargo, el tamaño del nido no cambia a lo largo de la temporada de cría y hay una consistencia significativa en el tamaño de los diversos nidos construidos por un mismo macho. Por tanto, la disminución en importancia del tamaño del nido para la hembra no se refleja en la conducta de construcción del macho. Más bien, la consistencia significativa indica que la conducta de construcción del nido del macho puede tener un determinante genético.

Palabras clave: Calidad del macho, calidad del nido, constancia en tamaño del nido, elección de la pareja, Pájaro Moscón, *Remiz pendulinus*.

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INTRODUCTION

Most studies on intersexual selection deal with the significance of cues females use in the mate choice process (Catchpole, 1980; Alatalo *et al.*, 1986a; Lifjeld & Slagsvold, 1988; Alatalo *et al.*, 1990; Reid & Weatherhead, 1990; Hill, 1990). Models of mate choice often assume that there is a genetic basis for female preference (Kirkpatrick & Ryan, 1991). This has been shown in several studies (i.e. Bakker, 1993; Wilkinson & Reillo, 1994; Houde, 1994), whereby consistency in female mate preference was calculated using repeatability of characters of males chosen by females on different mate choice occasions (Möller, 1994; Jennions *et al.*, 1995; Blanckenhorn & Perner, 1995).

However, consistency in female preference is not necessarily an indicator for a genetic basis of choice, and, conversely, a genetic basis need not to be necessarily reflected by consistency in female preference. Rather, one would expect that female mate choice criteria in many species can change according to the own quality, age, number and quality of potential partners and varying ecological situations (Petrie & Hunter, 1993) independently of a genetic basis. So, whether and how choice cues should be used is also influenced by the costs and benefits for a female. Choice cues can change even within a breeding cycle, which is supported by the fact that female choice can also occur after pair formation by actively soliciting extra-pair copulations (see Birkhead & Möller, 1992). In those cases, mate choice cues may change from parental quality features of their pair partners to genetical quality features of their copulation partners (Westneat *et al.*, 1990). Also in multiple brooded species with long breeding windows and a pronounced seasonality, one might expect that the importance of territory quality or male parental quality may change according to the ecological situation and probably shift to features directly related to male genetic quality when there is no ecological constraint. For instance, in many species the nutritional situation is a limiting factor at the beginning of the breeding season (first brood) but not at later breeding attempts (Hoi *et al.*, 1995).

To date, however, not much attention has been paid to variation in female choice preferences.

In this study we examine if female Penduline Tit (*Remiz pendulinus*) changes mate choice criteria throughout the breeding season. In the Penduline Tit — a small (9 to 10 g) European passerine — the nest plays a major role in mate attraction (Hoi *et al.*, 1994). In this species males devote a lot of time and energy to construct elaborate pendulous nests (Franke, 1938; Franz *et al.*, 1979; Franz & Theiss, 1983; Schleicher *et al.*, 1993). We could show that large nests are better insulated than small ones, and female choice is based on nest size (Hoi *et al.*, 1994). So, female Penduline Tits choosing large nests benefit mainly through reduced incubation effort (see, for instance, Weathers, 1985), and have more time for foraging (Grubbauer, 1995) or other self-maintenance behaviour (Nilsson & Smith, 1988). Additionally, females choosing large nests may enhance their reproductive success by avoiding cold stress and thereby increase hatching success (Grubbauer, 1995) and therefore the number of offspring (Hoi *et al.*, 1994). Females may have also more time for seeking extra-pair copulations during the egg-laying period due to a better insulation capacity of larger nests (Birkhead *et al.*, 1987; Smith, 1988; Birkhead & Möller, 1992).

Because insulation capacity of the nests is most likely to be important in the early breeding season, when the ambient temperature is low, one might expect a decrease in the significance of nests in the mate choice process with the progress of the breeding season.

Penduline Tit is an ideal study object for this subject because in our study area a) this species has a very long breeding season ranging from the beginning of April to the end of August; b) they breed first in riparian forests from April to the middle of June, and then the whole population seems to switch to Lake Neusiedl (80 km away) where they continue to breed from the middle of June until the end of August (see Franz, 1989); c) during the breeding season ambient temperatures vary widely from freezing during the early breeding season to above 30°C or even more during the hot and dry summer of the late season; and d) mate choice can be based on males as well as on nests (Grubbauer, 1995).

If nest quality becomes less important across the breeding season for Penduline Tit female mate choice, one might expect that female mate choice will switch to other factors, like male morphology or display behaviour. These may have implications for male parental quality.

To test this idea, we examined female choice across the season by comparing female preference for nest quality (using nest size) and male quality (using morphology, calling and singing behaviour). These aspects were considered both within and across the «early» and «late» breeding season.

METHODS

Study site

The field study was conducted in a riparian forest area in the eastern part of Austria about 60 km northeast of Vienna along the river March (48° 16' N, 16° 57' E) and in the region around Lake Neusiedl (47° 46' N, 16° 48' E) between 1992-1994. The riparian forest area was characterized by different kinds of willows, like *Salix alba*, *S. cinerea* or *S. fragilis*, and poplars such as *Populus alba*. The river bank was dominated by reed (*Phragmites australis*) and stinging nettles (*Urtica dioica*).

The region around Lake Neusiedl is dominated by the extended reed belt, whereas poplars and willows are subordinate here.

Penduline Tit shows a very distinct breeding pattern. The whole population appears to switch from the riparian forest, where they have their first breeding attempts (first egg-laying dates range from 16.4-10.6.), to Lake Neusiedl (first egg-laying dates range from 14.6-8.7.). So, the entire process of breeding site arrival and nest site establishment occurs twice within one year in this species.

Based on this, we termed the riparian forest period as «early breeding season» and the Lake Neusiedl period as «late breeding season».

Weather conditions change across the season: during April ambient temperatures can be well below freezing (mean ambient temperature for April: $\bar{x} = 10.6^{\circ}\text{C} \pm 3.05$ SE; May: $\bar{x} = 14.4^{\circ}\text{C} \pm 2.6$ SE), whereas in June and July the breeding situation is hot and dry (mean

ambient temperature for June: $\bar{x} = 19.6^{\circ}\text{C} \pm 2.86$ SE; July: $\bar{x} = 24.1^{\circ}\text{C} \pm 2.52$ SE).

To investigate the seasonally dependent variation of female mate choice criteria we compared the importance of different parameters: a) between chosen and not chosen males, and b) in relation to male mating order for the «early» and the «late» breeding season. A male was considered to be chosen only when egg-laying occurred to avoid errors due to sporadic visits of females. Males which were unable to attract a female with a certain nest are considered as not chosen.

Each male and female was considered only once in the analyses.

Investigated mate choice parameters

a) Parameter of nest quality.

To determine nest quality (see Hoi *et al.*, 1994) we measured the nest size using the height from the attachment to the bottom of the nest of completed nests or nests in advanced building stages.

b) Parameters of male quality.

To determine possible mate choice cues related to the male itself we measured: a) several phenotypic parameters (mask length, mask width, wing length) according to Svensson (1984), and b) male display behaviour during the mating period. During this period males use a certain call note to attract potential mates (see Franz & Theiss, 1983). In the presence of a female, but also after a successful mating, males use the song to link the female to their nests (Schönfeld, 1994).

We used the calling frequency (number of 30-s intervals with calls / 20 min) and calling intensity (mean number of calls / 30-s interval / 20 min) as well as song frequency (number of 30-s intervals with songs / 20 min) and song intensity (mean number of songs / 30-s interval / 20 min) as a measure of male courtship intensity.

Capture and Observations of Birds

Males were mist-netted and individually colour ringed during the mating phase (prior to or after mating) and females later on du-

ring incubation or feeding. Additionally, birds were provided with a numbered aluminium ring. Morphological characters were measured whenever the birds were captured.

Mask length and width were measured with a ruling caliper to the nearest of 0.1 mm. Wing length was measured with a ruler to the nearest of 1 mm. Only the size of right characters was used in the analyses.

Behavioural data were collected during the intermediate building stages («Swing» and «Basket», see Franz *et al.*, 1979) when unmated males try to attract a female. Five to seven behavioural protocols were done during daily visits for 20-min observation periods using time sampling in 30-s intervals. Male and female time on and off the nest, their nest building behaviour as well as male display behaviour were recorded.

Nest site quality was shown not to be important in female mate choice (Schleicher, 1993) and is therefore not examined here.

Statistical analyses

Spearman rank correlations were used to examine the relation of nest size, morphological and behavioural parameters with male mating day. Therefore, a male mating order was established using ranks from 1 to n where the first mated male was assigned a rank of 1. Only the first nest of each male within each breeding period was used to establish the mating order.

To investigate whether nest size varies throughout the whole breeding season («early» and «late») a Spearman rank correlation was done using «weeks» as a unit. For the analyses concerning nest size, breeding season and male characteristics in relation to whether or not males were chosen two-way ANOVAs were performed. Nest size, male morphology and male behaviour respectively were used as response variables. Breeding season («early», «late») and female choice (chosen, not chosen) were used as independent factors. Additionally, for the comparisons between chosen and not chosen nests and males both in the «early» and the «late» breeding season Students *t*-tests were used.

Most males build several nests within a season (up to eight nests). The consistency of

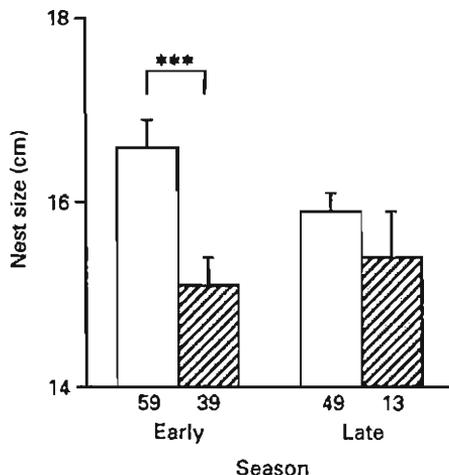


FIG 1.—Comparison of nest size (cm) between chosen (white bars) and not chosen nests (hatched bars) in the early and late breeding season. Given are means (\pm SE). Asterisks indicate significant differences (*t*-test: *** = $P < 0.001$).

[Comparación del tamaño del nido (cm) entre nidos elegidos (barras vacías) y no elegidos (barras sombreadas) durante la estación de cría temprana y tardía. Se ofrecen los valores medios (\pm ES). Los asteriscos indican diferencias significativas (test de la *t*: *** = $P < 0.001$)].

male nest building skill was examined by means of a repeatability analysis which quantifies the amount of within-male variance relative to the total within-and between-male variance in nest size (Falconer, 1981; Lessells & Boag, 1987; Boake, 1989). The repeatability measure (*R*) also provides an estimate of the heritability (Falconer, 1981) which should be lower than the repeatability (Möller, 1994) but can be used as an estimator for a heritable basis in male nest building skill.

RESULTS

The significance of the nest

The results of the two-ways ANOVA revealed a significant relation between mate choice and nest size (see Table 1), whereby chosen nests are larger than not chosen nests (Fig. 1). However, the seasonal factor revealed no difference in nest size between the

TABLE 1

Results of the two-ways ANOVAs to test the significance of nest size, male morphology and male display behaviour on female mate choice both early and late in the breeding season. A: factor 1 (chosen vs. not chosen males), B: factor 2 (early season vs. late season), A × B: interaction between both factors.

[Resultados de los ANOVAs de dos vías para comprobar el significado del tamaño del nido, de los caracteres morfológicos del macho y de su conducta de apareamiento en la elección de la hembra durante la estación de cría temprana y tardía. A: factor 1 (machos elegidos vs. machos no elegidos), B: factor 2 (estación temprana vs. estación tardía), A × B: interacción entre ambos factores.]

Dependent variable	A			B			A × B		
	F	df	P	F	df	P	F	df	P
Nest size	8.34	1,157	0.004	0.20	1,157	n.s.	1.83	1,157	n.s.
Male morphology									
Mask length	0.82	1,96	n.s.	0.49	1,96	n.s.	0.49	1,96	n.s.
Mask width	0.62	1,96	n.s.	0.46	1,96	n.s.	0.49	1,96	n.s.
Wing length	0.01	1,92	n.s.	0.15	1,92	n.s.	0.91	1,92	n.s.
Male display									
Calling frequency	1.62	1,77	n.s.	1.52	1,77	n.s.	0.01	1,77	n.s.
Calling intensity	0.55	1,77	n.s.	1.42	1,77	n.s.	0.09	1,77	n.s.
Song frequency	4.79	1,44	0.03	8.19	1,44	0.006	1.24	1,44	n.s.
Song intensity	0.03	1,44	n.s.	6.68	1,44	0.01	0.06	1,44	n.s.

TABLE 2

Correlation between female choice criteria and male mating day (ranked) for the early and the late season. Given are Spearman rank correlation coefficients (r) and P -values for significant relationships.

[Correlación entre los criterios de elección de pareja usables por la hembra y día de apareamiento del macho (ordenado por rangos) para la estación de cría temprana y tardía. Se ofrecen los coeficientes de correlación de Spearman (r_s) y los valores de P para las correlaciones significativas.]

	Early season	Late season
	Mating day	Mating day
Nest size	$r = -0.50, P < 0.001$ (33)	n.s. (49)
Male morphology		
Mask length	n.s. (59)	n.s. (42)
Mask width	n.s. (59)	n.s. (42)
Wing length	n.s. (59)	n.s. (41)
Male display		
Calling frequency	n.s. (19)	n.s. (24)
Calling intensity	n.s. (19)	n.s. (24)
Song frequency	n.s. (11)	$r = -0.63, P = 0.05$ (10)
Song intensity	n.s. (11)	$r = -0.64, P = 0.04$ (10)

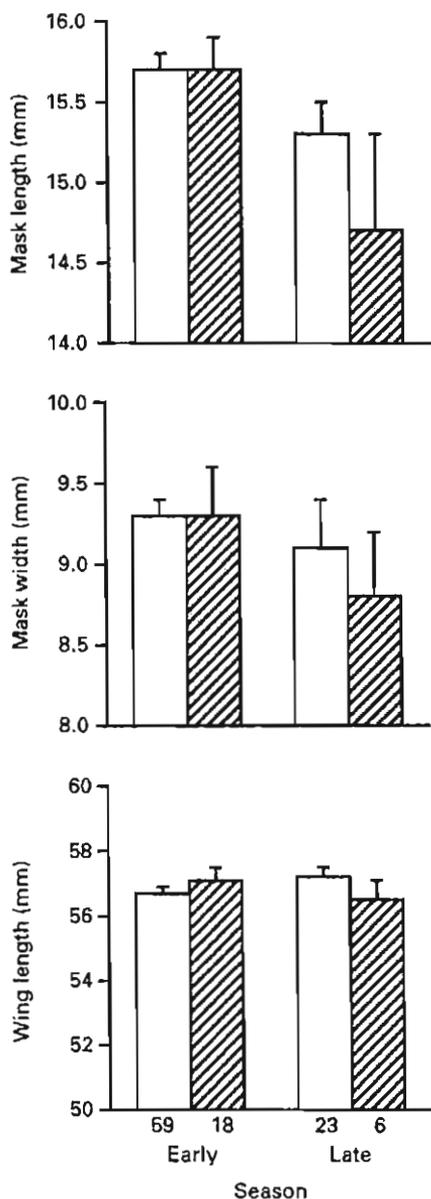


FIG 2.—Comparison of male mask length (mm), mask width (mm) and wing length (mm) between chosen (white bars) and not chosen males (hatched bars) in the early and late breeding season. Given are means (\pm SE).

[Comparación de la longitud de la máscara (mm), su anchura (mm) y la longitud del ala (mm) entre machos elegidos (barras vacías) y no elegidos (barras sombreadas) durante la estación de cría temprana y tardía. Se ofrecen los valores medios (\pm ES)].

«early» and the «late» breeding season (Table 1). There was also no variation in nest size throughout the whole breeding season ($r_s=0.1$, $P=0.21$, $n=160$, chosen and not chosen nests are pooled). The interaction between the two factors (choice and season) does not support that nest size is only important for female mate choice during one of the two breeding seasons. However, single comparisons for the «early» and the «late» season indicate a significant difference in nest size between chosen and not chosen nests in the early season (t -test: $t=3.86$, $P<0.001$, $n=59$ chosen nests/39 not chosen nests), whereas in the late season no difference was found (t -test: $t=0.99$, $P=0.32$, $n=49$ chosen nests/13 not chosen nests, Fig. 1). The different importance of nest size for female mate choice throughout the season is also supported by a correlation between male mating rank and nest size: in the early breeding season males with larger nests mate earlier, whereas in the late season nest size has no effect on male mating rank (Table 2).

Most males can build several nests (up to eight nests during one breeding season) and despite the changing ecological conditions (e.g. ambient temperature, habitat composition) there is a significant repeatability in nest size ($R=0.29$, $F=2.05$, $P=0.015$, $n=29$ males).

The significance of male morphology

The two-way ANOVAs did not show any significant difference in male morphology (mask length, mask width and wing length) between chosen and not chosen males both in the «early» and the «late» season (Fig. 2, Table 1) without significant interaction between both factors. Single comparisons for the «early» and the «late» season revealed also no differences (t -test, for all comparisons: $P>0.3$) between chosen and not chosen males. We also found no correlation between male morphology and mating rank for the «early» and «late» breeding season (Table 2).

The significance of male calling and singing behaviour

The two-way ANOVAs revealed neither an effect of calling frequency (number of 30-s

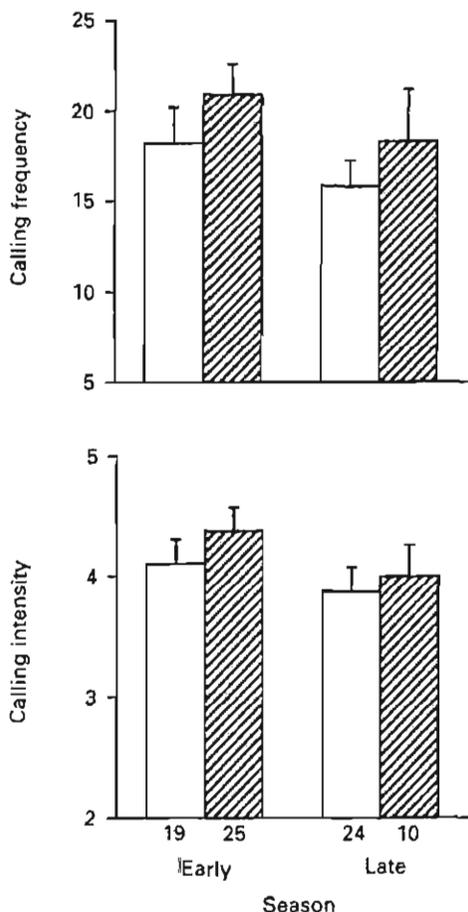


FIG 3.—Comparison of male calling frequency (number of 30-s intervals with calls / 20 min) and calling intensity (mean number of calls / 30-s interval / 20 min) of chosen (white bars) and not chosen males (hatched bars) in the early and late breeding season. Given are means (\pm SE).

[Comparación de la frecuencia de llamada (número de intervalos de 30 segundos con llamadas / 20 minutos) y de la intensidad de llamada (número medio de llamadas / intervalo de 30 segundos / 20 minutos) de machos elegidos (barras vacías) y no elegidos (barras sombreadas) durante la estación de cría temprana y tardía. Se ofrecen los valores medios (\pm ES)].

intervals with calls / 20 min) nor calling intensity (mean number of calls/30-s interval / 20 min) on mate choice (Fig. 3, Table 1). There was also no difference between the «early» and the «late» season and no significant interaction between both factors regard-

ing the two calling parameters. Single comparisons for the «early» and the «late» breeding season did not show any differences in male calling behaviour (t -test, for all comparisons: $P > 0.3$) between chosen and not chosen males. Additionally, table 2 shows that in the «early» and the «late» breeding season neither male calling frequency nor male calling intensity affects male mating success.

Concerning male singing behaviour we found no effect of song intensity (mean number of songs / 30-s interval / 20 min) on mate choice (Fig. 4, Table 1). However, song frequency (number of 30-s intervals with songs / 20 min) was higher in chosen males (Table 1). Furthermore, we found a decrease in song frequency but an increase in song intensity from the «early» to the «late» breeding season (Fig. 4, Table 1). The interaction did not indicate a change in the importance of male singing behaviour for female choice for any of the two breeding seasons. Additionally, simple comparisons did not reveal any differences (t -test, for all comparisons: $P > 0.1$) between chosen and not chosen males both in the «early» and «late» breeding season. However, table 2 shows that in the late breeding season males having a higher song frequency and song intensity were able to mate earlier.

DISCUSSION

Since the size of a nest is directly related to its insulation capacity and positively affects female reproductive success (Hoi *et al.*, 1994), females should prefer large nests. This preference should be highest in the «early» breeding season when the ambient temperature is low. In line with this, our results show that the significance of large nests in female mate choice is mainly related to the «early» breeding season. This is supported by the significant difference in nest size between chosen and not chosen nests especially in the «early» breeding season (Fig. 1) and by the negative correlation between nest size and male mating rank (Table 2). In the «late» season we found no effect of nest size for male mating day and no difference in nest size between chosen and not chosen nests. The loss in selectivity for nest size could be interpreted as

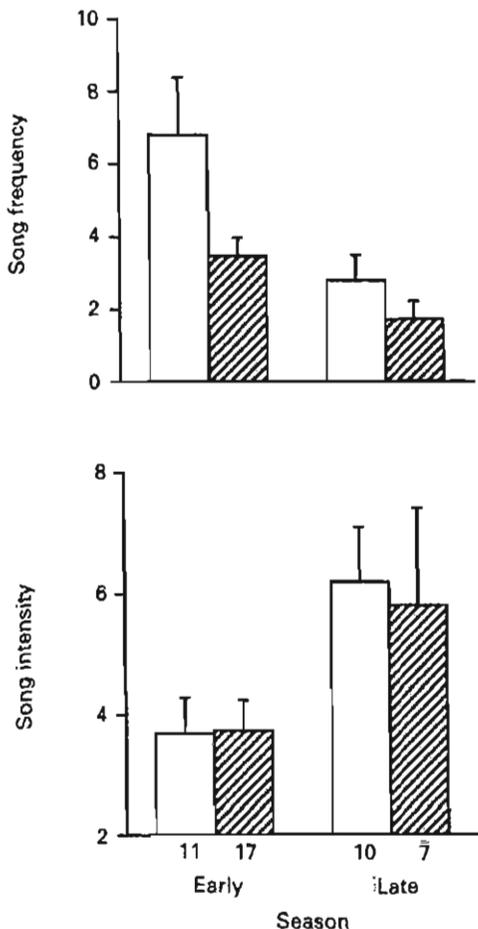


FIG 4.—Comparison of male song frequency (number of 30-s intervals with song strophes / 20 min) and song intensity (mean number of song strophes / 30-s interval / 20 min) of chosen (white bars) and not chosen males (hatched bars) in the early and late breeding season. Given are means (\pm SE).

[Comparación de la frecuencia de canto (número de intervalos de 30 segundos con estrofas de canto / 20 minutos) y de la intensidad de canto (número medio de estrofas / intervalo de 30 segundos / 20 minutos) de machos elegidos (barras blancas) y no elegidos (barras sombreadas) durante la estación de cría temprana y tardía. Se ofrecen los valores medios (\pm ES)].

the reduced importance of insulation capacity later in the season due to a higher and less fluctuating ambient temperature. Here it is assumed that the search for a good quality (large) nest is time and energy consuming (see

Parker, 1983). Besides insulation capacity, this change in female mate choice behaviour might also be influenced by changing mating opportunities (Persson & Öhrström, 1985, 1989; Franz, 1989; Schleicher *et al.*, 1993) or increased competition between mate-seeking females (Dale *et al.*, 1992; Hovi & Rätti, 1994).

In Penduline Tit, both males and females try to become polygamous (Persson & Öhrström, 1985, 1989; Franz, 1989). However, the opportunities for further matings change for males and females throughout the breeding season. Franz (1989) and Persson & Öhrström (1985) showed that early nests are mostly attended by females whereas in the late season males take care of the brood. One explanation for this observation is that males have better mating opportunities in the early breeding season because they can attract further females with additional nests. However, since nest construction is time consuming, to build additional nests later on would exceed the breeding season and therefore decrease male opportunities for additional matings the later they start building. This fact might also explain why the male propensity to attend late broods increases and why females have increasing opportunities to become polyandrous. According to this, females in the «late» season may benefit more by mating with additional males rather than by searching for a high quality nest. So, a «late» season strategy for females is to lay several smaller clutches which are attended by males rather than by incubating a large clutch by themselves (Persson & Öhrström, 1985; Franz, 1989; Hoi *et al.*, 1994). Indications for this include: 1) females generally start egg-laying in early nest building stages in the «late» season, and 2) there is a higher occurrence of clutches in non-completed nests, which are also incubated and do not differ in hatching success (pers. obs.).

In line with this our results suggest that in the «late» breeding season, female mate choice cues seem to be related to the male itself rather than to the nest. This is evidenced by the fact that males with a higher song frequency and song intensity are able to mate earlier (Table 2) and there is also a significant increase in song intensity in the «late» season. However, we could only detect a non-significant trend between chosen and not chosen males in

this regard. This may be due to the fact that sooner or later each male will become mated in the «late» season because 1) the operational sex-ratio is more female biased (due to a higher male propensity for performing parental care) and 2) females are probably less choosy at the end of the «late» season.

Why should female Penduline Tit choose male song features? Since females try to become polyandrous in the «late» season the use of male singing behaviour could be an honest indicator for male energetic condition (Reid, 1987) and for the propensity to provide paternal care (Trivers, 1972; Nisbet, 1977; Borgia, 1985). Grubbauer (1995) could show that singing behaviour of male Penduline Tit reflects male dominance status. This is very likely since singing and dominance behaviour are usually affected by the same physiological stimulator (i.e. testosterone) (Watson & Parr, 1981; Wingfield, 1984). Furthermore, Grubbauer (1995) could also show that male singing behaviour may be an expression of age and hence quality of males (Alatalo *et al.*, 1986b). Male dominance is important for reproductive success in particular to defend the nests against intruders, which may be potential nest material thieves (Schleicher *et al.*, 1993). Therefore, males which are more effective in repelling intruders (with costs of delayed nest building) should be the more attractive ones.

Although song features seem to be important, we surprisingly found a decrease in song frequency in the «late» season (see Fig. 4). Song frequency is mainly used to attract and to keep the female attracted to the nest in cases where intruder males approach the female (pers. obs.; see also Schönfeld, 1994). The occurrence of intruders and male-male competition for the access to females is probably less intense in the «late» season as pointed out earlier and mediated by a decrease in song frequency. The increase of song intensity in the «late» season suggests that this is the important feature for female choice.

Although Franz & Theiss (1983; see also Schönfeld, 1994) suggested that male calling behaviour is used to attract females, it does not seem to be important as a cue for female mate choice.

Concerning male morphology, our results do not indicate any importance of male phy-

sical attributes (see also Franz, 1989; Grubbauer, 1995) for female choice as it has been shown to be in other non-territorial bird species (Andersson, 1982; Borgia, 1987; Hill, 1990). Furthermore, former studies revealed that there is no relationship between nest size and male morphology (unpubl.data) and that nest site quality is also not important in female mate choice in this species (Schleicher, 1993).

Most males Penduline Tit build several nests during one breeding season (Franz, 1989, 1991; Schleicher, 1993). To enhance their reproductive success, males should try to mate as soon as possible to attract further females with additional nests (Franz & Theiss, 1983; Schleicher *et al.*, 1993). Due to female preference for large nests, and because female preference for large nests decreases across the breeding season, males should try to build large nests, moreso in the «early» breeding season. Due to the change in the importance of nest size, one would also expect a shift in male investment in constructing elaborate nests. Nevertheless, we found no seasonal change in nest size throughout the whole breeding season. Moreover, despite the changing ecological factors (e.g. ambient temperature, availability of nest material) across the breeding season, we found a significant and relatively high repeatability in nest size within one male. This result may also be strengthened if we consider that Penduline Tit switch between two different habitat types within one breeding season. So, like in the Village Weaver (*Ploceus cucullatus*) where males show a constancy in nest size (Collias & Collias, 1984), the significant repeatability of successive nests for one single male throughout the breeding season and a high variation between males indicates that nest building ability of males Penduline Tit may also have a genetic determinant.

In summary, we conclude that there are indications for a seasonal shift in female mate choice cues. At low ambient temperatures early in the season, nest size and hence insulation capacity is important in female choice whereas male quality becomes more important late in the season. Interestingly, uniparental male care is also more common late in the season. Both choice cues therefore seem to influence female reproductive success.

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