

# MATE CHOICE IS NOT IMPORTANT FOR FEMALE REPRODUCTIVE SUCCESS IN THE COMMON ROSEFINCH (*CARPODACUS ERYTHRINUS*)

MATS BJÖRKLUND

*Department of Zoology, Uppsala University, Box 561, S-751 22 Uppsala, Sweden*

**ABSTRACT.**—I studied mate choice in relation to female reproductive success in the Common Rosefinch (*Carpodacus erythrinus*) over a four-year period. Approximately 50–99% of the variance in female reproductive success was due to nest predation during incubation. Because males did not defend nest sites and females probably face time constraints, I conclude that they paired unselectively. This is supported by the lack of correlation between male phenotypic characteristics and pairing success and the random pattern in male pairing order. Received 22 March 1989, accepted 12 July 1989.

A CENTRAL issue in the understanding of avian mating systems is female mate choice (Oring 1982). Females are thought to choose in order to maximize fecundity (Halliday 1978, Searcy 1982, Kirkpatrick 1985, Andersson 1986). In species where males defend resources, that means that females primarily choose features such as good feeding territories, safe nesting places, or males' prospective parental effort, or at least cues that indicate such material benefits (Nisbet 1973, 1977; Halliday 1983; Alatalo et al. 1986; Yasukawa et al. 1987). If no immediate benefits are obtained from males (e.g. as in lek species; Vehrencamp and Bradbury 1984), the importance of male genetic quality should increase. Female mate choice may then be based on characters that are indicative of male quality, such as size or song rate (Zahavi 1977; Andersson 1982, 1986; Kodric-Brown and Brown 1984). Finally, if the variation among males in such characters is small, the availability of males is relatively high, and the time available for pairing is short, then nonrandom female mate choice no longer pays, and a random mating pattern in relation to male characteristics is predicted (Parker 1983, Hubbell and Johnson 1987, Lightbody and Weatherhead 1987).

Female choice is best understood from the female point of view. To maximize immediate reproductive success, females are likely to choose males that increase their probability of success. For example, if female reproductive success is determined to a large degree by territory quality, females are expected to choose males on the basis of their territories. Knowledge of the determinants of female reproductive success is therefore crucial in the understanding of fe-

male mate choice. Models of female mate choice commonly assume that females are free to choose among males (Bradbury and Gibson 1983), an assumption that is doubtful if, for example, males form dominance hierarchies (Beehler and Foster 1988). Thus, it is also necessary to examine the freedom of females to choose among males.

The Common Rosefinch (*Carpodacus erythrinus*) is a small (22 g), sexually dimorphic, cardueline finch. The first-year males and females are indistinguishable. Cardueline finches in general maintain only a small territory around the nest, and males do not defend territories before nesting. In contrast to other passerines, they feed their young largely on seeds rather than solely on insects (Newton 1972, Stjernberg 1979, Bozhko 1980). Individuals arrive from their winter quarters to their Swedish breeding areas in late May and begin to breed very soon after arrival.

The song of the Common Rosefinch is short (ca. 1.0 s) and can be classified into discrete songtypes (Björklund in press-a). A male with a particular songtype does not change to another songtype over a season, and songtypes are invariable with regard to number, shape, and ordering of syllables. Hence, males do not have song repertoires which might serve complex communication functions. Further, males do not have any visual displays, except that they select prominent song perches in high trees. Males feed their mates at a low rate during incubation but not during early pairing stages (Stjernberg 1979, pers. obs.).

Autumn migration begins in late July and ends in mid-August. This unusually early mi-

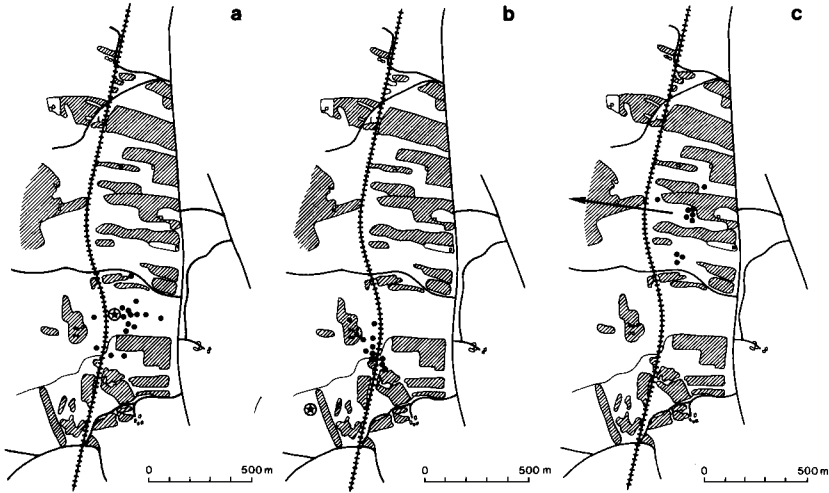


Fig. 1. Examples of the relationship between male song perch (dots) and subsequent nest site (stars) in 1988. Stippled areas are arable land, crossed line is railway, and other lines are roads.

gration is probably related to the fact that post-nuptial molt in the Common Rosefinch (unlike other European passerines) occurs after migration rather than before (Stjernberg 1979), shortening the breeding season considerably.

I studied female mate choice in the Common Rosefinch. In particular, I sought factors that determine female reproductive success and examined whether a choice of mate had an effect. I also examined whether females were free to choose among males and, if so, if they chose among prospective mates or simply accepted the first male they encountered.

#### METHODS

The study was performed at Rättvik, Central Sweden (60°52'N, 15°6'E) during May–July of 1985–1988 in an area of ca. 1.5 km<sup>2</sup>. The study area consists largely of deciduous forest of different height (usually 2–15 m) depending on the successional stage (Fig. 1). Pastures and newly abandoned pastures together with arable land constitute the remainder. In the abandoned pastures and the clear cuttings, there are scattered bushes usually 1–2 m in height. The bushes and trees are mainly willow (*Salix* spp.), birch (*Betula* spp.), aspen (*Populus tremula*), alder (*Alnus incana*), and bird-cherry (*Prunus padus*). Of special importance is the very rich abundance of currant bushes (*Ribes rubrum*) in which many of the nests were placed. The study area is a part of a larger area with arable land and gardens. Rosefinches, usually single males, occurred in these areas at very low densities.

As males arrived, they were caught (usually the

same morning), measured, and individually color-banded. I measured wing length (flattened), tail length, tarsus length (measured as the distance between the extreme bending points at the intertarsal joint and the toes), bill length, width, and depth (measured at the front of the nostrils). In 1988, plumage variability was recorded. Among males older than 1 yr, the throat, breast, and rump were always bright red, while the belly was either white or light red (never as intense as the breast). The head, tail, back, coverts, and remiges varied from no red to light red to bright red. Males were classified as having a high brightness if at least two of these body parts were bright red, and as having low brightness otherwise.

No females were caught. They did not respond to playback, as males did; and to avoid desertions, I did not try capture at the nest. Males captured in one year did not respond to playback the next year, although different tapes were used.

Males were observed, for 5-min periods with at least 30-min intervals, between 0300 (sunrise) and 1000. Only marked birds were followed. Numbers of songs and fights were recorded. Each male was observed several times per day during the pre-pairing and pre-nesting periods. Nestlings were banded and weighed on the sixth day after hatching, because open-nesting passerines' young can prematurely desert the nest upon disturbance (Stjernberg 1979). Occasionally, upon banding, the biggest chick tried to desert, but it was forced to stay by putting the other chicks on top of it. No further visits to the nest were made. I observed feeding frequency for 1 h at each nest each morning (days 1–6), a total of 88 h over 2 yr (1987–1988). In 1988, I followed 13 pairs for up to 30 min. The distance between the pair members and their activity were recorded every other minute. Move-

TABLE 1. Eigenvector loadings and variance explained for principal components extracted from a correlation matrix of body and bill characters.

Character	Principal component		
	1	2	3
<b>Body</b>			
Tarsus length	0.577	0.470	0.753
Wing length	0.577	0.530	0.658
Tail length	0.577	-0.703	0.0063
% Variance	47.8	35.1	17.1
<b>Bill</b>			
Length	0.577	0.738	0.086
Depth	0.577	-0.596	0.547
Width	0.577	-0.315	-0.833
% Variance	40.7	36.1	23.0

ments were divided into short (<20 m) and long (>20 m), and the member of the pair that initiated a movement was noted. We used a Sony Walkman Professional WM-D6C tape recorder with a Sennheiser ME-80 microphone to record males' singing upon arrival. Songs were analyzed by a UNISCAN sonograph.

To calculate body and bill size and shape, the principal components analysis (PCA) developed by Somers (1986) was used. Unlike ordinary PCAs, it produces an isometric vector of size (first principal component rather than an allometric) with all characters that describe size loaded equally without any shape component. The second and third components describe shape in body and bill, respectively, after the effect of size has been removed (Table 1). The PCA is based on 80 males. As a measure of pairing success of males, I used the residuals from the regression of pairing date on the arrival date, which is the deviation (in days) from the expected value of an average male arriving on a particular date. Hence, the term *pairing success* implies not how many females a male might attract but the relative order in which he is paired, controlling for the average delay for males that is due to the later arrival of females. The residuals were back-correlated with the *x*-variable (arrival date) to ensure that pairing success was not related to arrival date per se (Table 2).

The variance in female reproductive success was studied by calculating the opportunity for selection

(*I*) partitioned into episodes of selection (Arnold and Wade 1984). These episodes were variance in number of eggs laid ( $W_1$ ), variance in number of eggs that hatched ( $W_2$ ), and variance in number of young that reached 6 days of age ( $W_3$ ), which was used as the measure of fitness.

## RESULTS

*General breeding behavior.*—On average, males arrived 3–4 days before females (1985: male median date of arrival was 22 May, female 26 May,  $P = 0.015$ ,  $n = 19$ , two-tailed Mann-Whitney *U*-test; 1986: male 26 May, female 30 May,  $P = 0.020$ ,  $n = 31$ ; 1987: male 27 May, female 30 May,  $P = 0.027$ ,  $n = 28$ ; 1988: male 24 May, female 25 May,  $P = 0.012$ ,  $n = 24$ ). In general, arrival date accounts for most of the variance in pairing date (Table 2). The mean ( $\pm$ SE) number of days between arrival and pairing (controlling for the later arrival of females) was  $1.6 \pm 0.25$  days,  $n = 19$  in 1985,  $1.8 \pm 0.22$  days,  $n = 31$  in 1986,  $1.3 \pm 0.19$  days,  $n = 28$  in 1987, and  $1.1 \pm 0.20$  days,  $n = 24$  in 1988 (Fig. 2). Most males were unpaired for only a short period. Because of the earlier arrival of males, there were nearly always more males present than females, and newly arrived females could choose among several males (Fig 3). The pairing process is rapid and single females were not observed during the 4 yr of study.

Nest building and egg laying begin on average 9.3 days (SD = 3.03,  $n = 41$ , all years combined) after pairing. Because there was little variation in time between pairing and laying of the first egg, earlier pairing results in earlier egg laying. I observed no cases where males participated in nest building.

I observed 19 males in 1985, 31 in 1986, 28 in 1987, and 27 in 1988, all of which became paired. An important fact is that the number of first-year males (recognizable by the femalelike plumage) was very low: only 2–4 advertising males were present each year (Björklund in

TABLE 2. Regressions of arrival date (*x*) on pairing date (*y*) of Common Rosefinch males in 1985–1988.

Year	Model	<i>r</i>	<i>F</i>	df	<i>P</i>	Residuals vs. arrival	
						<i>r<sub>s</sub></i>	<i>P</i>
1985	$y = 0.73x + 10.07$	0.88	57.33	1, 17	<0.0001	-0.14	>0.50
1986	$y = 0.86x + 6.23$	0.87	87.03	1, 29	<0.0001	0.12	>0.50
1987	$y = 0.77x + 8.77$	0.85	68.69	1, 25	<0.0001	0.06	>0.50
1988	$y = 0.55x + 12.83$	0.73	24.45	1, 22	<0.0001	-0.05	>0.50

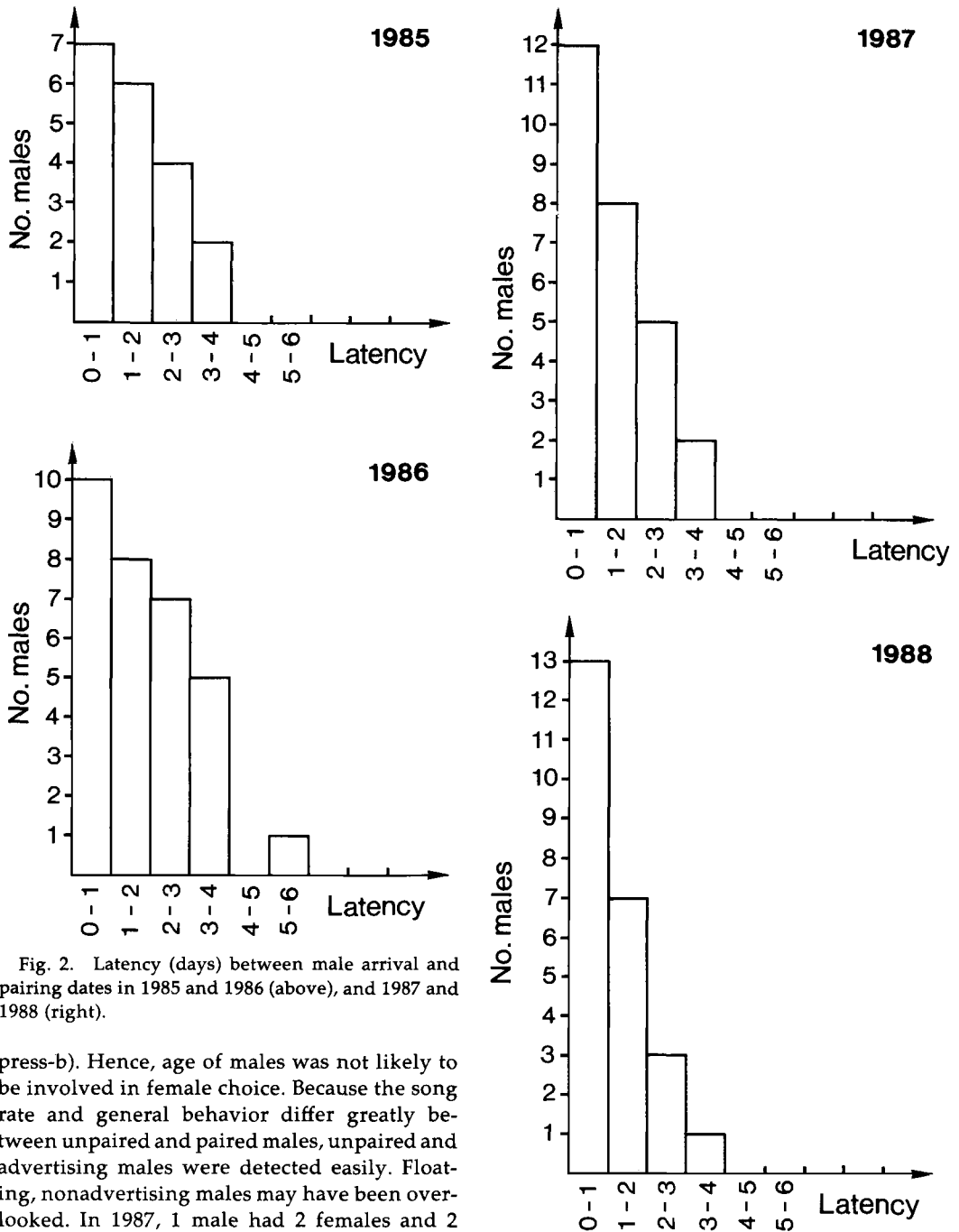


Fig. 2. Latency (days) between male arrival and pairing dates in 1985 and 1986 (above), and 1987 and 1988 (right).

press-b). Hence, age of males was not likely to be involved in female choice. Because the song rate and general behavior differ greatly between unpaired and paired males, unpaired and advertising males were detected easily. Floating, nonadvertising males may have been overlooked. In 1987, 1 male had 2 females and 2 nests. When paired, males greatly reduced their singing rates, and some even stopped singing altogether (1985: unpaired males  $\bar{x} \pm SE = 8.01 \pm 0.67$  strophes/min, paired males  $\bar{x} = 4.16 \pm 0.75$ ,  $F = 11.60$ ,  $df = 1, 190$ ,  $P < 0.001$ , tested against within-male variance; 1986: unpaired males  $\bar{x} = 8.30 \pm 0.59$ , paired males  $\bar{x} = 5.34 \pm$

$0.67$ ,  $F = 4.89$ ,  $df = 1, 275$ ,  $P < 0.001$ ; 1987: unpaired males  $\bar{x} = 7.94 \pm 0.52$ , paired males  $\bar{x} = 4.38 \pm 0.65$ ,  $F = 5.45$ ,  $df = 1, 200$ ,  $P < 0.001$ ; 1988: unpaired males  $\bar{x} = 7.78 \pm 0.27$ , paired

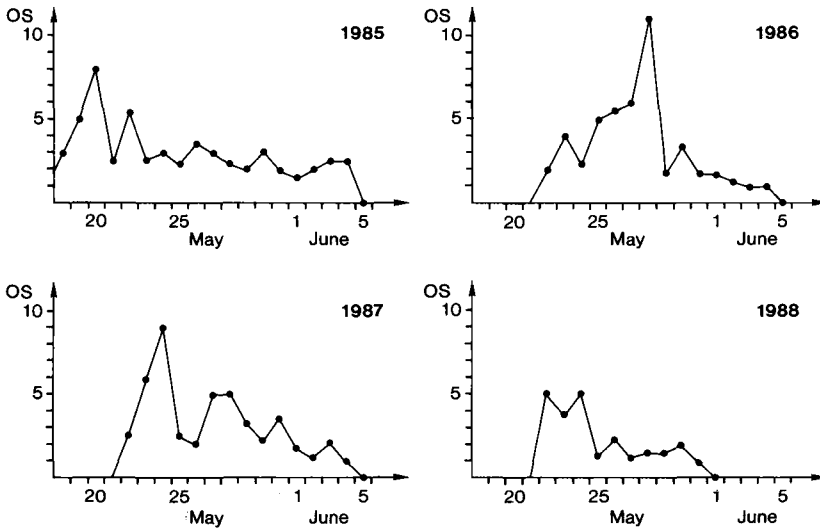


Fig. 3. Numbers of males available during the season measured as operational sex ratio (OS). OS = (No. males + 1)/(No. females arriving + 1).

males  $\bar{x} = 2.52 \pm 0.39$ ,  $F = 150.03$ ,  $df = 1, 138$ ,  $P < 0.001$ ). All males, including the bigamous male, started to sing again during egg laying and moved away from the nest during incubation, presumably to attract another female. Because many males left the study area during incubation, the number of females per male was probably underestimated. The distance moved could be considerable: one male (in 1987) sang 3 km from its first nest. All males, however, regularly visited the nesting females and later helped in feeding the young.

Males guarded their mates intensely. Overall, 862 min of observations were gathered ( $\bar{x} \pm SD = 63 \text{ min} \pm 41.1$ ,  $n = 13$  pairs, range 20–146 min/pair). Males were observed farther than 20 m from their mates ca. 22.5% of the time ( $SD = 16.4$ , range 0–56.3%,  $n = 13$  males). Further, when males initiated long movements, females followed the males in 31.6% (24/76) of the cases; but, when females initiated such a movement, their mates followed in 85.4% (74/87) of the cases ( $\chi^2 = 45.0$ ,  $P < 0.001$ ). There were no differences in initiation of short (53.8% for males vs. 46.2% for females,  $\chi^2 = 1.31$ ,  $P > 0.10$ ) or long movements (46.6% for males vs. 53.4% for females,  $\chi^2 = 0.37$ ,  $P > 0.10$ ). When males lost contact with their females, they started to sing (relative song frequency <20 m away: 28.7%, >20 m away: 76.8%,  $P < 0.025$ ,  $T = 77$ , Wilcoxon test, two-tailed).

*Determinants of female reproductive success.*—

The most important component of variance in female reproductive success was the number of eggs hatching (Table 3). This variation was due to predation, and each year ca. 37% of the nests were destroyed (Björklund in press-b). Nests close (<20 m) to an edge were much more likely to fail than nests farther away (Björklund in press-b). It is incumbent on females to choose safe breeding sites. It is therefore important to analyze if males defend such sites and if females choose males on the basis of safe nest sites.

Common Rosefinch males do not defend exclusive feeding territories (Newton 1972, Stjernberg 1979), but song perches were defended to some degree (two males rarely sang in the same tree at the same time). After pairing, two pairs might forage simultaneously in the same large tree. Song perches were in higher than average trees, in solitary bushes in open fields, on wires, and near forest edges. Nests were not necessarily near these song perches (see Fig. 1 for 3 examples). In many cases the pair moved away after pairing, often considerable distances (Stjernberg 1979). They were usually seen in the area on the first few days after pairing but, with time, moved farther away from the song perch (which might then be used by another male). This happened in 4/19 (21%) cases in 1985, 19/31 (62%) in males 1986, 16/28 (57%) in 1987, and 16/27 (59%) cases in 1988. I suggest (see Table 4) that females chose nest sites without regard to the position of male song

TABLE 3. Female reproductive success in 1985–1988. Sample sizes are in parentheses. *W* is fitness, *V* is variance, and *I* is opportunity for selection.

	1985 (13)		1986 (10)		1987 (13)		1988 (13)	
<b>Number of eggs laid</b>								
$\bar{W}_1$	5.08		4.90		5.00		5.08	
$V_{w_1}$	0.078		0.100		0.167		0.077	
$I_1$	0.0030	0.91%	0.0042	0.55%	0.0067	0.76%	0.0030	0.36%
<b>Number of eggs hatched</b>								
$\bar{W}_2$	3.85		3.00		3.00		3.64	
$V_{w_2}$	4.81		6.67		6.17		5.79	
$I_2$	0.324	98.1%	0.741	98.5%	0.685	78.6%	0.437	52.4%
<b>Number of 6-day-old young</b>								
$\bar{W}_3$	3.77		2.90		2.46		3.00	
$V_{w_3}$	4.69		6.32		4.94		5.54	
$I_3$	0.330		0.752		0.871		0.834	

perches. Thus, prospective nest sites were not defended by unpaired males, and females were not likely to choose males on the basis of resources males held or behavior.

In 1987 and 1988, a considerable proportion of variance in female reproductive success was due to a difference in the number of young reaching day 6. These losses were due either to unhatched eggs or to chicks that died at a very early stage. The number of chicks at first check (nearly always day 0) did not differ from the number of young that reached day 6. In one case, a nest was destroyed at day 5. The causes and frequency of unhatched eggs (failure to develop or not fertilized) were unknown. Newly hatched, unfeathered chicks are vulnerable to bad weather. In 1987, mean temperature during hatching period was ca. 5°C below normal (data from local national weather station), so if females were away during hatching, these losses could be due to environmental causes. It is therefore important to analyze whether the amount of paternal care is predictable from a male's behavior before pairing and if the amount of paternal care influences the quality of the young.

Common Rosefinches feed their nestlings largely on seeds. Mean feeding rate was  $\bar{x} \pm SE = 0.8 \pm 0.09$  feedings per hour (range 0.4–1.2,  $n = 9$  pairs) for females, and  $0.6 \pm 0.10$  feedings per hour (range 0.2–1.2) for males in 1987 ( $P = 0.05$ , sign test). In 1988, mean feeding rate was  $0.7 \pm 0.09$  feedings per hour (range 0.4–1.3,  $n = 9$  pairs) for females, and  $1.0 \pm 0.07$  feedings per hour for males (range 0.7–1.4,  $P = 0.10$ , Wilcoxon test, two-tailed). Although male parental

care probably does not influence the actual number of fledged young (see above), it can influence the condition of the young. If so, a positive correlation between male feeding rate and mean brood mass is expected when brood size and female feeding rate are held constant. Because male or female feeding rates, or mean brood mass (male feedings  $\cdot h^{-1} \cdot young^{-1}$  1987:  $\bar{x} \pm SD = 0.18 \pm 0.079$ ,  $n = 8$ , 1988:  $\bar{x} = 0.20 \pm 0.034$ ,  $n = 8$ ,  $P > 0.10$ , *U*-test; female feedings  $\cdot h^{-1} \cdot young^{-1}$  1987:  $\bar{x} = 0.21 \pm 0.084$ ,  $n = 8$ , 1988:  $\bar{x} = 0.15 \pm 0.078$ ,  $P > 0.10$ , *U*-test; mean brood weight 1987:  $\bar{x} \pm SD = 17.11 \pm 1.50$ ,  $n = 8$ , 1988:  $\bar{x} = 15.66 \pm 1.33$ ,  $n = 8$ ,  $P > 0.10$ , *U*-test, tests in all cases two-tailed), did not differ among years, data were pooled. Male feedings per hour for each young was not correlated with mean brood mass ( $r = 0.078$ ,  $n = 16$ ,  $P > 0.10$ ), nor was female feedings per hour for each young ( $r = 0.056$ ,  $n = 16$ ,  $P > 0.10$ ), nor male and female

TABLE 4. Distance between nesting site and the male's song perch. Figures given are number (*n*) of nests found and number (*n*\*) of nests including disappearing pairs assuming that these nests are >200 m from the song perch.

Distance class (m)	<i>n</i>	%	<i>n</i> *	%
<50	25	44.6	25	26.3
50–100 <sup>a</sup>	10	17.9	10	10.5
100–150	8	14.3	8	8.4
150–200 <sup>b</sup>	4	7.1	4	4.2
>200	9	16.1	48	50.5

<sup>a</sup> Median distance.

<sup>b</sup> Median distance including the disappearing pairs assuming that they nest >200 m from the song perch.

TABLE 5. Product-moment correlations between pairing success and male characteristics in 1985–1988. Numbers in parentheses following each year are sample sizes; if different from year sample size,  $n$  follows value.

Character	Pairing success			
	1985 (19)	1986 (28)	1987 (31)	1988 (20)
Body				
PC1	0.13	0.12	-0.02	-0.13
PC2	-0.11	-0.049	-0.21	-0.28
PC3	-0.11	-0.10	-0.048	0.33
Bill				
PC1	0.18	0.16	0.032	-0.15
PC2	-0.012	-0.094	0.32	0.31
PC3	0.17	-0.12	-0.042	-0.21
Song rate	0.11	-0.16	-0.39*	0.02
Mean frequency (kHz)	—	0.17 (26)	-0.15 (22)	0.31 (17)
Strophe length (s)	—	-0.13 (26)	0.11 (22)	0.27 (17)

\*  $P < 0.05$ .

feeding rate combined ( $r = -0.14$ ,  $n = 16$ ,  $P > 0.10$ ). The partial correlation of male feeding rate and mean brood mass, holding female feeding rate constant, was not significant ( $r = -0.14$ ,  $n = 16$ ,  $P > 0.10$ ). Hence, the actual male feeding rate did not influence the condition of the young. This does not necessarily mean that paternal care is unimportant, only that the variation in feeding rate is. I conclude that females are unlikely to exert mate choice on the basis of fine-level prospective paternal care.

*Female choice and male phenotypic characteristics.*—Females probably did not benefit materially from mate choice. This suggests that choice based on the genetic quality of males can be of greater importance. For genetic quality to be an important factor in mate choice requires a variance in genetic quality of males. This variance must be correlated with some phenotypic trait that is easily perceived by females, and females must have time to choose among males. There was a significant variation in song rate among males (1985:  $F = 5.56$ ,  $df = 15$ , 190; 1986:  $F = 4.05$ ,  $df = 31$ , 275; 1987:  $F = 2.33$ ,  $df = 26$ , 200; 1988:  $F = 1.04$ ,  $df = 21$ , 138, all years except 1988  $P < 0.001$ , ANOVA), but song rate correlated with pairing success only in 1987, where there was a negative correlation between song rate and pairing success (Table 5). In 1988, there was no significant between-male variation in song rate, probably because many males did not sing before pairing. No other morphological or behavioral characteristic that was measured correlates with pairing success in any year (Table 5).

Unfortunately, variation in plumage color was

recorded only in 1988, and only on males caught that year (males were not recaptured from previous years, see Methods). There was no relationship between pairing success and male plumage brightness (high:  $\bar{x} \pm SD = 0.65 \pm 1.29$ ,  $n = 5$ ; low:  $\bar{x} = 0.87 \pm 2.33$ ,  $n = 5$ ,  $P > 0.10$ , Mann-Whitney  $U$ -test). Thus, it is unlikely that females chose mates according to phenotypic variation in plumage.

If male dominance interferes with active female choice, then we would expect a correlation between pairing success and dominance in males. In the Common Rosefinch, size is a character determining dominance (Björklund 1989), and correlations between size and pairing success are expected. No such correlations were found (Table 5). It is likely that females are not constrained by male dominance to pair with the first unpaired, advertising male they happen to encounter upon arrival. Unconstrained and nonselective female choice would cause the variation in male pairing success to be random, and the distribution of number of days between arrival and pairing among males would be distributed randomly.

In all 4 yr, the number of days between male arrival and pairing (the later arrival of females controlled for) was not significantly different from a Poisson distribution (Poisson was used because mean and variance in latency were equal, see above, 1985:  $D = 0.16$ ,  $P > 0.10$ ,  $n = 17$ ; 1986:  $D = 0.15$ ,  $P > 0.10$ ,  $n = 31$ ; 1987:  $D = 0.18$ ,  $P > 0.10$ ,  $n = 28$ ; 1988:  $D = 0.21$ ,  $P > 0.10$ ,  $n = 24$ ) (Fig. 2). This also held for female arrival (1985:  $D = 0.069$ ,  $P > 0.10$ ,  $n = 17$  days; 1986:  $D = 0.13$ ,  $P > 0.10$ ,  $n = 13$ ; 1987:  $D = 0.09$ ,  $P >$

0.10,  $n = 11$ ; 1988:  $D = 0.21$ ,  $P > 0.10$ ,  $n = 10$ , Kolmogorov-Smirnoff test). Thus, the timing of pair formation in the Common Rosefinch can be regarded as a random process.

#### DISCUSSION

Females' reproductive success was largely determined by choice of nest site, which was unrelated to male behavior. The probability of success was independent of male physical characteristics or behavior. Consequently, I expected pairing to be random with regard to these characteristics: exactly what I found. However, the number of females per male was far from random. If females chose the first male they encountered, whether paired or unpaired, the number of females per male would be normally (Poisson) distributed (Sutherland 1985). Then, with a similar mean number of females per male ( $=1.0$ ), we would expect to find approximately equal proportions (1/3) of bachelors, monogamously paired males, and polygynously mated males. This was not the case in this population, where monogamy was the rule. Thus, females almost invariably chose unpaired males.

The frequency of polygyny can be underestimated. Common Rosefinch males resume singing and move away from the nest site around the onset of incubation; in some cases they move considerable distances (Stjernberg 1979). Two other questions (why females prefer to mate with unpaired males and why males resume singing in another place) are still open.

Female preference for unpaired males may result because males reduce or discontinue their singing after pairing. Consequently, newly arrived females may fail to find the relatively silent, paired males. One reason males reduce or stop singing when paired is mate guarding. Males that continue to sing from their perches cannot simultaneously guard their mates from extrapair copulations. Further, a singing, paired male may attract not only newly arrived females but also other males (Alatalo et al. 1982), which may lead to extrapair copulations. Mate guarding by the male is certainly important in the Common Rosefinch. Because males do not defend exclusive territories, which may help to reduce the frequency of extrapair copulation attempts (Møller 1987), paired males should stay near the female until after laying to guard against insemination by other males. Paired Common Rosefinch females are courted by oth-

er males, but their mates usually are not far away, and I never observed extrapair copulations. Thus, a decreased song rate can reduce the risk of extrapair copulations. The importance of mate guarding may also be the cause of the departure of pairs from the area soon after pair formation. Pairs may leave areas where the density of males is high to avoid harassment from other males.

The fact that the number of young or mean brood mass was not correlated with male parental care does not necessarily mean that the contribution of the male is unimportant. Because young are fed so seldom, growth is unlikely to be determined by the number of parental feeding trips. Instead, absence of a male during the nestling period may affect the time females can brood the young, which in turn can affect the survival of the young. This may explain female preference for unpaired males. Similarly, female preference for unpaired males may explain male movement away from the nest to seek subsequent mates (Alatalo et al. 1981).

Lightbody and Weatherhead (1987) argued that female choice can be regarded as neutral with regard to males or their territories if a number of conditions are met. Although these conditions were derived from the polygyny threshold model for the evolution of polygyny, they apply to mate choice in predominantly monogamous species as well. Six conditions are necessary: (1) females do not interact competitively or cooperatively while settling, (2) food supply in the territory is unimportant, (3) nest sites are not limited, (4) variation in territory features is not correlated with variation in female reproductive success, (5) variation in male "quality" is unrelated to female choice, and (6) paternal care is not necessary for female reproductive success.

The Common Rosefinch feeds in a large area around the nest, evidently up to several kilometers away (Stjernberg 1979). Furthermore, nest sites are by no means limited, and variation in male quality is unrelated to female choice, thus satisfying conditions 2, 3, and 5. Females occasionally fight after pairing and, because territories are established only after nest building, female interactions are unlikely to influence settling; this meets condition 1.

The main influence on female reproductive success was the probability of predation and this may suggest that territory quality is related to female choice. However, territories were es-



tablished only after nest building, and it is highly likely that females choose the nest site rather than the male (Björklund unpubl.). The choice of nest site is also unrelated to male movements before pairing, which satisfies condition 4. Finally, I demonstrated that paternal care was unrelated to the number of fledged young and that prospective paternal care was unpredictable from male premating behavior.

I believe that female choice in the Common Rosefinch is essentially neutral. At present, the frequency of neutral female choice is unknown, but Lightbody and Weatherhead (1987) cite studies where the postulated criteria are partially met. I suggest that it may be more common than assumed previously, and that it certainly is worth further study.

One factor likely to strongly influence the degree of choice is time, because it greatly influences the cost of searching for a mate (Alatalo et al. 1988, Slagsvold et al. 1988). Time constraints have been suggested as an explanation for a male Pied Flycatcher's (*Ficedula hypoleuca*) ability to obtain two females although he generally provides care for only one brood (Alatalo et al. 1981, 1986; Alatalo and Lundberg 1984; Slagsvold et al. 1988). Male Pied Flycatchers defend two or more territories (i.e. nest holes), generally quite a distance apart. Female choice in the Pied Flycatcher is probably not neutral because males defend a resource essential for reproduction, i.e. the nest hole. Subsequently, it has been shown that females choose among available nest holes rather than among males (Alatalo et al. 1986), although under certain circumstances features of the males defending these holes may have some influence on female choice (Slagsvold et al. 1988).

The influence of time differs between these two species. In the Pied Flycatcher, the clutch size decreases with time, and, under natural conditions, the availability of suitable nest holes is limited (Alatalo et al. 1981, and others). Consequently, the cost of searching for mates is related to an expected brood size decreasing with time. In the Common Rosefinch, the situation is more drastic. The pairing period is short and unpredictable, and females may end up unpaired if they spend excessive time choosing. The breeding season is also shortened because the Common Rosefinch arrives at the breeding ground ca. 3 weeks later than the Pied Flycatcher (Alatalo et al. 1981), and autumn departure starts early (late July to early August). This means

that the period to raise a brood and to gain energy for the migration is much shorter than most Holarctic migrating passerines.

The main influence on female reproductive success in Common Rosefinches was the probability of predation during incubation. In fact, given the circumstances under which broods fail, I concluded that predation was on females rather than eggs (Björklund unpubl.). The only pattern found was that nests close to an edge between bush land and arable land were much more susceptible than nests farther away from such an edge. There is thus considerable pressure on females to choose safe nest sites. Generally, females choose nest sites that are covered by leaves, which make it difficult for an airborne predator to locate (Björklund unpubl.). Conversely, cats and mustelids regularly patrolled these edges after dark. Female Common Rosefinches are known to stay on the nest when approached (Stjernberg 1979, Bozhko 1980). This may be fatal when the predator is a cat. It is worth noticing that this population is less than 25 yr old, and the predation pattern may be different from the pattern elsewhere. Thus, females choose nest sites according to one rule, although there are other rules that may be at least equally important. This creates a high variance in reproductive success in the population.

I conclude that pair formation in the Common Rosefinch is a random process with regard to male characteristics based on two facts. First, female reproductive success is unrelated to any resources males control, and females do not choose males on the basis of material benefits either controlled by the male (such as territory) or correlated with male quality (feeding rates). Second, because the number of arriving females cannot be predicted from one day to the next, the number of available males from which to choose is unpredictable. A hesitant female may end up unpaired, because the time available for pair formation is limited. These facts, and subsequent behavior, promote fast decisions and a low degree of selectivity.

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