

Mate choice by males from lines of Japanese Quail selected for male mating frequency

2. Preferences among plumage colors

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Key words : Mate choice. Japanese quail. Plumage colors.

RESUME

Le choix sexuel chez les coqs appartenant aux lignées de cailles japonaises sélectionnées pour leur fréquence d'accouplement. 2 - Préférences parmi les couleurs de plumage.

On a observé le choix du partenaire sexuel chez les coqs appartenant à des lignées de cailles japonaises sélectionnées pour une haute (H) ou une basse (L) fréquence d'accouplement et la lignée témoin (C), qui avait servi à la création des populations sélectionnées. Dès l'éclosion, les coqs au plumage d'une coloration de type sauvage sont élevés soit avec un groupe de coloration entièrement de type sauvage, soit avec un groupe de coloration mixte, composé de types sauvages et de mutants (albinos ou jaunes). Lors de la maturité, ils ont été soumis à des tests de choix simultané du partenaire entre des femelles de type sauvage et de l'un des types mutants. Quelle que soit la lignée ou le mode d'élevage, les coqs ont préféré les poules de type sauvage au type albinos. Ils n'ont pas montré de préférence entre les poules de type sauvage et jaune. Les coqs sélectionnés pour une haute ou une basse fréquence d'accouplement restent capables de distinguer entre les phénotypes de plumage femelles.

Mots clés : Choix du partenaire sexuel. Cailles japonaises. Couleurs de plumage.

SUMMARY

Mate choice by male Japanese quail were observed in lines genetically selected for high (H) or low (L) mating frequency and the control (C) line which served as the base for the selected populations. Males with wildtype plumage

Reçu le : 9 août 1983. *Accepté le* : 22 octobre 1983.

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coloration were assigned at hatch either to all-wildtype or wildtype and plumage mutant flocks (albino or yellow). When mature, simultaneous mate choice tests between wildtype and one of the plumage mutant females were given. Regardless of line or rearing experience, males preferred wildtype to albino hens. They did not exhibit a preference between wildtype and yellow hens. Males genetically selected either for high or low mating frequency maintain the ability to distinguish among female plumage phenotypes.

Although natural history studies indicate that Japanese quail utilize a monogamous mating system, promiscuity is generally observed in laboratory settings (Kovach, 1974). Mating behavior of male Japanese quail is routinely measured under laboratory situations (Ottinger, Schleidt, and Russek, 1982), and its frequency can be changed via artificial selection (Blohowiak and Siegel, 1983 a).

Mate choice relies on both genetic and learning components (Gallagher, 1978 ; Cooke, 1980). Innate releasing mechanisms, which Lorenz (1981) defined as " simple stimulus configurations whose releasing functions, obeying the laws of heterogeneous summation, add up to a qualitatively unitary effect ", may interact with environmental experiences in terms of open genetic programs described by Mayr (1974) thereby allowing for adaptive modification. There is considerable evidence that sexual imprinting and experience influence mate choice of Japanese quail (Bateson, 1978, 1979 ; Gallagher, 1978), with males generally exhibiting a preference for either hens of their own plumage phenotype, those of a similar plumage color, or those with which they were raised (Truax and Siegel, 1982 ; Blohowiak and Siegel, 1983 b).

Males of some species exhibiting promiscuous mating behavior appear to be indiscriminating in their choice of mates. This may be attributed to their higher levels of aggression, higher sex drives and lower thresholds of response to female releasers (Selander, 1972). Other studies, however, show that gallinaceous birds such as the domestic fowl (Lill, 1968) and the Japanese quail (Truax and Siegel, 1982) distinguish among mates by means of plumage coloration.

The objective of the experiment reported here was to examine mate choice of male Japanese quail (*Coturnix coturnix japonica*) from lines genetically selected for high and low male mating frequency. Choices included females with the same plumage type as the male versus other plumage phenotypes, which were either familiar (had early social experience with) or unfamiliar (no early social experience).

METHODS

Random samples of 28th and 29th generation (S_{28} and S_{29}) males from replicated lines selected for high (H) and low (L) mating frequency and the rambred control line (C) which served as the base population for the selected lines were used in this experiment. Although details of these lines have been

reported (Blohowiak and Siegel, 1983 a), a few points should be stated. Mating frequency by the control line has not changed over the period of this selection experiment. Chi-square tests demonstrated no differences between replicates, therefore, data for the replicates were pooled for analysis. The selected and control populations are quite different, not only in their frequency of mating (S_{28} generation means were 31, 10 and 1 for the H, C and L lines), but also as to whether or not males will mate. For example, in the S_{28} generation 3, 9, and 73 % of the males from the H, C, and L lines, respectively, were classified as nonmaters on the basis of their failure to mate in eight 8-minute trials. Reproduction of the lines is by natural mating.

All males used in this experiment had wildtype plumage. Females included wildtypes and the plumage mutants true albino and yellow, which is similar to the wildtype in markings while the base color is golden (Truax and Johnson, 1979). The mutant alleles had been introduced into a sample of the C line and maintained in the population via repeated backcrossing. These genotypes are now reproduced as closed populations.

An initial trial involved testing S_{28} males from the H, L and C populations. All males were hatched on the same day and raised in heterosexual flocks ($n = 80$, each) with wildtype flockmates until 28 days of age, at which time sexes were separated. A random sample of 15 males per line were tested in this trial. Each male had previous mating experience with wildtype females, during mating trials for the genetic selection of the lines; however, they were visually isolated from albinos until 85 days of age. At this time a series of four tests consisting of a simultaneous choice between an albino and a wildtype hen were given. The choice was presented among 24 neutral test cages measuring 25×34 cm. Hens were maintained in these cages and also had previous mating experience with wildtype males during the genetic selection trials. Males were tested randomly among four of the 24 choices. Attempts with each hen were recorded until a mating was completed, or for a maximum of one minute.

A second trial was designed to provide early social experience, without mating experience prior to testing. S_{29} males were randomly assigned at hatching to heterosexual flocks which provided experience with either all-wildtype, wildtype and yellow, or wildtype and albino flockmates. These flocks were reared in separate pens so that each flock was in visual isolation from the others. The number of males per line and experience are presented in *tables I, II, and III*. Plumage mutants were reared with each line so that there was a 2 : 1 ratio of wildtype to plumage mutant, and the number of wildtype males to wildtype females 1 : 1. At 32 days of age the wildtype males from the selected and control lines were removed from their rearing flocks and placed in unisexual groups. Mating preference tests as described for the initial trial, were conducted when the males were 63 and 64 days of age. Each male was given a series of simultaneous choices, four between an albino and a wildtype hen and four between a yellow and a wildtype hen. Placement of males with females was randomized within a color choice and similar to the tests of Trial 1. Tester hens were random samples of those raised in the mixed flocks so that all had early social, but not mating, experience with wildtype males.

For both trials, the cumulative number of attempted and completed matings across four tests were recorded according to plumage color of the hens and analyzed by binomial distribution with Yates' correction for small numbers (Ehrman and Parsons, 1981). Since non-independent hypotheses (total attempts and completions) were being tested on the same populations, a $\text{Tau} = 2$ was assigned for the Chi-square values in generation S_{28} and $\text{Tau} = 4$ was assigned in S_{29} (Jensen, Beus, and Storm, 1968).

RESULTS

In both generations males raised in all-wildtype flocks attempted and completed significantly more matings with wildtype than with albino hens (*table I*). This pattern was noted in all three lines with the exception of S₂₉ low-line males who completed few matings; in this case all matings were with wildtype hens.

High and control line males raised in mixed flocks of wildtype and yellow or wildtype and albino significantly ($p \leq 0.01$) preferred wildtype to albino hens (*table II*). Even those males raised with albinos avoided

Table I: *Mate preferences by lines of wildtype males raised in all-wildtype flocks for wildtype or albino hens.*

Tableau I : *Choix sexuel entre les poules de type sauvage ou albinos des lignées de coqs de type sauvage élevées dans les groupes « coloration sauvage ».*

Line	Gen	N	R	Frequency of mating			
				Attempts		Completions	
				A	W	A	W
High	S ₂₈	30	26	21	144**	4	85**
	S ₂₉	20	20	17	124**	5	73**
Control	S ₂₈	15	14	16	73**	4	40**
	S ₂₉	10	8	5	32**	2	21**
Low	S ₂₈	30	11	0	29**	0	13**
	S ₂₉	20	6	1	13**	0	3

** $p \leq 0.01$.

N = no. of males tested; R = no. of males responding.

A = albino; W = wildtype.

Table II: *Mate preferences by lines of wildtype males raised in wildtype and yellow or wildtype and albino flocks for wildtype or albino hens, S₂₉.*

Tableau II : *Choix sexuel entre les poules de type sauvage ou albinos des lignées de coqs de type sauvage élevées dans les groupes « coloration mixte » (sauvage/jaune ou sauvage/albinos), S₂₉.*

Expe- rience	Line	N	R	Frequency of mating			
				Attempts		Completions	
				A	W	A	W
Wild and Yellow	High	17	16	7	51**	0	26**
	Control	10	7	1	17**	0	9*
	Low	5	4	1	3	0	0
Wild and Albino	High	18	14	1	49**	1	19**
	Control	13	5	7	24**	1	1
	Low	17	1	3	1	0	0

** $p \leq 0.01$; * $p \leq 0.05$.

N = no. of males tested; R = no. of males responding.

A = albino; W = wildtype.

Table III : Mate preferences by lines of wildtype males raised in all-wildtype, wildtype and yellow or wildtype and albino flocks for wildtype or yellow hens, S₂₈.

Tableau III : Choix sexuel entre les poules de type sauvage ou jaune des lignées de coqs de type sauvage élevées dans les groupes « coloration sauvage » et « coloration mixte » (sauvage/jaune ou sauvage/albinos), S₂₈.

Expe- rience	Line	N	R	Frequency of mating			
				Attempts		Completions	
				Y	W	Y	W
Wild	High	20	20	53	71	30	40
	Control	10	8	13	8	8	12
	Low	20	3	1	5	0	1
Wild and Yellow	High	17	8	46	36	9	13
	Control	10	8	18	16	3	5
	Low	5	0	0	0	0	0
Wild and Albino	High	18	6	19	22	7	8
	Control	13	4	12	8	1	4
	Low	17	5	4	4	1	1

N = no. of males tested ; R = no. of males responding.
W = wildtype ; Y = yellow.

albino hens. When males were allowed to choose between wildtype and yellow hens no significant preferences were observed (*table III*). This indicates that regardless of the genetic background or early experience of the male no distinctions are made between these latter two phenotypes.

High-line males discriminated among females as evidenced by their preference for wildtypes to albinos. Although the lack of response to this test situation by many low-mating line males was expected due to their genetic background, males from the S₂₈ low-mating lines demonstrated that they distinguish between plumage colors such as wildtype and albino. The low percentage of high-line males raised in mixed flocks which responded to the yellow versus wildtype choice was not due to indecisiveness, but rather a consequence of maintaining males together during rearing and between trials. Males of these lines even mount other males indiscriminately.

DISCUSSION

Responsiveness by the C line was consistent with previous observations for this line in that males preferred wildtype to albino hens when raised with both phenotypes (Truax and Siegel, 1982 ; Blohowiak and Siegel, 1983 b). Early experience with albinos does not lead to sexual imprinting if reared simultaneously with the wildtype (Gallagher, 1978 ; Blohowiak and Siegel, 1983 b). Because initial preferences were the same as those observed in this experiment, experience with plumage coloration appears to fine-tune preferences as determined by genetic

mechanisms (Gallagher, 1978 ; Cooke, 1980 ; Blohowiak and Siegel, 1983 b).

The frequency of matings with yellow and wildtype hens was similar regardless of whether or not the males were raised with yellow flockmates an observation consistent with that of Truax and Siegel (1982). Also, yellow males raised both in all yellow flocks and with wildtypes did not show a preference between wildtype and yellow females (Truax and Siegel, 1982), even though yellow is lethal when homozygous (Truax and Johnson, 1979). The pattern of the yellow plumage may provide stimuli similar to that of the wildtype, while the albino may either lack such qualities (Bateson, 1978 ; Gallagher, 1978), or even release abnormal stimuli.

Truax and Siegel (1982) found no discrimination against albinos which had their body plumage dyed black. Similarly, Bateson (1978) observed familiar wildtype hens were preferred over novel white ones ; however, novel wildtype hens were favored overall. These experiments are indicative of beneficial gains to avoid mating with albinos. The white coloration may be so novel that albinos are perceived as too outbred to select as mates. Darwin (1871) reported that albinos of bird species were not observed to mate in the wild. A reviewer of this paper pointed out there may be a bias in this observation in that albinos were preferentially collected by man. The paucity of such observations may be related to morphological, physiological, and behavioral modifications due to the albino gene (Lee and Keeler, 1951) and to their attractiveness to birds of prey (Zeuner, 1963).

The benefits which can be gained by males being selective in choosing mates must exceed the costs of being selective (Wittenberger, 1979). Japanese quail in our bidirectionally selected lines and the randombred control line all showed the ability to select among potential mates even in a promiscuous mating system, and do so when presented with an extreme phenotype. Males from lines selected for high and low levels of mating distinguished among plumage phenotypes rather than mating indiscriminately. Such large phenotypic manifestations from a single locus, such as albino, can mask preferences which are exhibited among wildtype females of various genotypes (Blohowiak and Siegel, 1985). Our results, thus are not at variance with strategies of positive and negative assortative mating or inbreeding and outbreeding in maintaining an optimal balance of heterozygosity (Bateson, 1978, 1979, 1983 ; Thiessen and Gregg, 1980).

Acknowledgments: We wish to express special thanks to Dr. Ann Dunnington, Guy Barbato and Linda Dudley for their cooperation in various aspects of this research. This research was supported, in part, by NSF Grant BNS-7824493.

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