Z. Tierpsychol., 41, 307—331 (1976)
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ISSN 0044-3573 / ASTM-Coden: ZETIAG

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Spatial Proximity and Mate-specific Behaviour in a Flock of Budgerigars (*Melopsittacus undulatus*; Aves, Psittacidae)

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With 9 figures

Received: 22 March 1976

Abstract

The purpose of this study was to find out how much the behaviour of budgerigars to their mates is modified by the pair bond, and thus differs from their behaviour to other potential partners. Spatial cohesion and other behaviour patterns were analysed for partner-specificity. Many behaviour patterns are similarly partner-specific for all birds observed, although there are clear differences in the social behaviour of individuals. Partner-specificity of behaviour patterns is apparently based on individual recognition of mates. Causal and functional aspects of partner-specific behaviour in budgerigars are discussed.

Introduction

Pairs usually keep close together. Partners behave differently to each other than towards other conspecifics. These differences develop in the course of pairing and during their later association (Dilger 1960, Erickson 1973). Certain behaviour patterns are sometimes exclusively mate-specific (Brockway 1964b, Nicolai 1956). The duetting of many monogamous birds is an example of such mate-specific behaviour (Thorpe 1972, Wickler 1974). Agonistic behaviour is directed at the mate less often than at other conspecifics (Erickson 1973, Lamprecht 1973, Reyer 1975, Stamm 1962, Stettner et al. 1971).

Mate-specific behaviour can be based, e. g. on a common site attachment and/or on lack of opportunity for interaction with other potential partners; another factor found in most cases investigated is individual recognition. This study will attempt to show how much the behaviour of budgerigars to their mates differs from their behaviour to other potential partners. Mechanisms responsible for mate-specific behaviour will also be investigated.

Particularly the behaviour of birds is often described as inflexibly species-specific. But within many species individuals choose, for example, different sorts of food (Curio 1975). The exact description of behaviour necessary to characterize pair cohesion also shows whether social behaviour varies between individuals.

Budgerigars were chosen for this investigation as they are both monogamous and highly sociable; several pairs can be kept together in an aviary, so that the difference in the relationship of mates and nonmates can be investigated. Another advantage is that their behaviour has been thoroughly described and analysed, and much is also known of their (reproductive) physiology from studies in captivity (BROCKWAY 1964 a, b, c, 1965, 1967a, b, 1968, 1969, 1974, CINAT-THOMSON 1926, DOOLING and SAUNDERS 1975, HINDE and PUTMAN 1973, MASURE and ALLEE 1934, PUTMAN and HINDE 1973). Budgerigars are moreover readily obtainable, undemanding, and they can be bred independent of season.

A. Spatial cohesion

1. Definition of pairs

In watching the behaviour of a group of budgerigars in an aviary one soon observes that certain birds sit together repeatedly and interact in a specific way. The immediate impression is that they are mated. It is these birds which begin breeding together if nesting boxes are provided.

For clarity, only those animals having at some time bred together, or at least having attempted to do so, will be described in this paper as pairs.

2. Animals and observation methods

The spatial cohesion of budgerigars was studied in an aviary 230 × 245 × 90 cm, containing 6 pairs. The first series of measurements was made when the birds were about 3 months mated, the later measurements when they were about 12 months mated. Each bird was numbered for reference purposes. The position of each pair partner, or of 2 nonmates of different sex allocated to each other at random, or according to common site preferences, was recorded at 6 min intervals each day from 9—11 h.

Perches in the aviary were divided into numbered sections of about 30 cm, wire netting and the feeding area were similarly divided. Each location was characterized by its mean X, Y and Z coordinates in calculating distances between birds. Therefore the distance between two birds at any one site was recorded as 0, whether they sat touching or 30 cm apart.

3. Methods of analysis

Independence of the data: Continuous recording of the locations of 2 ♂♂ and 2 ♀♀ (total observation time 4 h) showed that after a 6 min interval their locations were unchanged in only 0 % and 2.5 % respectively of all cases. To detect any possible interdependence of the data, however, the autocorrelation function was calculated for the location series of each bird. Each series was shifted 1—20 steps, in some cases 1—40 steps, and so autocorrelated. As the correlation coefficients varied widely, the temporal shift at which the correlation fell to random could not easily be determined. To find a reproducible criterium for the establishment of the random niveau, the means of the last 10 or 20 correlation coefficients were calculated. From this mean ($\overline{r}$) and its standard deviation (σ) it is possible with the aid of the z-distribution to calculate the maximal value (r_{max}) at which the correlation coefficient still belongs, within 5 % probability of error, to the population of correlation coefficients characterized by the mean:

$$r_{max} = \overline{r} + 1.96 \cdot \sigma$$

Data for which the autocorrelation coefficient lay below this value were regarded as independent.

If for the ♂ of any pair of birds the values became independent of each other after one 6 min interval, whereas for the ♀ they first became so after 2, 3 or 4 intervals of 6 min, then the following calculations were made with only every 2nd, 3rd or 4th site registration. For most pairs the data for every 2nd site recording proved to be independent of each other.

Expected values for pair sitting: FERNALD (1973) described a method for calculating an expected value for pair-sitting at any particular site, from the measured frequency of perching at the given localities. Briefly, this states that if 2 birds A and B move quite independently of each other, then the probability of finding them together at a site i is:

$$p_{i(A/B)} = p_{i(A)} \cdot p_{i(B)}$$

This assumption of the independent movement of 2 birds can serve as a null hypothesis, against which the observed values are tested. This is possible only if the values are really independent of each other, so that the examination of data-independence is required.

The frequency (f_E) with which 2 birds can be expected to sit together at all n sites in the aviary is:

$$f_E = N \cdot \sum_{i=1}^{i=n} p_i \, A/B) = N \cdot \sum_{i=1}^{i=n} p_i(A) \cdot p_i(B),$$

where N is the number of all independent recordings. This manner of calculating a random expectation also takes into account any site preferences of the birds concerned. A deviation of observed values from the expected value cannot therefore be due to common preferences for or avoidance of particular sites.

Expected values for distance distribution: Correspondingly, the expected distance distribution between 2 birds A and B can be calculated from given location data (FERNALD 1973), again assuming independent bird movement. The distance between 2 birds is:

$$D_i = \sqrt{(x_A - x_B)^2 + (y_A - y_B)^2 + (z_A - z_B)^2}$$

x, y and z are the coordinates of the locations of birds A and B. The frequency of occurrence of a particular distance category D_i is:

$$N \cdot p_{(D_i)} = N \cdot \sum_{n=1}^{n_i} p_{(A_n)} \cdot p_{(B_n)}$$

N is the number of location registrations, $p_{(D_i)}$ the probability of occurrence of a value in the distance category D_i, n=1 to n_i is the number of possible location combinations for which the distance between the birds is in the distance category, $D_i \cdot p_{(A_n)}$ and $p_{(B_n)}$ are the probabilities of birds A and B being at locations between which the distance is D_i. In this way the expected distance distribution between the birds can be calculated.

The autocorrelation and site registrations were evaluated with a DEC computer PDP 11/40.

4. Pair sitting

Table 1 shows how often mates sat together. The corresponding expected values are also given. The mates sat together significantly more often than could be expected from a common site preference alone. There were no significant differences between birds paired for 3 months and for 12 months in respect of pair-sitting.

Mates do not therefore move independently of each other, although this does not necessarily mean that the birds attract each other. Their choice of location might perhaps be synchronized by variable external factors (fright stimuli, cover, temperature, light intensity, food etc.). But if so, then nonmates of different sex should also sit together more frequently than expected.

To investigate this possibility, each of the 3-months-paired ♂♂ was allocated a nonmate ♀ at random, and the locations of the 2 birds thus associated ('random-pair') were recorded 100 times. The results are shown in the upper half of Table 2. Such random pairs sat together less often than mates, and there was no significant difference between observed and expected frequencies of pair-sitting.

Table 1: Pair-sitting of mates*

	pairs	observed together (%)	expected together (%)
3 - months mated (N = 200)	1,1	18.0	6.7
	2,2	25.5	8.9
	3,3	40.0	7.7
	4,4	23.5	6.0
	5,5	22.5	8.3
	6,6	28.5	8.3
12 - months mated (N = 100)	1,1[a]	20.0	8.7
	4,4[a]	28.0	10.1
	7,7	34.0	10.4
	8,8[a]	22.0	9.3
	9,9	30.0	11.0
	10,10	38.0	18.3

* All pairs sat together significantly more often than expected (χ^2-test; $p < 0.001$). In calculating the significance the 1st and 2nd half of the data for each pair were taken separately and the observed and expected values calculated. These values were then subjected to the χ^2-test.

[a] For these pairs 1 of the 2 expected values was less than 5.

From the 200 location registrations of the 6 3-months-mated pairs, each ♂ was allocated a nonmate ♀ having the most site preferences in common. The locations of ♂ and ♀ were then recorded 100 times. The results are shown in the bottom half of Table 2. Such 'pairs' sat together more frequently than random pairs, but the expected value was also higher. There was no significant difference between observed and expected frequencies.

Table 2: Pair-sitting of nonmates

	Observed birds	observed together	expected together	
Birds allocated at random to each other	1,2	5.0	5.6	$\chi^2 = 1.5^+$ $p < 0.9$
	2,1	8.0	6.4	
	3,4	6.0	6.1	
	4,6	5.0	5.8	
	5,3	7.0	3.6	
	6,5	1.0	2.1	
Birds allocated to each other according to common site preferences	1,2	15.0	10.0	$\chi^2 = 3.4$ $p < 0.7$
	2,5	6.0	6.5	
	3,1	10.0	8.8	
	4,2	8.0	9.5	
	5,2	12.0	10.1	
	6,2	15.0	16.0	

[+] The values of the last 2 pairs were combined to make expected frequency larger than 5.

The frequency of pair-sitting was measured in both series for ♂1 and ♀2 (Table 2). At the time they were randomly matched, these two sat less often together than later on, when paired for common site preference, as between the 2 observation series they had developed a strong common preference for an additional 4 sites.

2 pairs exchanged mates between March and June 1973. Table 3 shows how much more often these birds sat together than expected. Both ♂♂ to begin

with sat with the first mate more often than expected, and with the later mate at about the expected frequency. In June it was the other way about.

Table 3: Mate exchange of 2 pairs. Frequency of pair-sitting. Figures stand for the difference between observed and expected values in % of all location registrations

♂♂ / ♀♀	2	5	Time of observation	No. of location registrations
2	16.8	1.9	March 1973	200
5	-1.1	14.7		
2	-0.4	23.3	June 1973	100
5	15.0	-0.9		

In all cases mates sat interdependently, and always perched side by side more often than was to be expected from common site preferences. Comparing the data in Tables 1 and 2, one must conclude that mates are not simply synchronized in location choice by external factors, for these should also influence nonmates. The results of measurements before and after the exchange of mates in pairs 2,2 and 5,5 (Table 3), makes such an interpretation even more unlikely.

The observed interdependence of the choice of location by mates is therefore understood here as mutual attraction.

5. Total distance distribution

If pairs sit together more often than expected, do they also cohere more closely at other times than unpaired birds? To study this question the observed and expected distance distributions were compared, with the exception of the first distance category (0—20 cm). The difference between observed and expected values in the region up to about 100 cm were positive for all pairs and random pairs, for greater distances negative (Fig. 1). Differences between the observed and expected distance distributions were significant for pairs 1—4, but not for pairs 5 and 6. The differences between the two distributions were also highly significant for 2 random pairs (1,2 and 4,6). All 12-months mated birds showed similar distance distributions (not shown here), which were not significantly different from those expected ($0.3 > p > 0.05$). These results indicate that budgerigars seek the proximity of conspecifics. They will repeatedly join the flock, usually containing the partner too. The differences therefore between observed and expected distance distributions for all birds in the flock will be positive in the region of smaller distances, but negative for the region of greater distances (here about > 1 m). So that the differences between observed and expected distributions indicate rather flock cohesion (gregariousness) than pair cohesion. However at very close range (0—20 cm) this attraction to flock-mates either ceases or is compensated by avoidance or aggression. Thus the difference between observed and expected distance distributions of nonmates approaches zero. This may indicate the magnitude of a budgerigar's 'individual distance' (Individualdistanz, Hediger 1941).

Presumably a greater number of measurements would have exposed clearer distinctions between the distance distributions of mates and nonmates.

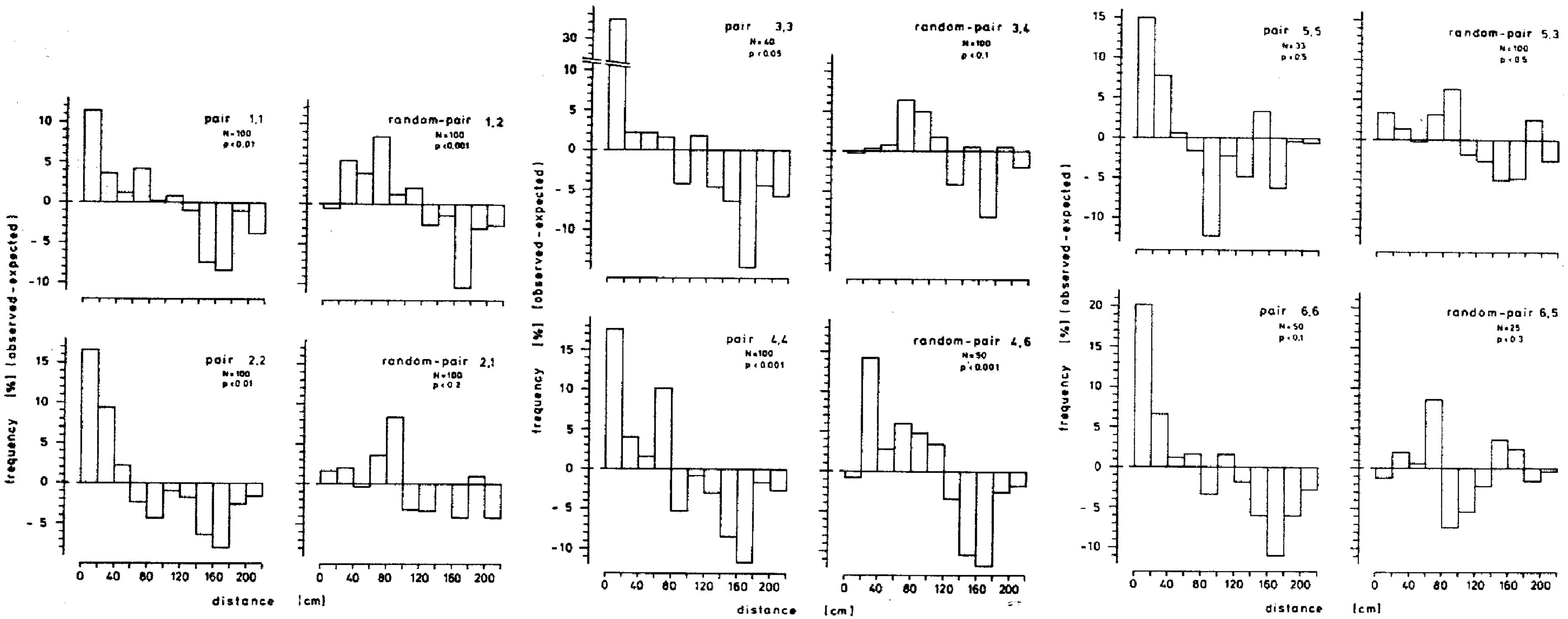


Fig. 1: Difference (in %) of the observed and expected distance distributions of 6 pairs and 6 random pairs. N = number of independent location registrations, p = significance of the difference of observed and expected distance distributions (χ^2-test)

6. The contribution of each partner to maintaining proximity

The more often an animal approaches its partner, the more it contributes to the spatial cohesion of the pair. But for both partners together, in a given period, frequency of approach equals frequency of leaving (±1). If one of the animals is especially active, it may approach the less active partner more often than the partner approaches it. It is equally probable that it leaves the partner more often. To avoid the effect of unequal activity, the frequencies of approach and leaving are here expressed in % of the total activity. If an animal devotes a greater share of activity to approaching its partner than to leaving it, then undoubtedly it contributes more to pair proximity than its partner does (for a detailed discussion of this measuring method see Hinde and Atkinson 1970).

The contribution of each partner to mate proximity was measured by two behaviour patterns: (1) flying or walking to the partner's location, (2) flying or walking away from the partner's location. To include all locomotory activity of the birds, all location changes which were neither (1) nor (2) were also recorded. Locations were again defined as in the pair-sitting protocols. These activities were registered for an hour regularly, between 9 and 11 h, for 2 birds at a time.

Table 4: Contribution of pair partners to maintaining proximity

	Observed birds	♂♂ Total site changes	♂♂ Towards partner (%)	♂♂ From partner (%)	♀♀ Total site changes	♀♀ Towards partner (%)	♀♀ From partner (%)
young pairs, mated approx. 2 months	2,2	239	21.8	18.1	309	14.6	17.8
	4,4	254	12.6	9.4	111	9.0	16.0
	5,5	188	20.2	17.0	18	11.1	50.0
♂ and ♀ exchanged	2,4	296	2.0	3.0	90	3.3	2.2
	4,2	170	4.7	5.3	137	4.4	2.9
old pairs, mated approx. 18 months	4,4	133	10.5	7.5	27	18.5	29.6
	7,7	159	25.1	22.6	55	16.4	25.5
	8,8	76	26.3	21.1	46	13.0	21.7
	9,9	145	26.2	23.4	49	22.4	28.6
♂ and ♀ exchanged	4,7	152	7.9	10.5	41	9.8	0.0
	7,4	443	10.4	10.6	23	0.0	0.0

Table 4 gives the results of these protocols. On the whole the ♀♀ were less active (fewer location changes) than the ♂♂ ($p < 0.002$; Mann-Whitney U-Test, two-tailed: Siegel 1956). In absolute values, all ♂♂ approached their partners more often than they were approached by them ($p = 0.008$; U-Test). The percentage of total activity spent approaching the mate was greater for the ♂♂ of 6 of the 7 pairs than for the ♀♀. All ♂♂ approached their mates more often than they left them.

As a control, data was measured as if partners were exchanged in 2 pairs of young birds, and in 2 pairs of older birds, e. g., as if the young pairs were ♂2, ♀4 and ♂4, ♀2 (Table 4). ♂♂ and ♀♀ both approached and left their own mates significantly more often than they did their exchanged partners ($p \leq 0.006$; U-Test). That is, all birds showed more interest in their true mates than in the exchanged partners. The ♂♂ left their exchanged partners more often than they approached them, exactly contrary to their behaviour to their true mates.

The exchanged partners 4,7 and 7,4 showed an unusually close relationship, as the 2 ♀♀ preferred a common site. The data is therefore biased by site preferences. The great difference however between observations of true mates and the control protocols shows clearly that mates and nonmates have quite different relationships.

B. Partner-specificity of other behaviour patterns

1. Animals and methods of observation

The aviary contained 5 pairs, of which only 4 were observed. At the time of observation all pairs had bred together twice successful the second time 4 months previously. They had been paired for a little over 12 months.

Each bird of these 4 pairs was observed singly for 4 h, from 9—11 and 16—18 h. Observations on all 8 birds were made within 12 days.

A protocol of behaviour patterns was made, using an apparatus described by FERNALD and HEINECKE (1974) for recording behavioural events on paper tape. Every second throughout the observation period this apparatus automatically punched a code fed to it from a keyboard. For every observed behaviour pattern it was recorded whether the bird sat alone, with a nonmate ♂ or ♀ or with its mate.

This method of recording data precludes statements concerning the behaviour of any animals with which the observed one interacted. Nor is it possible to tell to which of the 4 nonmate ♂♂ or ♀♀ a behaviour pattern was addressed.

2. Methods of analysis

The paper tape protocols were analysed for frequency, duration and sequence of behaviour patterns.

Differences in the frequency of addressing behaviour patterns to the mate and to nonmates of the opposite sex were either checked for each bird individually with the Binomial test or, if the numbers were too small, the data for all birds together was checked with the Wilcoxon matched-pairs signed-ranks test or the Randomization test (Tests described in SIEGEL 1956). All probabilities given are two-tailed when not otherwise stated. The correlation between duration and frequency of the behaviour patterns was calculated after SPEARMAN (SIEGEL 1956).

Sequence analysis: The behaviour patterns were so defined that direct autotransitions were excluded. If in a sequence: 'pattern 1, pause, pattern 1', the pause was shorter than 10 s, then behaviour pattern 1 was recorded as following directly upon itself. If the pause exceeded 10 s, the sequence was recorded as 'pattern 1, resting, pattern 1'. Other transitions were analysed accordingly. The expected values for the frequency of transitions between behaviour patterns were calculated from the total data according to the formula:

$$\text{Expected frequency} = \frac{\text{Row total x Column total}}{\text{Total of all transitions}}$$

If a behaviour pattern followed upon another more frequently, but preceded it less frequently than expected, this disparity was not tested for significance. If in both cases the observed values deviated in the same direction from the expected values, the χ^2-test was applied to determine significance, if the expected values were 5 or more, and the sum of the observed and expected values 20 or more.

The behaviour pattern 'resting' was not analysed, as it was not positively defined (see below).

3. Definition of behaviour patterns

Most budgerigar behaviour patterns have been exactly described by BROCKWAY (1964 a, b; based partly on DILGER 1960). Only deviations from

Brockway's representations, and details important for methodological reasons will be mentioned here.

Resting: (Resting and sleeping, Brockway 1964a, p. 200) A budgerigar shows none of the protocolled behaviour patterns for 10 s or longer. Shorter intervals between 2 activities will be called *pauses* in the following.

Feeding: (Brockway 1964a, p. 200) The head is held close to food and directed at it. The beak need not necessarily be in contact with the food. The pattern 'feeding' ends when the bird looks up, changes location or interacts with others.

Preening: (Brockway 1964a, p. 199—200) This behaviour category comprises 5 activities: 1. scratching head or beak with the foot, 2. preening with the beak, 3. cleaning feet with the beak, 4. shaking, 5. rubbing the head on wings and back. If these various patterns merged they were protocolled as a single preening event.

Singing: (Loud warble, Brockway 1964b, p. 303) Sitting relaxed in a normal posture or with the head under the wing a budgerigar sings continuously. The eyes may be shut. The song is never directed and contains none of the visible precopulatory displays described by Brockway (1964b).

Courtship singing: (Loud warble with interspersed visible precopulatory displays, Brockway 1964b, p. 303—322) As opposed to singing, courtship song is always clearly directed, most often at other budgerigars, but sometimes at branches or wall irregularities. The bird sings continuously and shows additional behaviour patterns never shown in undirected singing: 1. head-bobbing, 2. nudging, 3. head-shaking, 4. flying or walking approach to or retreat from object courted, 5. beak-hooking. These are all typical courtship behaviour patterns. ♂♂ sometimes attempt mounting while courtship singing to a ♂ or a ♀, even in the absence of soliciting for copulation.

Brockway combines the acoustical components of singing and courtship song under 'loud warble', to which 'soft warble' may be added in courtship. Here these 2 behaviour complexes are protocolled separately, in view of the clear orientation of the courtship song, and the precopulatory displays contained in it. The differentiation corresponds to that for Estrildid finches, into 'undirected' and 'directed' song ('ungerichteter' and 'gerichteter' Gesang, Immelmann 1959).

Allopreening: (Reciprocal preening, Brockway 1964a, p. 198—199) One budgerigar nibbles the head plumage of another.

Beak touching: ('I.N.T.', Brockway 1964b, p. 300) The beaks, turned towards each other and nearly touching, are rotated against each other, whereby they may occasionally touch lightly. The birds utter a warble, pleasant to us. This behaviour seldom occurs without the acoustical component but it is described by Brockway without this. Beak touching can also be directed at a partner by one bird only: such cases were not recorded.

Courtship feeding: (Brockway 1964b, p. 299—300) A bird regurgitates food and feeds another in beak-to-beak contact. As feeding may occur in a great variety of body positions, regurgitation is the surest sign of which bird does the feeding.

Adult food begging: (Brockway 1964b, p. 300) Adult food begging occurred only in ♀♀. The head is turned towards a ♂, the upper mandible quivers up and down; some ♀♀ accompany begging with a sharp cheep, not unlike the begging call of the young. Brockway never heard a call during 'adult food begging'.

Copulation: (Soliciting copulation and copulation, Brockway 1964b, pp. 314—318) Budgerigar ♀♀ solicit with raised head and tail and flattened back, somewhat abducted legs and slightly lowered wings. If a ♂ mounted a ♀ thus soliciting a copulation was recorded, whether cloacal contact occurred or not.

Supplanting attack: (Flying into or onto another individual, Brockway 1964a, p. 205) A bird flies straight at the place where another is sitting. Usually the attacked bird evades by flying off immediately, or the attacker can alight upon him and dislodge him, e. g. from a perch.

Beak thrust: (Brockway 1964a, p. 203) The birds thrust at each other with opened beaks. The beak is closed if the thrust hits the opponent, but thrusts are often wide of the mark.

Sidling at: (Sidling toward in head-erect-toward and head-body-erect-toward body position, Brockway 1964a, p. 213—214) A bird edges on foot so close to another that he yields place. Head and body of the sidling bird are held at an angle of 0—45° to the other budgerigar.

Flying away: (Brockway 1964a, p. 213) A budgerigar evades an approaching conspecific by flying away.

Sidling away: (Brockway 1964a, p. 213) A budgerigar evades an approaching conspecific by climbing or walking away.

4. Duration of pair sitting

On an average, ♂♂ and ♀♀ sat respectively 20.3 and 20.9 min/h together with their mates. ♂♂ and ♀♀ of pairs 7, 8 and 9 sat longer with their mates than with all other nonmates of the opposite sex (Fig. 2). ♂4 and ♀4 sat longer with the 4 nonmates of the opposite sex than with their mates, but they sat much longer with the mate than with any one of these nonmates. This still applies if they did not sit with each of the other birds of the opposite sex equally long (as assumed in Fig. 2), but only with 2 (Randomization test, p = 0.008). Some ♂♂ showed preferences for certain ♀♀, which were however in no case so pronounced that a ♂ sat exclusively with one other ♀ besides his mate.

This continuous measurement of the duration of sitting together shows roughly the same results as the measurement of pair-sitting in 6 min intervals (A.4).

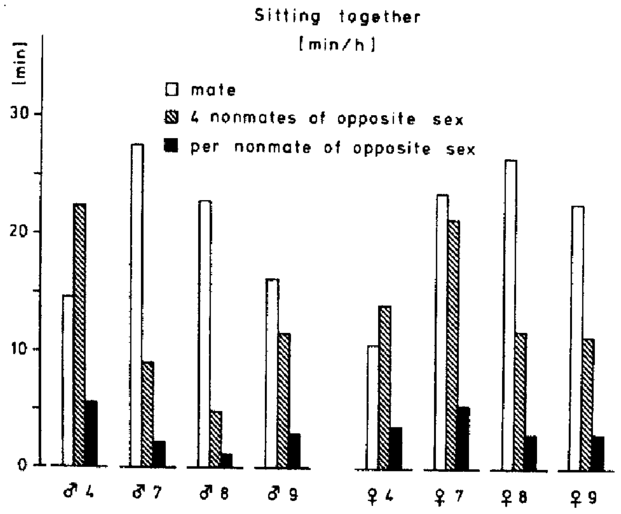


Fig. 2: Duration of sitting together with the mate and with nonmates of the opposite sex

5. Definition of partner-specific behaviour

"An animal directs many behaviour patterns exclusively or nearly exclusively towards certain individuals, although it also meets others." "If a behaviour pattern is partner-specific (*partnerbeschränkt*), then the reason for the specificity can only be that the presence of the partner creates a different . . . stimulus situation than the presence of a stranger" (LAMPRECHT 1973, translated).

According to this definition, frequent pair-sitting or prolonged sitting together as described in A.4 and B.4 constitutes mate-specific behaviour. If 2 animals sit together for long periods, the probability of interactions occurring between them is higher than between animals sitting together for short periods only. But the notion of partner-specific behaviour is that the tendency, not the opportunity, to direct various behaviour patterns at the partner, is different from the tendency to direct them at others; so that the frequency of occurrence of a behaviour pattern has to be calculated for equal periods of sitting together.

In this paper, therefore, partner- (or mate-)specific behaviour will be defined as behaviour which, in equal periods of sitting together, is directed at the mate significantly more often or less often than at nonmates of the opposite sex. Behaviour frequencies will always be calculated for 30 min of sitting together, either with the partner or with other birds of the opposite sex (potential partners).

6. Preening

The total duration and frequency of preening were correlated (♂♂: $r_S = 0.9$; $p < 0.01$. ♀♀: $r_S = 0.77$; $p < 0.05$). Here only the frequencies per 30 min sitting together will be considered, as the analysis of duration gives no additional information.

With the exception of ♂8, all ♂♂ preened more frequently beside the mate than beside other ♀♀. Conversely, all ♀♀ with the exception of ♀7 preened more often sitting beside male nonmates (Fig. 3). These differences however are significant only for ♂7, ♂9 and ♀9, the 2 ♂♂ preened mate-specifically more often than when sitting with other birds, the ♀ less often.

The connection of preening with other behaviour patterns will be described below (B.14).

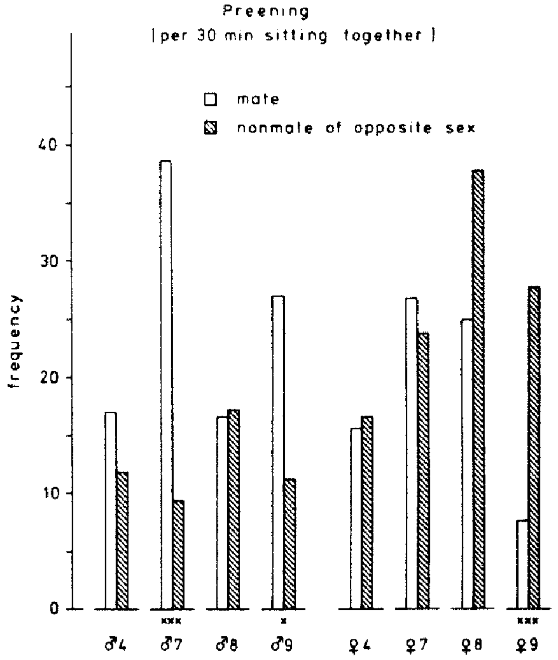


Fig. 3: Frequency of preening beside the partner and beside birds of the opposite sex. Crosses below the columns symbolize the significance of the difference (Binomial test). ×: $p < 0.05$; ××: $p < 0.01$; ×××: $p < 0.001$

7. Singing

Duration and frequency of singing were significantly correlated for the ♂♂ ($r_S = 0.9$; $p < 0.01$), but not for the ♀♀. With the exception of ♀7, who sang very little, all budgerigars sang most frequently when sitting alone

Table 5: Frequency of singing per 30 min sitting in company or alone

	Partner	Nonmates of opposite sex	alone	p⁺ (Binomial test)
♂ 4	6.2	5.4	11.0	n. s.⁺⁺
♂ 7	2.7	2.5	18.0	= 0.002
♂ 8	9.6	14.0	34.6	= 0.003
♂ 9	19.5	25.4	36.5	n. s.
♀ 4	6.4	11.8	31.6	= 0.003
♀ 7	0.0	3.8	0.0	n. s.
♀ 8	3.7	0.0	19.6	= 0.002
♀ 9	2.0	2.6	26.0	= 0.001

⁺ The significance was calculated in each case two-tailed for the larger of the 2 first values over against the value for sitting alone.

⁺⁺ n. s. = not significant.

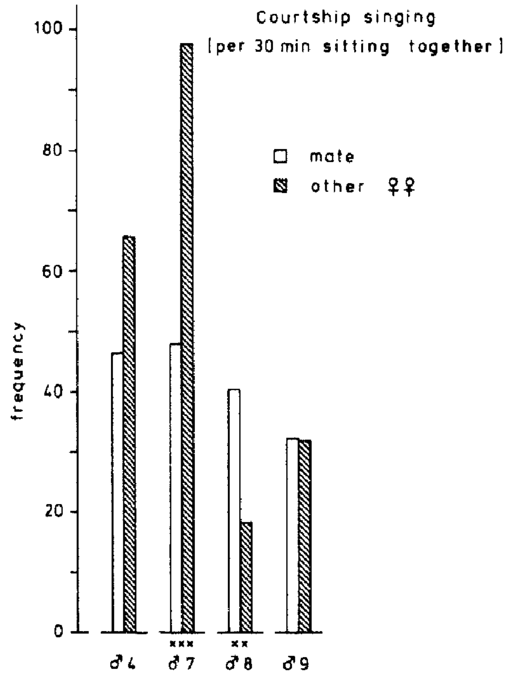
(Table 5). Singing while sitting with the mate and while sitting with other potential partners was of roughly the same duration and frequency.

When with the mate, ♂♂ followed singing with courtship song less often than when with other ♀♀ (χ^2-Test; $p < 0.01$). Otherwise there were no clearly defined differences between the 2 situations (sitting with the mate or a nonmate ♀) for behaviour patterns preceding and following singing.

8. Courtship singing

For the total observation time, all ♂♂ save ♂4 courted their own mates more frequently than all other ♀♀ together. Assuming that ♂♂ courted ♀♀ not their partners equally often, it was calculated that all ♂♂ including ♂4 displayed more frequently to their partners than to any other ♀. Nevertheless, courtship singing is not a mate-specific behaviour pattern. If frequency is related to the time of sitting together, the opposite results are obtained in some cases. As the total duration of courtship singing per 30 min interval was significantly correlated with its frequency ($r_S = 0.88$; $p < 0.01$), only frequencies will be compared in the following. ♂♂4 and 7, per 30 min sitting together, courted other ♀♀ much more often than their own mates. ♂9 courted his mate and the other ♀♀ with roughly equal frequency, and only ♂8 courted his mate more frequently than other ♀♀ (Fig. 4).

A given ♂ may interrupt his courtship song to his mate or to another ♀: the probability of interruption was greater for any ♂ while addressing whichever ♀ he courted less frequently. An example is shown in Fig. 5 for ♂4, who addressed courtship song to his partner less often than to other ♀♀.



The curves in Fig. 5 represent survival curves, as used in demography. The percentage of all recorded cases of courtship singing lasting longer than the time marked off on the abscissa was plotted at intervals of 2 s. The slope of the curves gives the probability of interruption of this behaviour pattern at any moment. As can be seen, the probability that the courtship song of ♂ to his partner is interrupted is roughly constant, and exceeds the probability of interruption or song addressed to other ♀♀.

Fig. 4: Frequency of courtship song to mate and to other ♀♀ per 30 min sitting together. Symbols as in Fig. 3

The courtship song of the 4 tested budgerigars was therefore not mate-specific either in frequency or duration. But courtship song was addressed to the mate in a different context than to nonmates (Table 6). The courtship song of a ♂ was followed significantly more often by courtship feeding when the mate was addressed. From the total data for the ♂♂ it can be seen that when the mate was courted, preening followed more often and fleeing more seldom than when nonmates were song-courted (χ^2-test; in both cases $p < 0.01$).

Of the ♀♀ only ♀4 regularly song-courted other budgerigars. During the whole observation period she addressed her mate 8 times and other ♂♂13 times.

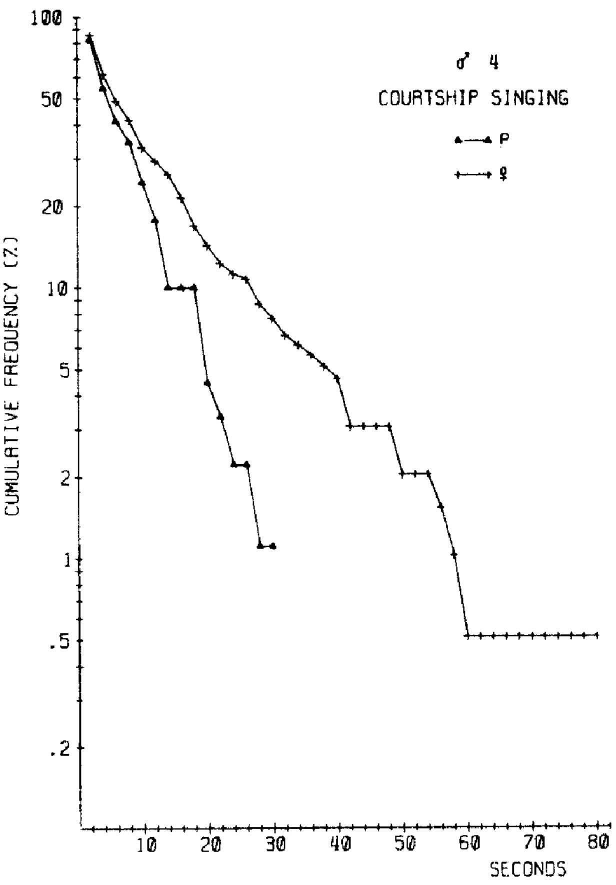


Fig. 5: Survival curves of courtship song for ♂4 to his partner (P) and to other ♀♀ (♀). For further explanation see text

Table 6: Behaviour patterns frequently following courtship singing[+] (Frequency in %)

Courting bird	Courted bird	Resting	Courtship singing	Preening	Courtship feeding	Fleeing[++]
♂ 4	Partner (N = 90)	7.8	34.4	4.4	16.7	6.7
	Other ♀♀ (N = 195)	6.7	20.0	4.1	1.0	43.6
♂ 7	Partner (N = 176)	4.0	26.7	16.5	13.1	14.8
	Other ♀♀ (N = 116)	2.6	29.3	4.3	0.0	36.2
♂ 8	Partner (N = 123)	8.9	28.5	8.1	10.6	24.4
	Other ♀♀ (N = 12)	16.6	8.3	8.3	0.0	8.3
♂ 9	Partner (N = 70)	7.1	12.9	14.3	21.4	8.6
	Other ♀♀ (N = 49)	8.2	14.3	10.2	2.0	18.4

[+] Pauses up to 9 s between 2 behaviour patterns are ignored in the sequence analysis.
[++] Sidling away and flying away combined.

9. Allopreening and beak touching

Allopreening occurred relatively seldom. It could not therefore be positively stated that each bird allopreened its mate more often than other birds, but for all animals together this was significant (Randomization test, p=0.008). In 32 h of observation the birds allopreened their mates 54 times, but never nonmates.

Equivalent results were obtained in 36 h of observing 6 other birds, roughly 6 months paired. They allopreened their mates 84 times, but never nonmates.

♀2 beak touched with a male nonmate once, 52 times with her mate. All other birds beak touched only with their own partners (significant in each case). Beak touching occurred an average of 16.6 times per 30 min sitting together with the partner, and was the most frequent mate-specific behaviour pattern.

The context in which allopreening and beak touching occurred is described below (B.14).

10. Courtship feeding and adult food begging

All ♂♂ except ♂4 fed their own mates significantly more often than nonmate ♀♀ (Table 7). Throughout the observation period only ♀4 fed her mate once. This contrasts with BROCKWAY's (1964 b) observations. She states that ♀♀ frequently feed their mates. In this study, however, only sick budgerigar ♂♂ were often fed by their mates. NICOLAI (1956) reports the same of bullfinches.

Table 7: Courtship feeding per 30 min sitting together

	Partner	other ♀♀
♂ 4	11.8	3.7
♂ 7	19.3	0.0
♂ 8	6.9	0.0
♂ 9	20.0	0.0

Courtship feeding followed courtship feeding in 52 % of all cases. There was a close connection between courtship singing and courtship feeding (see also B.14).

Table 8: Adult food begging per 30 min sitting together

	Partner	other ♂♂
♀ 4	14.8	0.0
♀ 7	0.3	0.0
♀ 8	1.1	0.0
♀ 9	4.3	0.0

Begging for food in ♀♀ was absolutely mate-specific. It occurred very rarely (Table 8). Although ♀♀ occasionally accepted food from nonmate ♂♂, they did not beg from them. While breeding, budgerigar ♀♀ often begged for food from their mates.

11. Copulation

Out of the breeding season copulation is rare. In 32 h of observation 8 copulations with the mate and 4 (by ♂4) with a nonmate (♀1) were noted. The partner-specificity of copulation was measured at the beginning of 2 breeding seasons, when the aviary contained 6 pairs of budgerigars, whose activities were occasionally recorded. In this way a total of 164 observations of copulation was reached. Mates copulated with each other 159 times, nonmates 5 times.

These 5 copulations were between ♀10 and ♂9 and between ♀1 and ♂4. ♀10's mate was sick and did not copulate with her. ♀1's partner fled whenever she was aggressive, so that this pair rarely copulated. ♀10 and ♀1 always had the same copulation partners, ♂9 and ♂4 respectively, who remained constant for some months. These ♀♀ directed mate-specific behaviour patterns mostly to their mates, however, and only exceptionally at their copulation partners (never allopreening, very rarely beak touching); the same applies for the 2 ♂♂ involved, who were firmly mated.

12. Aggressive behaviour

3 behaviour patterns, supplanting attack, beak thrust, and sidling at the other fall under this heading; according to Brockway (1964 a) this order denotes a decreasing aggressive tendency.

Table 9: Aggressive behaviour of ♂♂ (per 30 min sitting together)
(Means of data for all 4 ♂♂)

	Partner	other ♀♀	♀♀ / Partner
Supplanting attack	0.09	0.47	5.2
Beak thrust	0.46	1.10	2.4
Sidling at	0.74	0.94	1.3

As ♂♂ rarely showed these behaviour patterns to all the ♀♀, Table 9 gives only the mean of the data for all 4 ♂♂. According to these data, the ♂♂ seemed to be less aggressive to their mates than to other ♀♀.

The ♀♀ were much more aggressive than the ♂♂, but never used supplanting attack against their mates, and only twice against other ♂♂. ♀8 beak-thrust at her mate per 30 min sitting together just as often (or seldom!) as she did at other ♂♂. ♀♀4, 7 and 9 beak-thrust less often at their mates (♀7 and ♀9 significantly) than at other ♂♂ (Fig.6). The ♀♀ did not sidle at their mates significantly more often (♀♀4 and 8) or less often (♀♀7 and 9) than at other ♂♂.

Per 30 min sitting together the ♀♀ beak-thrust at nonmate ♂♂ on an average 11.6 times as often as at the mate (20.9/1.8 times), but sidled at nonmate ♂♂ only 1.5 times as often as at their mates (10.6/7.0 times). The 2 ratios are significantly different (χ^2-test; $p < 0.001$). The ♀♀ were obviously inhibited in showing aggressive behaviour patterns to their mates. They were however quite aggressive to other ♂♂. This inhibition acted more strongly on the more aggressive beak-thrust than on the less aggressive sidling. In accordance with the concept 'biting inhibition' used for cichlid fish (Lamprecht 1973, Reyer 1975) it will here be termed beak-thrust inhibition. From the small number of data collected for the ♂♂, it appears that these too have a beak-thrust inhibition towards the mate.

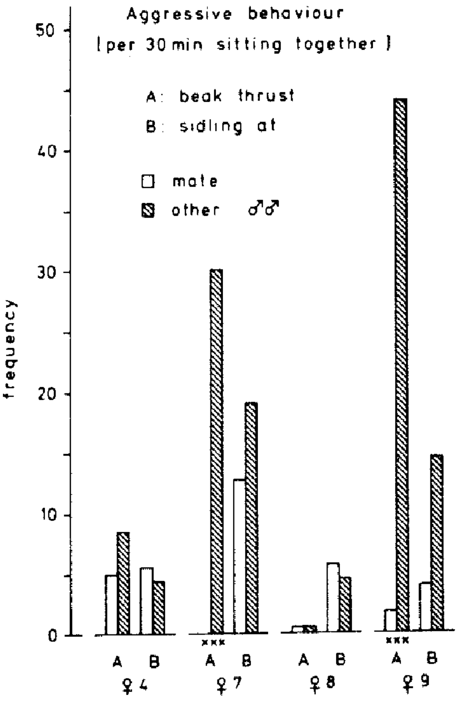


Fig. 6: Aggressive behaviour of budgerigar ♀♀.
Symbols as in Fig. 3

Beak-thrusting by the ♀♀ drove off their mates on an average in 20% of all cases (3/14), other ♂♂ in 10% (13/170). Sidling at the mate by the ♀♀ drove them off in 25% (20/80) and other ♂♂ in 30% (28/92) of all cases. None of the ratios given are significantly different from each other. The aggressive behaviour of the ♀♀, therefore, was not very efficient in increasing the spacing between them and either mates or other ♂♂.

But aggressive behaviour does not only serve to space out conspecifics. According to HASSENSTEIN (1973) it can also serve to lessen needs, and subsides after having reached the state striven for. If the aggressive behaviour patterns of the budgerigar ♀♀ were effective in this respect, it should only rarely be necessary for them to be repeated.

The possibility that there was a difference in this respect between aggressive behaviour to the mate and to other ♂♂ was investigated with the aid of sequence analysis. Beak-thrust of the ♀ at her mate was followed by one of the 3 aggressive behaviour patterns in only 14% (2/14) of all cases, her beak-thrusts at other ♂♂ were followed by further aggressive behaviour in 59% (100/170) of all cases. After sidling at the mate, further aggressive behaviour patterns were observed in 10% (8/80), but after sidling at other ♂♂ in 37% (34/92) of all instances. These differences are significant (for beak-thrust: $p < 0.05$; for sidling at: $p < 0.01$).

It can be concluded that with their mates ♀♀ reached a condition in which further aggressive behaviour was unnecessary more speedily than with other ♂♂.

13. Fleeing

Under this heading the 2 behaviour patterns 'flying away' and 'sidling away' will be combined. The latter, according to BROCKWAY (1964 a) indicates the weaker flight tendency.

Only few data are available for the ♀♀ (Table 10). All ♀♀ sidled away from their mates more often than they did from other ♂♂. This applies for each of the 4 ♀♀. It is impossible to decide whether this indicates a relative dominance of the male partner over the ♀, or is an artefact of the small amount of data.

♂♂ fled from ♀♀ much more often than the reverse. All ♂♂ fled significantly less often from their mates by flying away, and ♂4 and ♂7 sidled away significantly less often, than they did from other ♀♀ (Fig. 7). Fleeing therefore was mate-specifically rare. The ♂♂ fled most frequently after having addressed courtship song to the mate or to other ♀♀.

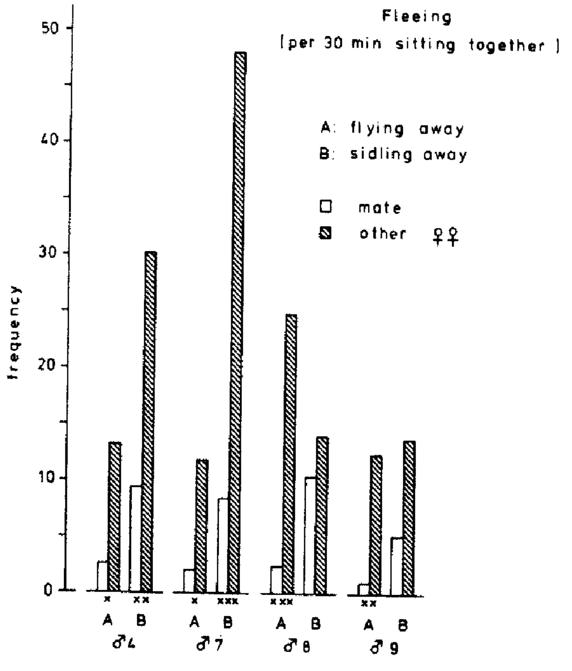


Fig. 7: Fleeing in ♂♂.
Symbols as in Fig. 3

Table 10: Fleeing in ♀♀ per 30 min sitting together (Means of data for all 4 ♀♀)

	Partner	other ♂♂
flying away	0.07	0.65
sidling away	2.30	0.70

These results accord well with those of the analysis of the aggressive behaviour of ♀♀, demonstrating their beak-thrust inhibition over against their mates.

14. Connection between allopreening, beak touching, courtship feeding and other behaviour patterns

Allopreening, beak touching and courtship feeding are the 3 most clearly partner-specific behaviour patterns. Their interrelation and relationship to other behaviour patterns were differently interpreted for the *Agapornis* parrot by STAMM (1962) and WICKLER (1969). While STAMM inclined to consider beak touching as derived from allopreening, WICKLER, going by similarities of form and orientation, considered it more likely that beak touching had developed from courtship feeding. The same question arises for budgerigars. BROCKWAY (1964 b) implied that beak touching might be connected with preening.

To investigate this question for the budgerigar, all behaviour sequences containing these patterns were examined. As we are concerned with partner-specific behaviour, and as only ♂♂ courtship feed, only those male behaviour patterns appearing while in the partner's company are shown in Table 11, so that line and column totals often differ. The expected values for this matrix segment were calculated from the total matrix of 7022 transitions for the 4 ♂♂. Sequences for ♀♀ were also analysed; as these results agree with those for the ♂♂, they will not usually receive special attention.

Table 11: Behaviour sequences of ♂♂ while sitting together with their mates

		following act								
		PRE	SIN	C. S.	ALL	B. T.	C. F.	AGG	FLE	Total
preceeding act	PRE	76 11.4	9 3.7	61 18.5	8 1.0	48 7.3	1 6.4	1 0.6	6 4.5	210
	SIN	9 3.7	34 1.2	16 6.1	1 0.3	4 2.4	0 2.1	1 0.2	1 1.5	66
	C. S.	59 18.5	14 6.1	124 30.0	0 4.3	19 11.8	67 10.3	6 0.9	68 7.3	357
	ALL	3 1.0	2 0.3	3 4.3	2 0.9	4 0.7	0 0.6	0 0.1	0 0.4	14
	B. T.	43 7.3	2 2.4	27 11.8	10 0.7	25 4.7	4 4.1	0 0.4	8 2.9	119
	C. F.	0 6.4	0 2.1	61 10.3	0 0.6	0 4.1	82 3.6	0 0.3	1 2.5	144
	AGG	3 0.6	0 0.2	5 0.9	0 0.1	0 0.4	0 0.3	1 0.1	3 0.2	12
	FLE	11 4.5	1 1.5	57 7.3	0 0.4	6 2.9	0 2.5	1 0.2	7 1.2	83
	Total	204	62	354	21	106	154	10	94	1005

Expected values in the matrix have been calculated from the total matrix of 7022 behaviour transitions of the 4 ♂♂. Abbreviations: PRE = Preening; SIN = Singing; C.S. = Courtship singing; ALL = Allopreening; B.T. = Beak touching; C.F. = Courtship feeding; AGG = Aggressive behaviour patterns (supplanting attack, beak-thrust and sidling at combined); FLE = Fleeing (flying away and sidling away combined).

Allopreening was observed only 21 times in all. Beak touching and preening preceded allopreening more often than was expected, and also followed it more often. These trends could not be statistically established from the few available data. Beak touching in ♀♀ also preceded allopreening more often than expected (15: 1.3), but never followed it. Autotransitions of allopreening were clearly observable in ♀♀.

Beak touching occurred significantly more often than expected before and after preening and courtship singing. It followed more often than expected upon itself, upon allopreening and upon fleeing. No connection was found between beak touching and courtship feeding.

Courtship feeding very often followed upon itself. Before and after courtship singing, ♂♂ fed their partners significantly more often than expected. Transitions between preening and courtship feeding were fewer than expected.

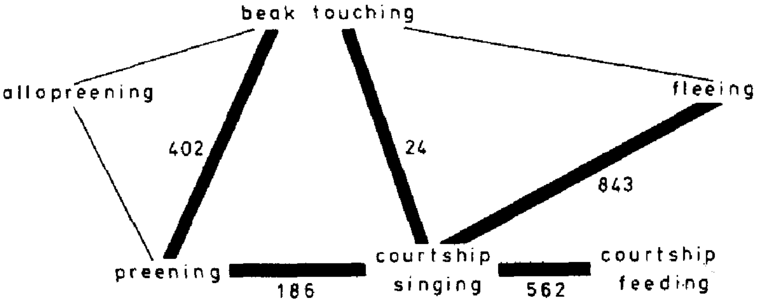


Fig. 8: Transitions between some behaviour patterns. The lines show which transitions occur more often than expected. Thick lines: significantly more often than expected. χ^2 values (df = 1) are shown beside the lines

Fig. 8 shows the significant relationships between the behaviour patterns mentioned above. The connection between preening and courtship feeding seems more likely to be inhibitory (comp. Table 11), although both occur very frequently together with courtship singing.

If 2 patterns often occur in sequence, then there is a high probability that they derive from common (internal or external) factors (HINDE 1973). 3 of the ♂♂ observed preened more often when sitting beside the mate, one when sitting beside nonmates. They all, however, touched beaks exclusively with their partners. The connection between preening and beak touching cannot therefore be dependent only on an (internal) tendency to preen. In addition to this tendency, specific external stimuli from the partner are apparently necessary to release beak touching. Similar considerations apply to the connection between courtship song and courtship feeding.

From the results of the sequence analysis it appears probable that for the budgerigar, a closer motivational connection exists between (allopreening), beak touching, and preening on the one hand and courtship singing and courtship feeding on the other. This conclusion cannot of course be directly extended to cover the relationship of the corresponding behaviour patterns in *Agapornis*.

C. Interindividual differences in behaviour

Qualitative differences in the behaviour of various budgerigars first impress the observer, such as individual body positions in courtship singing and singing, and differences in song patterns and general activity. Such individual differences cannot be documented from the material available.

There were in part remarkable differences between observed individuals in the absolute frequency with which different behaviour patterns occurred. Considerable individual differences also existed in the probability of occurrence of the various behaviour patterns either beside the mate, beside another bird or sitting alone. Examples are preening (Fig. 3), courtship singing (Fig. 4), aggressive behaviour of ♀♀ (Fig. 6), and fleeing of ♂♂ (Fig. 7).

A comprehensive representation of these differences between individuals has been attempted in Figs. 9a and 9b. The columns show in which situation the animals employed a behaviour pattern, namely alone (A), sitting with the mate (M), with nonmate ♂♂ (♂) or with nonmate ♀♀ (♀). The situation in which a given ♂ or ♀ showed a particular behaviour pattern most frequently per 30 min was taken for this ♂ or ♀ and the particular behaviour pattern as 100 %, and the relative frequencies of the same behaviour pattern in the other situations calculated with reference thereto. The resulting frequency distributions for all 4 ♂♂ and 4 ♀♀ are shown for every behaviour pattern separately in a vertical sequence.

Fig. 9a shows, e.g., that ♂4 most frequently preened sitting alone, less often sitting beside his mate, still less often beside ♂♂ and least often beside nonmate ♀♀. The absolute

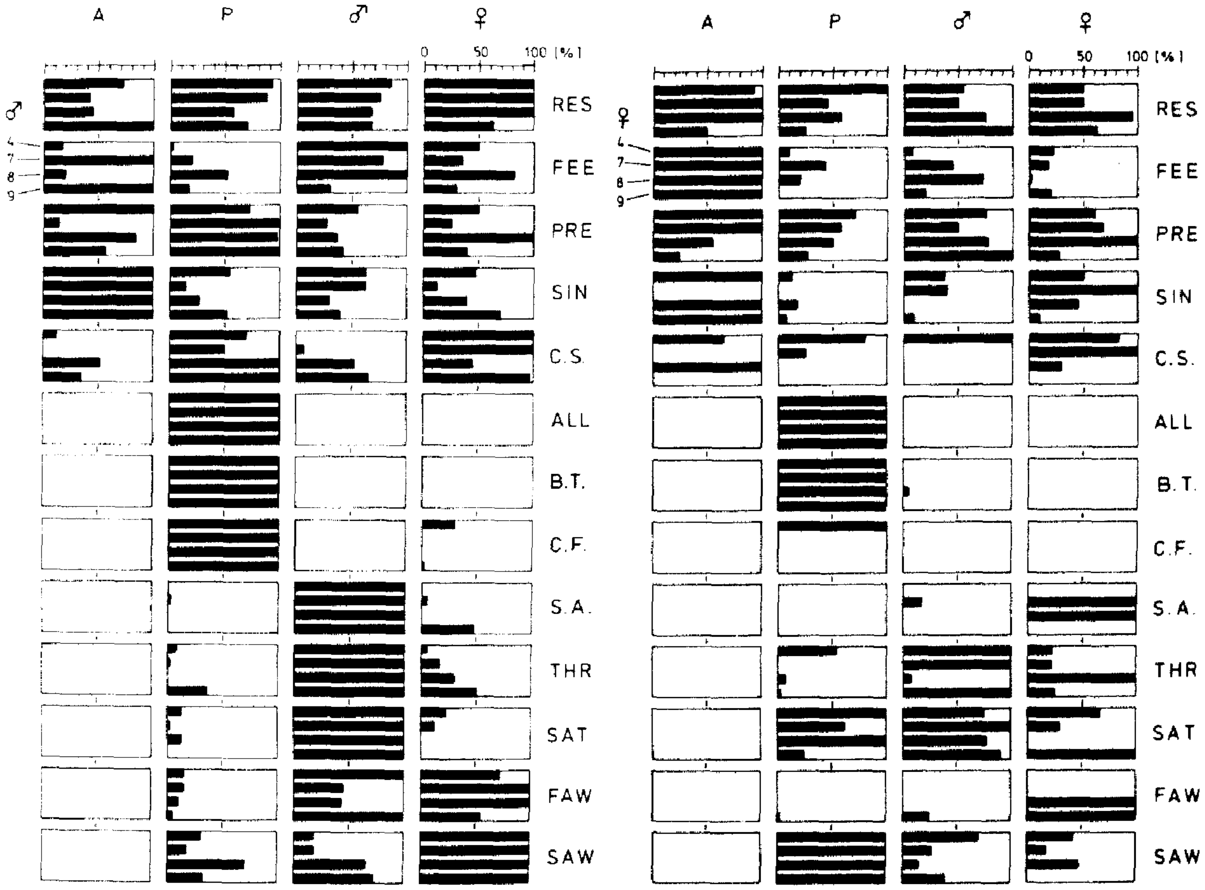


Fig. 9: Interindividual behaviour differences. 9a: 4 ♂♂. 9b: 4 ♀♀. A = Alone; P = Partner; RES = Resting; FEE = Feeding; PRE = Preening; SIN = Singing; C.S. = Courtship singing; ALL = Allopreening; B.T. = Beak touching; C.F. = Courtship feeding; S.A. = Supplanting attack; THR = beak thrust; SAT = Sidling at; FAW = Flying away. SAW = Sidling away. Further explanations in the text

values of these frequencies per 30 min sitting together were compared with the corresponding values for all other ♂♂ by means of the χ^2-test. In this way the probabilities of occurrence of the various behaviour patterns in different situations were compared for all ♂♂ and all ♀♀.

In the probabilities of occurrence of preening the ♂♂ differed significantly ($0.01 > p < 0.001$), with the exception of ♂4 and ♂8, as did the ♀♀ ($0.01 > p < 0.001$) save for ♀4 with ♀7 and ♀4 with ♀8. For singing, only the difference between ♂7 and ♂9 was significant ($p < 0.01$), while all ♀♀ except ♀4 with ♀8 and ♀8 with ♀9 showed significant differences ($0.01 > p < 0.001$). With the exception of ♂8 and ♂9 all ♂♂ showed significant differences in respect to courtship singing. ♀♀ did not courtship sing often enough to allow for a test of differences. With regard to aggressive behaviour (beak-thrust and sidling at combined) ♀4 was not significantly different from ♀7 and ♀8, but all other combinations were different ($0.05 > p < 0.001$). In fleeing (flying away and sidling away combined) ♂9 showed a distribution different from all other ♂♂ ($0.05 > p < 0.001$), the latter showing no differences among themselves.

When 2 birds interact it is difficult to place, in one of them, the cause of a certain characteristic in the behaviour of either. As all the behaviour patterns here compared occurred within a more or less social context, we must ask whether the behaviour of the tested individuals was really different, or whether the differences were caused by various external stimuli. As all animals had the same opportunities to interact with other budgerigars in the aviary, and the abiotic environment was the same for all of them, all animals were exposed at least potentially to the same environmental stimuli. As they nevertheless behaved differently, either they chose differently from the many available stimuli, or reacted differently to the same stimuli. In either case, variations in the organization of behaviour of different individuals are exhibited.

Discussion

Possible influences of captivity

In Australia budgerigars breed in cavities of all sorts near watercourses (FORSHAW 1973), and distances between pairs are inordinately greater than in an aviary. Neighbouring pairs probably interact very rarely, especially as ♂♂ spend much time foraging far from the hole. Under these conditions it is scarcely possible to measure partner preference. The situation in the free-ranging flock is not known. Conditions in aviary tests are likely to be very artificial, and what we observe are which behaviour patterns are made particularly mate-specific by a special internal mechanism. This mechanism is probably rarely needed in the wild, and so is all the more conspicuous in captivity, giving investigations on birds in captivity an independent value. The value of comparative behaviour studies of hamadryas baboons is similarly appraised by KUMMER and KURT (1965).

In the zebra finch, a few generations of domestication are sufficient to make mechanisms releasing social behaviour less specific. Furthermore, long-domesticated zebra finches in Europe seem to behave 'hyper-sexually' (IMMELMANN 1962). Similar consequences of domestication may also have appeared in budgerigars. This could possibly explain the unspecificity of courtship singing. However, this question can be solved only by studying birds living free. The great number of partner-specific behaviour patterns found in this study suggests that a substantial part of the original behavioural specificity still exists.

Which mechanism effects partner-specificity?

It has been shown in part A. that common site preference is not enough to maintain partner-specificity. As pair partners reunite after losing sight of each other, they must recognize each other by means of individual characteristics (i. e., distinguish and remember). The least requirement is that one partner should be able to recognize the other. The observed partner-specificity of many behaviour patterns in ♂♂ and ♀♀, however, indicates that both partners of a pair recognize the other individually. This is supported by teleonomic considerations, as otherwise the naive partner would be at the mercy of 'deception' by others. Individual recognition is the simplest mechanism accounting for all observed partner-specificity. A demonstration of the ability for individual recognition in both sexes is given by Trillmich (1976).

Not all social behaviour patterns are partner-specific, however, nor are all partner-specific behaviour patterns specific to the same degree. Individual recognition of the partner can explain why all partner-specific behaviour patterns are directed almost without exception at one individual, but not why only certain behaviour patterns are partner-specific. The causes for the latter limitation must be sought in other properties of the individual.

Internal causes of partner-specific behaviour patterns

Pair sitting, approach to a partner, allopreening, beak touching, courtship feeding, copulation, the beak-thrust inhibition of ♀♀ and the infrequency of fleeing in ♂♂ were partner-specific in all budgerigars observed. These behaviour patterns cannot all be attributed to one unitary drive. Allopreening and beak touching were closely connected to a preening tendency, courtship feeding to the courtship tendency. Copulation was also partner-specific. Beak touching and allopreening cannot be regarded as low-threshold sexual activities; these behaviour patterns were never or rarely displayed by 2 ♂♂ and 2 ♀♀ to their nonmate copulation partners.

Aggression and flight, again, belong to quite different behaviour complexes. Lamprecht (1973) and Reyer (1975) suggested, on the basis of investigations on fish, that aggressive behaviour is partner-specifically inhibited by the perception of the partner's individual characteristics. This explanation can be adopted here for the beak-thrust inhibition of ♀♀. The partner-specific low rate of fleeing in ♂♂ is adequately accounted for by the low rate of female attack upon their mates.

Fischer (1965), and Wickler and Seibt (1972), suggested the existence of an attachment drive underlying the partner-specific behaviour of the greylag goose and the shrimp *Hymenocera,* which could explain both the triumph ceremony of the greylag goose and the pair-sitting of *Hymenocera.* But other motivations, e. g. sexual and preening tendencies, are most likely involved in budgerigar partner-specific behaviour patterns, as well as a possible attachment drive. Accordingly, simultaneous activation of the attachment drive and of one of the above-named tendencies should lead to a partner-specific behaviour pattern specific for that particular mixed motivation. A hypothetical model assuming just such interactions between internal variables has been evolved by Bischof (1975) for the interrelation between fear and attachment behaviour.

Functional aspects of pair cohesion

WICKLER and SEIBT (1975) interpreted the increasing acquaintance of individuals, and the construction of an expectation of how the partner will act or react, as a process of adjustment, making life simpler by reducing the occurrence of the unexpected. As the results here given demonstrate a clear diversity in the organization of individual behaviour, such an economy in its relationships would benefit the individual. Individual recognition and an enduring pair-bond are 2 factors favouring the construction of such an expectation of how the partner will act or react.

There are already clear references in the literature to the mutual adaptation of mates. GWINNER (1964) reports that ravens showed courtship display less often in the course of a long partnership, while several pairs developed diverse 'rituals' in courtship feeding. DILGER (1960 and pers. comm.) gave similar reports on *Agapornis* parrots and FISCHER (pers. comm.) on greylag geese. The studies of v. HELVERSEN and WICKLER (1971) and GÜNNIGMANN (1973) on the construction of the Drongo (*Dicrurus adsimilis*) duetting showed that different pairs sing different duets. The song of a pair-partner is determined partly by his own song-program, partly by responses to the song elements of the mate. This response relationship apparently develops through learning, in the course of pair formation. There are even indications that the birds learn to predict particular sequences of elements in the song of the partner. All these examples show that the animals have learned more and more accurately to assess the partner's reactions and readiness to act, and to adjust their (re-) actions accordingly.

Budgerigars are sexually stimulated by the song of conspecifics (BROCKWAY 1969), and in this way their gonads probably remain active throughout the year in the wild, as shown for zebra finches (FARNER, pers. comm. in IMMELMANN 1963); pairs form outside the breeding season in the flock, and stay together throughout the year. IMMELMANN (1963) calls this type of pair formation and pair bond maintenance the '♂-♀' type, in contrast to the '♂-nest' type or '♂-territory' type more common in the temperate zone. The permanent cohesion of pairs in the flock outside the breeding season probably developed under the selective pressure of the unpredictability of rainfall, creating favourable breeding conditions in arid central Australia (IMMELMANN 1963). When rainfall starts, permanent pairs can begin breeding with minimum delay (a few days to 2 weeks) and so achieve maximum reproductive success in the brief spell propitious for rearing young. For 2 gull species, COULSON (1966) and MILLS (1973) could show that pair partners retaining the pair bond of the previous season have greater breeding success than birds with equivalent breeding experience paired for the first season.

Acknowledgement

I would like to thank Prof. Dr. W. WICKLER for enabling me to carry out these observations, for many helpful discussions and suggestions throughout the work and for his constructive criticism of the manuscript. For discussions and criticism I am also most grateful to Dr. R. FERNALD, who in addition spent much time teaching me FORTRAN IV, to Dr. J. LAMPRECHT, Dr. J. NICOLAI, Dipl.-Biol. C. RECHTEN, Dipl.-Biol. I. SCHEURMANN, Dr. U. SEIBT and Dipl.-Biol. P. WIRTZ. I thank Miss B. KNAUER for drawing the graphs, and Mrs. P. RECHTEN for the translation, and the many incidental discussions.

Summary

It was attempted to show how much the behaviour of budgerigars to their mates is modified by the pair bond, and thus differs from their behaviour to other potential partners.

Pairs sit together much more frequently than unpaired birds, or than can be expected assuming independent movement of birds having given site preferences. In addition to sitting together, all birds show a tendency to stay closer to each other than expected. This tendency is presumably responsible for flock cohesion in budgerigars. ♂♂ are more active than ♀♀, and contribute more to the spatial cohesion of pairs.

Partner-specific behaviour is defined as behaviour shown significantly more often or less often to the partner than to others, within a certain period of sitting together. Of the behaviour patterns studied, allopreening, beak touching, courtship feeding, adult food begging and copulation are partner-specific in all birds. Agonistic behaviour is partner-specifically rare. Other behaviour patterns such as courtship singing, singing and preening are not equally partner-specific for all birds.

The partner-specific behaviour patterns beak touching and allopreening are coupled with a tendency to preen, courtship feeding with a tendency to courtship song. There are clear differences in the social behaviour of individuals.

Possible influences of captivity on the behaviour investigated are discussed. The partner-specificity of the behaviour patterns mentioned is based on individual recognition of the partner. As partner-specific behaviour patterns appear in many different motivational connections, a single cause cannot be assumed. The function of a firm pair bond could be to help partners adjust to each other; it could also be an adaptation to the unpredictability of favourable breeding conditions in the natural habitat.

Zusammenfassung

Es wurde zu klären versucht, wie stark die Verpaarung das Verhalten von Wellensittichen zum Paarpartner im Vergleich zu ihrem Verhalten zu anderen möglichen Partnern verändert. Paare sitzen weit häufiger zusammen als nicht verpaarte Vögel und als auf Grund der Annahme unabhängiger Bewegung der Vögel bei gegebenen Ortsbevorzugungen zu erwarten ist. Über dieses Zusammensitzen hinaus zeigen alle Vögel eine Tendenz, dichter als erwartet beieinander zu bleiben. Diese Tendenz ist vermutlich die Ursache für den Schwarmzusammenhalt der Wellensittiche. Zum räumlichen Zusammenhalt tragen die aktiveren ♂♂ mehr bei als die weniger aktiven ♀♀.

Partnerbeschränktes Verhalten wird als Verhalten definiert, das in gleichen Zeiträumen des Zusammensitzens signifikant häufiger oder seltener gegenüber dem Paarpartner als gegenüber anderen Tieren gezeigt wird. Von den näher untersuchten Verhaltensweisen sind Kraulen, Schnabelberühren, Füttern, Futterbetteln und Kopulation bei allen Vögeln partnerbeschränkt. Aggressives Verhalten und Fluchtverhalten sind partnerbeschränkt selten. Andere Verhaltensweisen wie Ansingen, Singen und Putzen sind nicht für alle Vögel gleichartig partnerbeschränkt.

Die partnerbeschränkten Verhaltensweisen Schnabelberühren und Kraulen treten häufiger zusammen mit Putzen, Balzfüttern häufiger mit Ansingen auf. Zwischen Individuen bestehen im Sozialverhalten deutliche Unterschiede.

Mögliche Gefangenschaftseinflüsse auf das untersuchte Verhalten werden diskutiert. Die Partnerbeschränkung der genannten Verhaltensweisen beruht auf individuellem Erkennen des Partners. Da partnerbeschränkte Verhaltensweisen in vielen verschiedenen Motivationszusammenhängen auftreten, kann man für sie keine einheitliche Ursache annehmen. Funktionell könnte der feste Paarzusammenhalt beim Wellensittich Paarpartnern erleichtern, sich aufeinander einzustellen, und außerdem eine Anpassung an die Unvorhersagbarkeit günstiger Brutbedingungen im natürlichen Biotop sein.

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