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The Influence of Separation on the Pair Bond in Budgerigars (*Melopsittacus undulatus*; Aves, Psittacidae)

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With 7 figures

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Abstract

In a group of budgerigars, former pair partners resumed the bond after periods of up to 70 days spent in unisexual groups. The bond was measured from mate-specific behaviour. Choice of partners according to common site preference or degree of quality rather than individual characteristics could be excluded. Mates paired again when reassociated, after 20 days of separation spent with other potential partners. Birds having paired for equal periods with two successive mates preferred the more recent when both were available. Predictability of interactions is suggested to be an important variable influencing choice of a partner after separation.

The maintenance of a pair bond does not merely require that animals should be able to distinguish between 2 or more individuals; they must also be able to remember the mate's characteristics during periods of separation. To re-cognize the partner they must check that the observed characteristics tally with those memorized. Only thus can the partner-specificity of certain behaviour patterns be achieved.

Birds have been proved to be capable of remarkable feats of memorizing. White-throated sparrows still recognize each other after 17 days (WESSEL and LEIGH 1941), black-crowned night herons after 20 days (NOBLE, WURM and SCHMIDT 1938), Bobwhite quails after 3 weeks (STETTNER, MISSAKIAN and LOREN 1966), chickens after 30 days (ENGELMANN 1951), bullfinches after 6 months (NICOLAI 1956), ringdoves up to 7 months (MORRIS and ERICKSON 1971) and sea birds (e. g. Adélie penguins, PENNEY 1968, kittiwakes, COULSON 1966) even after a year. Presumably fidelity to the nest site is an aid to sea birds in finding their last year's mate.

According to CINAT-THOMSON (1926), the pair bond in budgerigars dissolves after 4—5 days of the partner's absence. She always separated the birds 1—4 days after pairing. BROCKWAY (1964), on the other hand, quotes evidence that pairs mated for several months can be separated for weeks without destroying the pair bond.

This paper describes 4 experiments investigating how long and under what conditions the pair bond of budgerigars (and therefore the recollection of pair partners) survives periods of separation. Budgerigars are especially

suitable for these experiments, as relationships are clearly indicated by mate-specific behaviour (described in TRILLMICH 1976).

The experiments were to provide answers to the following questions:

1. After how long a separation can a pair bond still be proved? (Experiments 1 and 2).
2. Does the bond to a former partner dissolve sooner in association with budgerigars of the same or of the opposite sex? (Experiments 3 and 4).

Methods

Criteria of recognition after separation

After a separation, it was observed whether the birds again addressed partner-specific behaviour (allopreening, beak touching, courtship feeding) to their former mates. Such behaviour is shown to a former partner only when the old bond is still extant, or is latent and resumed after recognition, or when a new random mating has occurred with the former partner. The probability that a new bond has by chance replaced an old one can be calculated; if it is very remote, then the alternative possibility, i.e., that the birds have recognized each other, must be accepted.

If in a group a first ♂ fails to recognize his mate after a separation, and tries to form a new bond with any ♀, then the probability of choosing his former mate by chance from among N ♀♀ is 1/N. If it is assumed that a mated ♀ is no longer available to mate-seeking ♂♂, then for a second ♂ seeking a mate among N ♀♀ the probability of finding his former mate by chance would be 1/N-1, etc.

Accordingly, if in a group of 6 pairs 4 birds pair with former mates after a separation, the probability for the chance occurrence of this is:

$$p = \frac{1 \cdot 1 \cdot 1 \cdot 1}{6 \cdot 5 \cdot 4 \cdot 3} = 0.0028$$

This estimation of the probability of 'correct' chance pairing after a separation is rather too high than too low, because:

a) The probability of a chance 'correct' pairing after a separation would be much less if it is assumed that to form a pair, *both* birds must exercise a choice. If each chose independently of the other, then the probability of their chance reunion would be, for the first pair, $1/N^2$.

b) The above calculation presumed that the ♂♂ first mating chose their former partners. Otherwise, the former partner of the chosen ♀ is unable to mate with her. The probability of mating with his former partner is zero for this bird.

c) If it is assumed that ♀♀ already paired are still accessible to ♂♂ as yet unpaired, then the probability of choosing the correct former partner is, for all ♂♂, 1/N.

Methods of observation

All birds in an aviary were observed simultaneously. Allopreening, beak touching and courtship feeding were immediately protocolled. If material accumulated for some pairs, attention was concentrated on birds interacting less often. The recorded frequencies of partner-specific behaviour do not therefore represent the absolute number of interactions during an observation period, but principally the distribution of interactions among individuals. As the protocolled behaviour patterns in adult birds are exclusively (allopreening) or essentially (beak touching and courtship feeding) directed at the partner, this frequency distribution is a faithful representation of pair formation in a budgerigar group.

In a method check, a naive observer was able to identify all 4 pairs in an aviary within an hour.

Method of presentation

In the first experiment in which they took part, each of a pair of birds was given the same number, which they retained throughout the experiments even if they later changed mates. For this reason pair partners may not always have the same number. ♂♂ and ♀♀ are so arranged in the figures that partner-specific behaviour between birds formerly mated is shown in the diagonal of the matrix.

The figures give the frequencies/h of the observed behaviour patterns; total observation times are given in the legends.

In the first h after reunion, budgerigars showed partner-specific behaviour much more frequently than later on. For this reason observations made during the first h after the birds were reassociated, and those made in the course of the next few days, are usually given separately. In this way partner-specific behaviour occurring immediately after separation, during the first meeting of ♂♂ and ♀♀, is emphasized. Directly after having been brought together again, the birds had scarcely had an opportunity to build a relationship to a new partner; so that the old bond should be particularly obvious, if it had not been annihilated by separation.

Results

1. After how long a separation can a pair bond still be proved?

Experiment 1: 20-day separation

The experiment was conducted with 7 pairs. Age and history of the birds are contained in Table 1.

Table 1: Age and history of birds in experiment 1

Pair	age (months)		No. of matings*		Duration of present mating (months)
	♂	♀	♂	♀	
1,1	18	18	1	1	15
2,2	18	18	1	2	10
3,3	18	18	1	1	15
4,4	18	18	1	1	15
5,5	18	16	2	1	10
6,6	18	18	1	1	12
7,7	18	18	3	2	1.3

* Including the present one.

All birds were well mated before being separated (judged by partner-specific behaviour). During the 20-day separation all ♂♂ were housed together in an aviary, all ♀♀ were placed in another aviary, unknown to both them and the ♂♂. No homosexual pairs formed during the separation. Terminating separation, all ♂♂ were released simultaneously to the ♀♀ in their aviary in the morning. Fig. 1 shows the total of partner-specific interactions during the first h of reassociation (left of capitals) and in further 3 h of observation in the evenings of the 1st, 2nd and 3rd days (right of capitals). Pairs 1—3, 6 and 7 already showed many partner-specific interactions in the first h of reunion. Pair 7 formed immediately, although the birds had been mated for only 40 days before separation. Pair 4, too, formed again during the observation time.

♂5 beak touched with ♀5 (his former mate) in the first 15 min after reassociation. He then persistently followed ♀2, to whom he had been mated 10 months previously for a period of 6 months. ♀5 was observed to follow ♂5 time and again, from which it can be assumed that she still had a special relationship to him.

Of the 14 birds 12 paired as before. The possibility of this occurring at random is $p = 0.0002$. It may therefore be concluded that the pair partners recognized each other individually after a 20-day separation, and formed pairs again on this basis.

An alternative possibility is that ♂♂ chose according to the quality of the ♀♀. Investigation of this contingency was included in the next experiment.

♂♂ \ ♀♀	1	2	3	4	5	6	7
1	2.0 A 1.0 24.0 B 9.3 F 1.0						
2		3.0 A 1.0 9.0 B 6.0 F 2.7					
3			3.0 A 0.7 12.0 B 4.7 F 0.7				
4				A 0.7 4.0 B 6.3 F 4.7			
5		A 0.3 B 4.3 F			A 1.0 B F		
6						A 0.3 10.0 B 9.7 F 0.3	
7							A 3.7 16.0 B 4.7 F

Fig. 1: Partner-specific behaviour after 20-day separation. A = Allopreening, B = Beak touching, F = Courtship feeding. Figures left and right of capitals denote observations for 1st h, and average for 3 further h respectively. Square 5 : 2 shows a pair which broke up 10 months before the experiment began. Interactions between former mates lie on the diagonal. The top row gives identification nos. of ♀♀, the left hand column those of ♂♂

Experiment 2: 70-day separation

In addition to the mnemonic performance of the budgerigars, this experiment investigated whether the ♂♂ seek out ♀♀ according to general quality rather than individual characteristics. This concept seems from the outset very improbable in budgerigars, but it can be tested experimentally if each ♂ is allowed to choose without the interference of other ♂♂. If all ♂♂ choose according to the same criterion of quality, their choice should invariably fall upon the same ♀.

7 pairs participated in this experiment, pairs 10,10 and 11,11 had been mated by being caged together, ♀3 and ♂12 were mother and son. For further details see Table 2.

Table 2: Age and history of birds in experiment 2

Pair	age (months)		No. of matings		Duration of present mating (months)
	♂	♀	♂	♀	
1,1	32	32	1	1	27
5,7	32	32	3	3	11
8,12	20	32	3	3	1
9,9	32	32	3	4	2
10,10	19	19	2	1	4
11,11	19	19	2	3	1
12,3	19	32	1	2	5

The 7 pairs had lived together in an aviary for a month before separation. At this time all birds showed partner-specific behaviour only to the partner. The ♀♀ spent the separation period in an aviary formerly unknown to all birds, while the ♂♂ stayed in the original aviary.

♂♂ \ ♀♀	1	7	12	9	10	11	3	t [min]
1	A B 39 F							10
5	A B 9 F	A B 58 F						30
8	A B 32 F	A B 6 F						60
9				A B 4 F				60
10	A B 12 F				A B 67 F	A B 9 F		60
11						A B 31 F		60
12							A 2 B 33 F	60

Fig. 2: Partner-specific behavior after 70-day separation. Each ♂ was introduced singly to the 7 ♀♀. Total no. of behaviour patterns observed during time spent by each ♂ (extreme right column) in the ♀♀'s aviary. Further explanations in text. Symbols as in Fig. 1

On the 70th day the ♂♂ were released singly to the ♀♀ in their aviary, the order being 1, 12, 5, 8, 9, 11, 10. Each was watched for 10—60 min (Fig. 2), and removed again before the next ♂ was introduced. In this way each ♂ could choose between all ♀♀ without the interference of others.

Of the 7 ♂♂ tested, 4 showed partner-specific behaviour exclusively with their former mates (♂♂ 1, 9, 11 and 12; see Fig. 2). The remaining 3 ♂♂ interacted with more than 1 ♀, and all showed some partner-specific behaviour to ♀1. All 3 ♂♂ except ♂8 first showed partner-specific behaviour to their former mates; but only ♂10 showed preference for his former mate as long as observation continued. ♀♀7, 9 and 10 fiercely repulsed advances made to their mates by other ♀♀, especially by ♀♀ 1 and 10, who approached every ♂ released. Of the ♀♀, at least these 3 defending their mates took an active part in the process of rebonding.

♂♂ \ ♀♀	1	7	12	9	10	11	3
1	A 24.0 B 0.8 F						
5	A B 7.3 F	A 64.0 B 5.3 F 0.8	A B 6.5 F 1.5				
8	A 7.0 B 3.0 B 0.8						
9			A 1.0 B 0.5 F	3.0 A 0.5 19.0 B 1.8 F			
10		A B F 0.3			A 4.5 75.0 B 16.0 F 1.3		
11	A B F 0.3					A 0.3 7.0 B 9.8 F	
12							20.0 A 6.3 38.0 B 10.8 F 1.8

Fig. 3: Partner-specific behaviour after 70-day separation. All ♂♂ were introduced simultaneously to the ♀♀. Figures left and right of capitals denote observations for 1st h, and average for 4 further h respectively. Shaded squares indicate with which ♀♀ the ♂♂ interacted when introduced singly (Fig. 2). Symbols as in Fig. 1

All ♂♂ were released in the ♀♀'s aviary next morning simultaneously. Fig. 3 gives the total of observed partner-specific behaviour patterns in the first h (left of capitals) and in 4 h of observation during the next 2 days (right of capitals). In the first h all ♂♂ except ♂8 interacted almost exclusively with their former mates. In the following 2 days ♂5 showed partner-specific behaviour consecutively to ♀1, ♀12, and then mainly to ♀7, his former mate. ♂8 remained almost constantly with ♀1, thwarting most approaches of ♂1, who obviously recognized his formre mate but could not compete. The other 4 ♂♂ continued to show partner-specific behaviour almost exclusively to their former mates. The 4 pairs (or 5 counting pair 1,1) were those which had addressed partner-specific behaviour exclusively or essentially to each other in the individual tests of ♂♂ (Fig. 2). The probability that 4 pairs out of 7 reunited at random is $p = 0.0012$, or, calculated for 5 pairs, $p = 0.0004$. Budgerigars can therefore renew an earlier pair bond after a separation lasting 70 days.

Conclusions from experiments 1 and 2

According to these observations ♀1 was the most attractive of the tested ♀♀. But she took precedence only for her former mate and ♂8. In a 3rd separation experiment, however, (see below), ♀1 remained unpaired during a 20-day separation from her mate — and that in the presence of 2 unpaired ♂♂, one of which was ♂8.

Probably ♀1 drew the attention of the ♂♂, after 70 days of separation, by approaching them immediately and following them constantly. This unusual behaviour was also observed in ♀10, and may have been caused by the long separation of ♂♂ and ♀♀.

As in the individual tests ♂♂9, 11 and 12 practically ignored ♀1, and ♂10 heeded her less than he did his former mate, it is assumed that no standard of quality valid for all ♂♂ existed among the budgerigars taking part in this experiment.

The 'correct' reunion of the budgerigar pairs after 20 and 70 day periods of separation can therefore be explained only by the individual recognition of partners.

2. Does the bond to a former partner dissolve sooner in association with budgerigars of the same or of the opposite sex?

Experiment 3: 20-day association with birds of the opposite sex

The birds in the first 2 experiments were confined during separation with others of the same sex. The old partner-bond might dissolve sooner if birds of the opposite sex — potential partners — were present during separation. To investigate this hypothesis the separated mates were first kept for 20 days in association with budgerigars of the opposite sex.

Two groups, each containing 4 pairs of birds, took part in the experiment. 5 of the 8 pairs had been paired by caging them together. Details of the birds' history are given in Table 3.

The pairs had been mated for about 3 months; groups 1 and 2 were placed in aviaries optically and acoustically isolated from each other and each group was observed for 2 h. At this time all pairs were firmly mated (Fig. 4, left). The ♂♂ of the groups were then exchanged, and the new groups thus formed retained for 20 days.

During separation of the original pairs, 2 new pairs formed in each group (Fig. 4, centre).

Table 3: Age and history of birds in experiment 3

Pair	age (months) ♂	age (months) ♀	No. of matings ♂	No. of matings ♀	Duration of present mating (months)	
1,1	30	30	1	1	27	Group 1
5,7	30	30	3	3	9	
10,10	17	17	2	1	2	
13,9	30	30	2	3	3	
8,11	17	17	2	2	3	Group 2
9,12	30	30	2	2	3	
11,14	17	17	1	1	3	
12,3	17	30	1	2	3	

After 20 days of separation the ♂♂ were returned to the groups containing the original partners. 7 of the 8 former pairs recombined within 25 min. Pair 8,11, which had stayed unmated during the separation, did not recombine, and neither partner showed obvious interest in any other bird (Fig. 4, right). The 4 ♂♂ and 4 ♀♀ which had formed new pairs during the separation (always both partners of a pair) all resumed the old pair bond; 2 of these pairs (13,9 and 9,12) did not allopreen however during the 7½ h of observation after reassociation.

The probability of the random occurrence of such a re-mating is $p = 0.002$. The budgerigars must have recognized each other after 20 days spent apart but with other birds of the opposite sex, although some formed new pairs during this time.

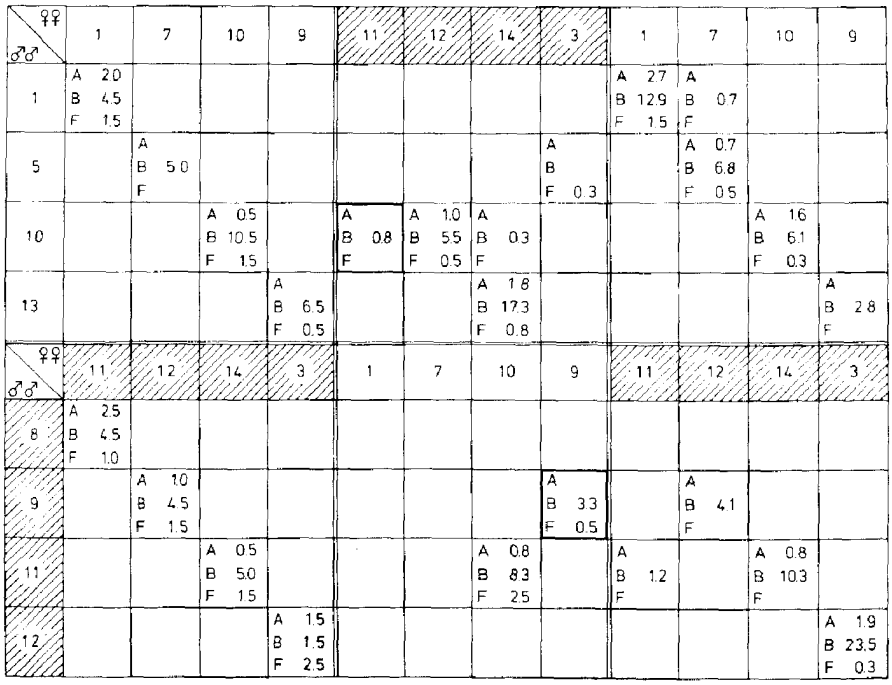

Fig. 4: Partner-specific behaviour in 2 budgerigar groups. On left: Average for 2 h observation before separation. Centre: Average of 4 h of observation during 20 days spent with birds of the opposite sex, from the other group; heavy outlines denote pairs which split up at least 3 months before the experiment began. On right: Average of 7½ h observation after close of 20-day separation from first partners. Birds of group 2 shown in shaded squares. Explanations in text. Symbols as in Fig. 1

All birds were then placed together in an aviary but not systematically observed. It can be stated, however, that pairs 1,1, 5,7, 10,10, 11,14 and 12,3 stayed together; ♂9 paired immediately with ♀9; ♀♀11 and 12, and ♂♂13 and 8 remained unpaired for a week. That is to say, the 2 pairs which had not allopreened after reunion split up. In 5 of the 8 pairs the primary mates stayed together.

Experiment 4: Primacy versus recency

For the birds in experiment 3, the second mating periods were much shorter than with their first partners (comp. Table 3). Experiment 4 was designed to show whether the birds would still prefer the former mate if they had spent equally long with a second partner, and bred with both.

All birds were newly obtained from the dealer and had just moulted into adult plumage. It is not known whether any had been previously mated.

2 groups of 4 pairs were placed in separate aviaries, nesting boxes were provided and the pairs were left together for 57 days, until or almost until the end of egg-laying. All pairs except 18,18 laid 4 or 5 eggs (left, Fig. 5).

♀♀ of the 2 groups were then exchanged, and the 2 new groups thus formed were provided with fresh nesting boxes in optically and acoustically separate aviaries, where they remained for 57 days. In this situation ♂♂16 and 17, and 19—22 mated with a ♀ each. ♂18 did not pair during this time. ♂15 paired with 2 ♀♀ (20 and 21); he copulated with both, was allopreened by both and fed both. ♀22 died of egg binding. ♀18 laid only 2 eggs, all others 4—5 (Fig. 5, right).

On the 57th day after separation from the primary mates all birds were reassociated in an aviary without nesting boxes. They were thus free to choose between the primary and the more recent partners. Fig. 6 (left of capitals) shows that in these circumstances the birds remained with their more recent partners. During 7 days (5 h observation) no bird showed any partner-specific behaviour over against the primary mate.

♀♀ / ♂♂	15	16	17	18	19	20	21	22
15	5 eggs					4 eggs	4 eggs	
16		5 eggs			5 eggs			
17			5 eggs					1 egg †
18				0 eggs				
♀♀ / ♂♂	19	20	21	22	15	16	17	18
19	4 eggs						4 eggs	
20		4 eggs			4 eggs			
21			5 eggs			5 eggs		
22				5 eggs				2 eggs

Fig. 5: Pairs in 2 budgerigar groups. Left: First mating, Right: Second mating. Birds of group 2 are identified by shading. Symbols as in Fig. 1

♂♂ \ ♀♀	15	16	17	18	19	20	21
15						A 0.2 0.8 B 4.1 F 2.7	3.6 A 0.9 16.6 B 12.0 0.4 F 1.7
16					A 0.7 3.6 B 0.9 1.4 F 1.1		
17					A 0.2 B 0.4 F 0.3	A B 0.6 F	A B F 0.4
18							
19			1.8 A 0.6 6.8 B 5.1 0.4 F 1.4				
20	1.2 A 0.5 8.2 B 15.2 0.6 F 1.3						
21		0.6 A 0.5 16.4 B 12.9 2.2 F 1.8					A B F 0.3
22			A B 0.1 F 0.2	0.4 A 1.2 5.2 B 9.4 0.6 F 1.1		A B F 0.1	

Fig. 6: Partner-specific behaviour in the simultaneous choice between 1st and 2nd partners. Left of capitals: Average of 5 h observation time without nesting boxes. Right of capitals: Average of 10 h observation time after nesting boxes were provided. Birds of group 2 are identified by shading. Explanations in text. Symbols as in Fig. 1

After 7 days the birds were provided with nesting boxes for 19 days; all bred with the recent mate (Fig. 6, right of capitals). ♂18 again stayed unpaired. ♂17, whose recent mate had died (♀22), courted ♀♀19—21, in whose company he had recently been, but not his primary mate. ♂21 fed his primary mate 3 times. Except for this case, which of course is by no means conclusive, there was no indication that the birds retained any sort of relationship to the primary partner after breeding with a second.

Experiment 2 showed, however, that budgerigars can remember a mate for 70 days when kept for that time in unisexual groups. Was there still any demonstrable relationship, however faint, to the first mate? To solve this question the birds were again sorted, after 19 days with nesting boxes, into

♂♂ \ ♀♀	15	16	17	18
15		A B 3.7 F 0.3	A 0.3 B F	
16		A B 0.7 F	A B 0.3 F	
17		A 9.0 B F	A 0.3 7.0 B 4.0 0.3 F	A B 4.7 F 0.7
18	A 1.0 B 15.0 F 1.7	A 5.0 B 0.3 F		A B 0.3 F

♂♂ \ ♀♀	19	20	21
19	A 5.3 B 27.3 F 2.0	A B 4.7 F 0.3	
21			A 1.3 B 24.7 F 3.7

Fig. 7: Partner-specific behaviour in group 1 (above) and group 2 (below), after the birds were reassociated with the primary partners. Left of capitals: Average of 3 h observation without nesting boxes. Right of capitals: Average of 3 h observation after nesting boxes were provided. Explanation in text. Symbols as in Fig. 1

2 groups consisting of the primary partners, one group containing 4 ♂♂ and 4 ♀♀ and the other 3 ♂♂ and 3 ♀♀.

During 10 days before nesting boxes were provided very little partner-specific behaviour was shown by birds in either group (Fig. 7, left of capitals). ♂20 died at the end of this period, and therefore does not appear in Fig. 7. ♀16 in group 1 seemed at first to be forming a pair with ♂18, but then showed partner-specific behaviour only with ♂17, who had begun courting his primary mate.

As soon as nesting boxes were hung in the aviary, the birds began forming firm pairs. In group 1, ♂17 paired with both his primary mate and ♀18. ♂♂ 15 and 18 mated with ♀♀ 16 and 15 respectively, not their primary mates, and ♂16 stayed unmated, although he showed interest in his primary partner, now mated to ♂15.

In group 2 (now only 2 ♂♂ and 3 ♀♀) ♂21 and his primary partner became firmly mated. On the 1st observation day ♂19 beak touched with ♀20, but subsequently paired with ♀19 (Fig. 7, right of capitals); in this pairing ♀19 was apparently more active than ♂19, as she supplanted ♀20.

3 out of 7 ♂♂ paired again with their primary mates when separated from their second mates. 2 other ♂♂ showed interest in their primary mates, approaching them frequently. The random probability for the formation of 3 pairs as before is $p=0.042$ ($1/3 \cdot 1/2 \cdot 1/4$). For the ♀♀, however, the probability of such a random mating is $p = 0.125$ ($1/2 \cdot 1/4$) because in group 2 their choice was between 2 ♂♂ only; so that in this case it cannot be maintained with certainty that the birds still preferred and therefore had recognized their first partners. In comparison with the results of the other separation experiments it can be stated that a 57-day separation from a partner, and breeding with a second partner in this interval, strongly reduces the preference for the primary mate.

Discussion

Pair partners reunite after a separation of up to 70 days if kept in a unisexual group during this time. The pairs cannot have reunited on the basis of a common site preference, as in experiments 1 and 2 they were reassociated in aviaries in which they had never been together before. Nevertheless most birds directed their partner-specific behaviour mainly towards the partner. They must have remembered and recognized him (her) therefore.

The period of separation weakens the bond, however; pairs broke up after separation more often than pairs living normally together. Long separated budgerigar pair partners show courtship feeding and beak touching less partner-specifically at first than equally long mated pairs having been together all the time. This lack of selectivity usually dwindles within a few h, until beak touching is once again directed exclusively at the mate. Or it may lead to approaching another bird and a change of partners. From these experiments it is impossible to say whether this lack of selectivity stems from uncertainty in recognizing a partner, or whether the threshold of this normally partner-specific behaviour is lowered by the long separation from birds of the other sex.

Most birds kept in unisexual groups during separation had apparently preserved a latent bond to the mate. The capacity to preserve a latent bond for some time is probably a byproduct of the exact learning of all the characteristics and properties of the partner. If pair partners in the wild lose contact for some time outside the breeding season, when the birds range over great distances, it is unlikely that they will ever find each other again. Preservation of the bond to the first partner would then even be detrimental, as the birds

might forego favourable breeding conditions which they might have utilized with a new partner.

Budgerigars in the wild do not live in unisexual flocks, however. Experiments 3 and 4 were therefore designed to establish how the birds would react to the original mate after a separation, if they could mate with a second partner in the interval.

The significance of familiarity for the reunion of mates

ZAJONC (1971), working with human subjects, was able to demonstrate that "the mere repeated exposure of an individual to a given stimulus object is a sufficient condition for the enhancement of his attraction toward it". Similarly in lambs the strength of the attachment response increases with time of exposure and the attachment might be reversed by a long time of exposure to a second stimulus (CAIRNS 1966).

The observations on the budgerigars' partner-choice in the separation experiment suggest that the aforementioned 'latent bond' is a byproduct of the familiarity of partners. Familiarity does not here mean individual recognition only, but a high degree of certainty with which 2 individuals can predict the outcome of interactions on the basis of precise knowledge of each other. Length of acquaintanceship presumably correlates with the precision of knowledge about an object. Possibly the birds chose according to this kind of familiarity. This concept agrees well with ZAJONC's and CAIRNS' findings and could explain all experimental results satisfactorily.

In the first 3 experiments the first partner was always the best known in the group of available birds. In the choice situation in experiment 4 the second partner, with whom the birds had most recently bred, was the best known. Quite evidently, all birds preferred to retain the existing bond with the second partner rather than seek a possible renewal of the bond to the first. Later, however, separated from the second partners, they seemed to prefer the primary mate.

It is to be expected that the longer mates have known each other, the longer is the period of separation after which they will still prefer each other. But this preference, or the period it bridges, certainly does not increase linearly with the previous duration of the pair bond, as on the 100th day budgerigars will hardly learn as many new details about the partner as on the 1st or 10th day of their association.

The findings of CINAT-THOMSON (1926) and BROCKWAY (1964) correspond exactly with predictions possible from such a concept. CINAT-THOMSON (l. c.) separated newly-paired budgerigars. It needed only a short separation to cancel out any advantage to the birds from choosing the former partner, as they scarcely knew him better than any other bird. In the cases mentioned by BROCKWAY (1964), and the experiments reported here, all birds could gather a great deal of experience with first partners before they were separated. They therefore still preferred the first partners even after several weeks of separation.

Breeding with a familiar partner can yield advantages, as is shown for gulls by COULSON (1966) and MILLS (1973). These authors also showed that breeding success or failure with a given partner strongly influences the probability of remating in the next breeding season. Further possible advantages of staying with a well known individual are discussed by WICKLER and SEIBT (1975).

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Summary

Experiments were designed to show for how long the budgerigar pair bond can survive a separation of partners. In addition tests investigated whether, in the interval of separation from the first mate, experience with a second partner weakened the earlier pair bond more than spending the time without potential partners.

Mates resumed the bond after a 70-day separation when they had spent the intervening time in a unisexual group. The resumption of the bond was measured from mate-specific behaviour patterns addressed to the former partners. The ♂♂ did not choose according to a general quality standard among the ♀♀, but recognized their former mates individually.

Birds having been mated for 2 months or more, and parted for 20 days which they spent with other potential partners, paired again with the first partner when reassociated. Birds which paired for 57 days each with 2 successive partners, and bred with both, preferred the second mate when offered a choice at the end of the second 57-day period. When they were then separated from the second partner, and placed in groups containing the first, only a few birds paired again with the primary mate. A period of bonding to a second partner, therefore, exerts a stronger influence on the first pair bond than a longer separation spent without potential partners.

The results of the 4 experiments could be explained by the degree of familiarity of birds. Familiarity here means not only individual recognition, but the capacity to anticipate the partner's actions correctly from exact knowledge. After all separation experiments the budgerigars usually chose the most familiar bird as their new partner.

Zusammenfassung

Die Experimente sollten zeigen, wie lange Trennungszeiten die Bindung von Wellensittich-Paarpartnern überdauern kann. Außerdem wurde getestet, ob die Verpaarung mit einem Zweitpartner die Bindung an den Erstpartner stärker schwächt als eine gleichlange Trennung von ihm ohne Paarungsmöglichkeit.

Paarpartner nahmen nach bis zu 70tägiger Trennung die Bindung an den alten Partner wieder auf, wenn sie in der Trennungszeit nur mit gleichgeschlechtlichen Vögeln zusammen gehalten wurden. Die Bindung wurde am Auftreten partnerbeschränkten Verhaltens mit dem früheren Partner gemessen. Die ♂♂ wählten die ♀♀ nicht nach einem Güteklassenmerkmal aus, sondern erkannten ihren früheren Partner offensichtlich individuell wieder.

Vögel, die 2 oder mehr Monate verpaart waren und für 20 Tage getrennt vom Erstpartner mit anderen möglichen Partnern zusammen gehalten wurden, verpaarten sich nach der Trennung wieder mit dem Erstpartner. Vögel, die

nacheinander mit 2 Partnern je 57 Tage zusammen waren und mit beiden brüteten, blieben beim Zweitpartner, als sie anschließend zwischen Erst- und Zweitpartner wählen konnten. Danach wurden sie vom Zweitpartner getrennt und zusammen mit anderen Vögeln zum Erstpartner gesetzt. Unter diesen Bedingungen wählten einige Vögel wieder den Erstpartner. Bindung an einen Zweitpartner hatte einen stärkeren Einfluß auf die Bindung an den Erstpartner als eine etwa gleich lange Trennung von ihm ohne Verpaarungsmöglichkeit.

Die Ergebnisse dieser 4 Experimente könnten mit der Bekanntheit zwischen Paarpartnern erklärt werden. Bekanntheit bedeutet dabei nicht nur individuelles Erkennen, sondern darüber hinaus die Fähigkeit, auf Grund genauer Kenntnis des Interaktionspartners dessen Aktionen voraussagen zu können. Die meisten Vögel verpaarten sich nach jeder Trennung wieder mit dem bestbekannten gegengeschlechtlichen Vogel.

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