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Recognition of the Individual Nesting Box in Budgerigars, Melopsittacus undulatus Shaw (Aves, Psittacidae)

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With 4 figures

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Abstract

The behaviour of 6 budgerigar QQ at their own nesting box was compared with their first reactions to a strange nesting box at the familiar site. In most cases QQ behaved differently in the two situations. All of 10 QQ preferred a strange nesting box at the familiar site to their own nesting box at a strange site. It is concluded that budgerigar QQ recognize their own individual nesting box but orient predominantly by the nest site.

For birds the site of the nest is a substantial aid for orientation to and recognition of the nest. The more stable and striking the site, and the less evident the nest structure, the more important the site becomes for nest recognition. Much less attention is often paid to the nest and its eggs or chicks (BEER 1970, BÖHRINGER 1960, DIRKSEN 1932, GOETHE 1937, NICE 1964, NOBLE and LEHRMAN 1940, PEEK et al. 1972, TINBERGEN 1953).

In species where pairs breed clustered without clearly defined nest boundaries, the nest site does not help the birds recognize their own eggs and young with any certitude, and parents learn to make out eggs and chicks individually (Buckley and Buckley 1972, Miller and Emlen 1975, Tschanz 1959). Birds inflicted with brood parasites also react to slight distinguishing features of the eggs (Rothstein 1975, Smith 1968, Victoria 1972).

Is this capacity to distinguish features of the nest, eggs and chicks completely overlaid in some species by the site attachment of the parent bird? Or is their reaction to an alteration at the nest so slight that an observer may easily miss it? To investigate these questions budgerigars were used. These colonial birds readily breed in artificial nesting boxes which can easily be substituted for different ones or changed in their appearance. The budgerigars' behaviour at their own nesting box at its usual site was compared with their first reactions to a strange box. The birds were also offered their own box at unfamiliar sites, under various conditions, to ascertain the relative interitables, of site and box characteristics.

Test animals and methods

Six and seven budgerigar pairs were kept in two aviaries approx. 7 m³ and 5 m³ respectively. Each pair took possession of a $25 \times 15.5 \times 17$ cm box (Fig. 1). The ability of the QQ to recognize their nesting boxes was tested in the interval between the laying of the first egg and the hatching of the first chick. The period chosen ensured that the QQ had a firm attachment to their nesting boxes, but that no activity, e. g. chick calls, emanated from it. Maximally 4 experiments were conducted with one Q on any day. Between tests the

Maximally 4 experiments were conducted with one Q on any day. Between tests the QQ were left undisturbed for at least 35 min, usually however for an h or more. If on one day several tests were made with one Q, the various test conditions (see below) were offered

in alternation.

A running protocol of a number of behaviour patterns of the Q was commenced within 10 s of the experimental alteration of the situation. A polygraph record (Easterline Angus Event Graph, Series 'S' 20 channels) was made of the occurrence and duration of the following:

1. Aggressive behaviour (beak thrust, supplanting attack)

2. Preening

3. Beak-meeting ritual of pair partners4. Change of location (walking or flying)

5. Alighting on box roof6. Alighting on box perch

7. Peering into box

8. Entering box.

The protocol was terminated when a Q entered a box. In some tests only the frequency

and times of alighting on the perch and the time of entering the box were noted.

Analysis: The protocols could be exactly analysed to within .5 s. The numbers of behaviour patterns 1—7 in the protocol were counted. The latency until the first occurrence of behaviour patterns 5—8 and the intervals between patterns were measured. The significance of the differences was assessed using the Mann-Whitney U-Test (SIEGEL 1956). The values given are one-tailed significances, as earlier observations had indicated that QQ take longer to enter strange nesting boxes than their own.

Test situations

1) Control experiment

A box containing a brooding \mathcal{Q} (e.g. Box 16, Fig. 1) was taken down and the \mathcal{Q} driven off. An identical box as yet unused for breeding (Box 18, Fig. 1) was placed beside it and both boxes opened. The eggs were momentarily placed in the second box and returned to the first, both boxes were closed and the first restored to its former position. Box 18 was then hidden away out of the birds' sight.

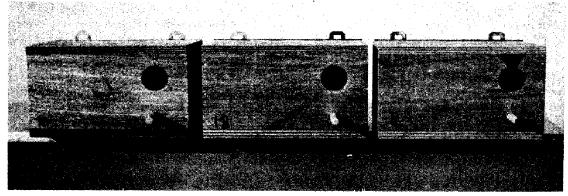


Fig. 1: From left to right: Box 16, example of a nesting box in constant use (Q 4). Box 18, offered as a strange box in the Box Substitution 18 tests. Box 8, distinguished by black markings and offered as strange nesting box in the Box Substitution 8 tests

2) Box Substitution 18 (BS 18)

This commenced as in the Control experiment, but the eggs of the test Q were left in Box 18 and this was substituted for the original, which was then hidden. At the end of the

test (when the Q had entered Box 18), the original nesting box was immediately substituted for Box 18, to minimize habituation of the Q to the strange box.

3) Box Substitution 8 (BS 8)

Similar experiments were conducted with Box 8 (Fig. 1), of which the end cross-section of the perch and a segment above the entrance hole were painted black.

4) Box Transposition (BT)

The first 2 of these experiments involved 2 QQ having the same sized clutch. The boxes were taken down and the QQ driven off, the eggs exchanged and the boxes then tranposed. The immediate reaction of one Q was noted. Nest boxes and clutches were restored to their original sites as soon as both QQ had entered the boxes.

In the last 4 BT experiments boxes were transposed complete with eggs.

5) Change of Site (CS)

For these experiments the Q to be tested was driven from her box, which was hung elsewhere in the aviary, its original site remaining vacant.

Results

Habituation to the test situation

It was necessary to find to what extent the experiments were influenced by habituation and/or increase of broodiness. For 3 experimental conditions, therefore, (Control, BS 18 and BS 8), the partial correlation (Weber 1967) between the latency (time until the \mathcal{P} enters the box) and the test serial numbers on the one hand and the number of eggs on the other was calculated. The number of eggs and the serial number in the Control experiment and in the BS 18 series were highly correlated (Control: r = 0.93; BS 18: r = 0.94), but not in the BS 8 experiment (BS 8: r = 0.06). The partial correlation coefficient was calculated for all 3 test situations (Table 1). Except for an ex-

Table 1: Partial correlation coefficients of period before entering the nesting box to number of eggs and to test number for three different test situations

			우 † N = 10	우 2 N = 10	११ 4 - 6 N = 13
Partial correlation of period before entering box to	no. of eggs	Control BS 18 BS 8	- 0.02 + 0.43 -	+ 0.16 + 0.25 -	- - + 0.20
	test number	Control BS 18 BS 8	- 0.25 - 0.44 -	- 0.43 - 0.25 -	- - - 0,62

tremely small one, all partial correlation coefficients of egg number to latency of entering the box are positive. For all conditions the correlation of latency with the running test number is negative, and with one exception always exceeds that with egg number. Habituation, therefore, had a greater influence on the results than broodiness increasing with egg number. As this underlying trend is more or less clear from the data, the values for the Control experiment were paired up with those from BS 18 and BS 8 under trial numbers, and the significance of their differences established by the Randomization Test (SIEGEL 1956). The results tallied with those of the Mann-Whitney U-Test. In Tables 2 and 3 only the significances of the Mann-Whitney U-Test are given, as this is valid for small numbers of experiments.

Comparison of the Control and the BS 18 Tests

Before alighting on the box birds changed location more often in the BS 18 situation than in the Control situation. This was the only indication that the

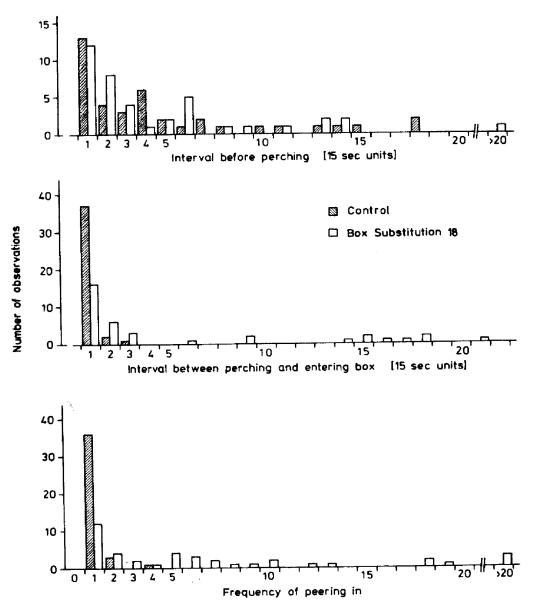


Fig. 2: Comparison of the budgerigars' reactions to their own nesting boxes and to the strange box 18. Data is given for QQ 1-6 (n = 40)

99 noticed a difference from their accustomed boxes even before alighting on the strange box.

	Σ \$\$ 1 - 6	9 1	\$ 2	\$ 3	\$ 4
No. of BS 18 tests	40	10	10	5	5
Time before alighting on perch	n. s.**	n, s.	n. s.	n. s.	n. s.
between perching and peering in	= 0.0016	< 0.001	= 0.05	n. s.	= 0.016
between perching and entering nesting box	< 0.00003	< 0.001	< 0.001	= 0.048	n. s.
before entering nesting box	= 0.017	< 0.001	< 0.025	n, s.	n, s.
Frequency of Preening	n. s.	n, s,	n, s,	< 0.075	n. s.
Beak - touching	n. s.	n, s,	< 0.05	n. s.	n. s.
Change of locality	= 0.015	= 0.001	n, s,	n, s.	n, s.
Perching	= 0.04	= 0.001	n. s.	n. s.	N, S,
Peering in	< 0.00003	< 0.001	< 0.001	= 0.028	n. s.

Table 2: Comparison between Control tests and BS 18*)

Statements valid for the total data of all \Im did not apply for each individual bird, however. Columns 2—5, Table 2, show that for \Im 1 and \Im 2, and with some reservations \Im 3 and \Im 4, appreciable differences exist in some measurements for the Control and BS 18 situations. Fig. 3 gives a comparison of some data for \Im 1 in both situations. The altered circumstances did not affect the behaviour of \Im 5 and \Im 6.

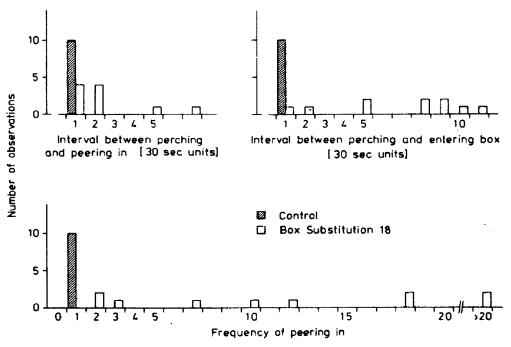


Fig. 3: Comparison of the reaction of Q 1 to her own and to the strange nesting box 18

^{*)} All significances p < 0.1. Mann-Whitney U-test (one-tailed)

^{**)} n.s. = not significant

The test series shows that 991-4 noticed a difference between their own and the strange nesting box, although they rapidly accepted the strange nesting box.

Comparison of the Control and BS 8 tests

Additional tests were made with 994-6 with the painted Box 8 (Fig. 1), which looked quite different from all others. This box was accepted on an average quite quickly, by 94 in 90 s (n = 3), 95 in 55 s (n = 5) and 95 in 65 s (n = 5). Table 3 shows the significance of the differences between the Control and BS 8 tests. The total data for all 95 in this comparison contain several highly significant differences (Col. 1, Table 3). Under these conditions 95 4 and 6 also showed individual significant deviations from their behaviour at their own boxes.

	Σ 22 1 - 6	ያ 4	ዩ 5	¥ 6
No. of BS 8 tests	13	3	5	5
fime before alighting on perch	< 0.01	= 0,018	n. s.**	= 0.048
between perching and peering in	n. s.**	n. s.	n. s.	= 0.075
between perching and entering nesting box	< 0.05	= 0.071	n. s.	= 0,028
before entering nesting box	< 0.001	= 0.018	n. s.	< 0.028
Frequency of				
Preening	n. s.	n, s,	n. s.	n. s.
Beak - touching	n. s.	n, s,	n. s.	n, s.
Change of locality	< 0.01	= 0.018	= 0.075	= 0.075
Perching	n. s.	n. s.	n. s.	n. s.
Peering in	< 0.025	n. s.	n. s.	= 0.075

Table 3: Comparison between Control tests and BS 8*)

**) n.s. = not significant

With a greater difference between the familiar and the strange boxes, 2 at least of the less sensitive 99 showed altered behaviour, although they also rapidly accepted the painted box.

Comparison of the Control and the Box Transposition test (BT)

Tests were continued to determine whether perhaps a general feature, e. g. 'unused, fresh box' as opposed to 'used box' was responsible for the observed difference in behaviour. Boxes occupied by 2 $\varphi \varphi$ with equal clutches were transposed, and in 2 tests the φ known to be more sensitive was observed. Both $\varphi \varphi$ tested behaved as the birds had done in BS 18. They changed location frequently (15 and 16 times respectively) before alighting on the box, and hesitated a long time, each peering in 8 times before entering. Under BT conditions the interval before entering was significantly different for both birds together from that of the Control tests ($n_{BT} = 2$; $n_{Control} = 15$; p = 0.05). A difference in the frequency of peering into the box could also be established (p = 0.01).

^{*)} All significances p < 0.1. Mann-Whitney U-test (one tailed)

These two experiments indicate that the \mathfrak{P} tested did not merely differentiate between used and unused boxes, but could identify their own nesting boxes by specific characteristics.

Further Box Transposition tests

In the first 2 box transposition tests the \mathfrak{P} flew past their own boxes to the strange box at the accustomed site. Apparently the site was more important to the birds than the appearance of the box. Box transposition tests were made on 6 other breeding \mathfrak{P} to confirm this.

Of 4 occupied boxes, a pair 68 cm apart (distance between hole centres) and a pair 42 cm apart were transposed complete with clutch. The first boxes held 3 and 4 eggs, the second boxes 2 and 5 eggs. Although there was long vacillation and repeated approach and retreat, in the end all 9 were sitting

on a strange clutch in a strange box on the familiar site.

In 2 further tests \mathfrak{PP} were offered their own box with clutch at the site of an unoccupied box which was then hung, with the same number of eggs, in place of the familiar box. The test box pairs were only 37 cm and 32 cm apart. After prolonged vacillation both \mathfrak{PP} entered the unused box at the familiar site. After 1 s one \mathfrak{P} emerged again but re-entered later, having paid no attention to its own box. The nesting box site was demonstrably more important to all budgerigar \mathfrak{PP} tested than the appearance of the box.

Changed Site tests

Although the nesting box site was more important, it was evident from the box transposition tests that box characteristics were nevertheless heeded. Would the 99 select their own box if the original site remained vacant?

A box was lowered 54 cm to the left (Fig. 4a: distance between hole centres). The approached an occupied box 42 cm to the right of the familiar site, then alighted twice on the perch of its own box, entering after 3 min. No attention was paid to an empty box 42 cm to the left.

A second \$\text{9}\$'s box was displaced 32 cm from its usual site (Fig. 4b). It visited the box 4 times, entering after 8 min 25 s. It had only once alighted on the roof of an occupied box 44 cm to the right of the familiar site.

The box of a third \mathcal{P} was raised 37 cm to the left (Fig. 4c). The \mathcal{P} alighted on the box after 1 min 30 s, flew 10 times to an unoccupied box 35 cm from the familiar site and 6 times to its own box, which it entered after 11 min 50 s.

Fig. 4: Situation in the three Changed Site tests. Broken lines indicate original box site, left vacant in the test. Arrows point to new position of the bird's own box (shaded). Cross-hatched boxes are occupied by QQ other than the test bird. For further explanation see text

All 3 99 hovered briefly at the familiar site of the nesting box before seeking in the vicinity. In the last 2 tests the 99 may have recognized the box, or merely chosen the nearest to its original site; whereas the first chose (see Figs. 4a—c), from 2 empty boxes, the correct one further from the usual site.

Discussion

1. Methodological problems

According to Franck (1966), successive choice tests measure the releasing value of the stimuli involved rather than their orienting value, whereas in simultaneous choice experiments the orienting value is emphasized. Many studies on individual recognition of nests, eggs or chicks have been made as successive choice tests, recording only whether or not a change was accepted. With this method one is tempted to conclude that the birds cannot recognize the nest, etc., specifically. Such a conclusion would be unwarranted, however, as the test determines the releasing value of the objects rather than individual recognition. The assumption that birds accepting strange nests, eggs or chicks cannot distinguish these objects from familiar ones (as announced by PEEK et al. 1972) is refuted by the test results with the budgerigars. All birds eventually accepted the strange box at the familiar site, although most birds showed clearly that they discriminated between the two. The fine distinction between accepting a strange object in lieu of a familiar one, and not discriminating between the two, is even better demonstrated by another experiment. BÖHRINGER (1960) offered a house martin (Delichon urbica) as close a replica as he could make of its own nest; it was accepted without evident hesitation. But in a simultaneous choice experiment between the original and the replica, equidistant from the familiar site, the house martin chose its own nest.

I therefore suggest that, in further experiments on individual recognition of nests, eggs or chicks, mere observation of acceptance or rejection of substituted objects is insufficient; as many behavioural reactions of the test bird as possible should be recorded immediately after the situation changed, as habituation may affect the results. The results of substitution tests should then be compared with controls, in which the object is removed and immediately replaced. If with this method an alteration in behaviour still cannot be demonstrated, simultaneous choice experiments should be carried out to avoid drawing erroneous conclusions regarding the birds' ability to discriminate.

2. Relative importance of nesting box and nest site characteristics

In budgerigar \$\forall \text{ the sight of a nesting box released an entry reaction sooner if the box was familiar. In the described experiments the nature of the features involved was not determined.

The few Changed Site tests indicated that the \Im can also recognize their own nesting boxes at a strange site. In addition to releasing an earlier entry, the characteristics of the familiar box possibly oriented the \Im to it. This proposition has to be tested with more experiments.

The usual site at which the box hung had a much stronger orienting influence than the features of the box. In all tests offering the \$\times 2\$ a strange nesting box at the usual site and their own at a strange site, they ignored the latter and after some hesitation entered the former, even if it looked quite

different. Although they were able to recognize their own individual nesting boxes, the \$\Pi\$ were predominantly influenced by the site and accepted strange boxes on it.

3. Possible adaptive value of nest, egg and chick recognition

For most nest-building or hole-nesting birds, displacement of the nest or hole, of eggs or altricial chicks means loss of the brood. Under what conditions might it be adaptive for them to pay attention to characteristics of their nests and eggs or chicks, as the tested budgerigars paid attention to features of their own boxes?

It could be vital for a parent bird to interpret alterations at the hole or nest as danger signals, and then to proceed with caution. In this way lurking predators and nest or hole competitors could be detected and possibly driven

off.

Selection for the ability to discriminate between the own and strange eggs could be brought about by brood parasites (ROTHSTEIN 1975). SMITH (1968), observing various colonies of Zarhynchus wagleri and Cacicus cela, showed that the birds accepted or rejected parasite eggs according to the ensuing advantage or disadvantage to their brood. If not directly apparent, such brood parasites might be detected through alterations at the nest or hole entrance, and once noticed, the danger could be reduced by e. g. mobbing, or remaining on guard at the nest. Recognition of the individual nest would

therefore serve to enhance a bird's reproductive success.

As long as the nest remains in a fixed position, the site alone is sufficient for certain recognition of the eggs or young. Common murres (Uria aalge) and Royal terns (Sterna maxima) have no nests, or merely shallows dells, and the eggs may become moved from the laying site; these species recognize their eggs individually (Murres: TSCHANZ 1959, Terns: Buckley and Buckley 1972). A similar correlation, between chick mobility and the time of the parents' first observed individual chick recognition, was demonstrated by MILLER and EMLEN (1975) from the data of authors testing chick recognition in terns and gulls with successive choice tests. They concluded (in accordance with Davies and Carrick 1962) "Apparently, the onset of the period for learning individual chick characteristics has become geared through natural selection to the rate of development of chick mobility..."

4. Learning individual characteristics and/or rating individual characteristics over site characteristics

As the nesting box recognition tests with budgerigars have shown that site-dependent acceptance by no means excludes individual recognition, although the nest is normally at a fixed site, it seems that the results of the tests on gulls and terns allow another deduction, which does not exclude that

of Miller and Emlen (1975):

The parents may learn to recognize the individual characteristics of their chicks much earlier than they begin using this ability to discriminate, e. g. in rejecting strange chicks. Various gull and tern species may begin rating individual characteristics over site characteristics at a different time after chick hatching. To keep parental investment (Trivers 1972) in carriers of strange genes to a minimum, the particular time of this shift of relative importance from site-dependent recognition to individual recognition would have been

adapted through natural selection to the rate of development of the chick's mobility and to the probability of its moving into a neighbouring territory. Whether individual recognition of chicks really exists, even before strange chicks are rejected, could be tested only with experiments of the kind suggested above.

Summary

The behaviour of budgerigar \mathfrak{PP} at their own nesting boxes was compared with their first reactions to a strange nesting box. All \mathfrak{PP} entered the strange boxes after some minutes. 3 of the 6 test birds took significantly longer to enter the strange box, and also showed other behaviour differences in the 2 situations. When tested with a paint-marked box, the behaviour of 2 of the 3 less sensitive \mathfrak{PP} also changed. These differences in behaviour are considered to be signs of individual recognition of the own nesting box. All tested \mathfrak{PP} preferred a strange box at the familiar site to their own box at a strange site. Although they recognize their own nesting boxes, they orient principally by the nest site and will accept strange boxes there. In 3 tests with the familiar site left vacant, \mathfrak{PP} found their own nesting boxes at a strange site.

Methodological problems arising from the use of successive choice tests in attempting to prove individual recognition are discussed. The possible adaptive value of nest, egg and chick recognition is indicated. MILLER and EMLEN (1975) considered that gulls and terns begin to reject strange chicks as soon as they have learnt the individual characteristics of their own. Some species may possibly be able to recognize their own chicks at an earlier stage, but first begin to put individual characteristics before site characteristics when chick mobility separates the two.

Zusammenfassung

Das Verhalten von Wellensittich- \PP gegenüber ihrem eigenen Nistkasten wurde mit ihren ersten Reaktionen auf einen fremden Nistkasten verglichen. Alle \PP schlüpften nach wenigen min in den fremden Nistkasten ein. 3 der 6 Testvögel brauchten aber signifikant länger, bis sie in einen fremden Nistkasten einschlüpften und zeigten noch weitere Verhaltensunterschiede in beiden Situationen. Im Test mit einem teilweise schwarz angemalten Nistkasten zeigten 2 der 3 weniger störungsempfindlichen \PP verändertes Verhalten. Diese Veränderungen im Verhalten werden als Anzeichen für individuelles Erkennen des eigenen Nistkastens gewertet. Alle getesteten \PP zogen einen fremden Nistkasten am gewohnten Platz dem eigenen an einem fremden Platz vor. Wellensittich- \PP können also zwar ihren eigenen Nistkasten erkennen, orientieren sich aber vorwiegend nach dem bekannten Ort und nehmen dort auch fremde Nistkästen an. In 3 Tests suchten \PP ihren eigenen Nistkasten an einem ungewohnten Platz auf, wenn an ihrem gewohnten Platz kein Nistkasten hing.

Methodische Probleme, die beim Nachweis individuellen Erkennens mit Sukzessivwahlversuchen auftreten, werden erörtert. Es wird auf den möglichen Anpassungswert von Nest-, Eier- und Jungenerkennen hingewiesen. MILLER and Emlen (1975) meinten, daß Möven und Seeschwalben beginnen, fremde Junge zurückzuweisen, sowie sie die Individualmerkmale ihrer eigenen Jungen erlernt haben. Möglicherweise kennen einige dieser Vogelarten ihre Jungen

aber schon früher, beginnen jedoch erst dann, Individualmerkmale als wesentlicher zu bewerten als Ortsmerkmale, wenn die Jungen sich vom Platz des Nestes wegbewegen können.

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