

Zusammenfassung. Eine Endodesoxyribonuclease wurde aus den Eiern des Seeigels *Arbacia punctulata* isoliert. Das Enzym braucht sowohl Ca^{2+} als auch Mg^{2+} um

maximale Aktivität mit *Tris*-HCl bei pH 8.5 zu erreichen. Die Matrizenaktivität von Samenchromatin für DNA-Synthese konnte durch Ei-Endonuclease stimuliert werden.

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Effect of Territorial Conditions on the Maintenance of Pair Contact in Duetting Birds

Many species of tropical birds communicate by antiphonal duets. In some species more than two individuals may sing together. Thereby they perform trios, quartets and quintets. The analysis of the temporal patterning of these performances has shown that the vocal contributions of individuals living in pair contact occur in a coordination which is more clear and precise than that between the contributions of not mated birds. There is evidence that a well developed vocal coordination will support the maintenance of pair contact between the duetting birds¹⁻⁵. The vocal coordination is developed by social learning and improved by repeated exercise⁶.

Based on field observations, we worked out an experimental program which allowed us to test the function of well coordinated antiphonal songs. The program was carried out on the behaviour of the central African thrush, *Cossypha heuglini* H., captured and now living under controlled conditions in our laboratories (6 individuals). Like other species duetting antiphonally, these thrushes are extremely territorial^{7,8}. In general, mated *Cossyphas* claim and defend their territories together and predominantly by singing 'counter-duets'⁴. When separated from its mate for more than 2 weeks, a *Cossypha* may start to develop antiphonal duets performed with new song partners. Our question: Would a bird, which 1. has learned to answer song patterns of more than one partner with antiphonal responses, and 2. is exposed to two of these partners simultaneously, demonstrate a clear preference for that one of the partners which shows the better coordination with the bird's own singing behaviour?

In order to investigate this question, we removed male *Cossyphas* (symbol: $m1 = \delta$) out of aviary rooms wherein they had lived in normal pair contact: each of them with 1 female and sometimes (additionally) with 2 youngsters of their own. Each removed male ($m1$) was replaced by another adult and already mated *Cossypha* male (symbol: $m2 = \delta$). For avoidance of aggressive attacks, these birds were kept in cages (1m \times 0.5m \times 0.5 m). Almost 3 weeks after such a replacement, the unremoved female started to accompany the songs of the $m2$ male by the same vocal patterns which it had uttered formerly in the duets with its $m1$ male. They did so inspite of the following facts: 1. the song patterns vocalized by the $m2$ were different from those uttered by the $m1$; 2. the duets performed by the $m2$ and the female did not show the regular timing (coordination) between the duet contributions which was observed in the duets performed by the $m1$ and the female. Like these, the duets between the $m2$ and the female, however, occurred predominantly in consequence of certain auditory or visual stimulations^{6,7}.

Another 2 weeks later, when the antiphonal duets between the $m2$ and the female could be released with high probability ($p > 0.9$; stimulation with stuffed bodies of *Cossyphas* = dummies of rivals), we removed the $m2$ male out of the females rooms. Then we started 3 types of experiments. Each of them was carried out to examine the vocal behaviour of the *Cossyphas* when again brought together: The female, its mate ($m1$) and the $m2$ male. Again the male birds were kept in cages, both of identical construction.

Experiment 1. The cages with the males were installed simultaneously in the female's room but outside of its territorial area (Figure 1; position A and B). Immediately after the start of the exposure of the 2 males to the female, the vocal activity of the birds (measured individually in the number of the vocalized duet contributions) increased to a maximum value (100%). About 7 min later, the female, which had first approached the cages of the males, retired to its territorial area. In parallel, the vocal activity of the birds began to decline. The activity of $m2$

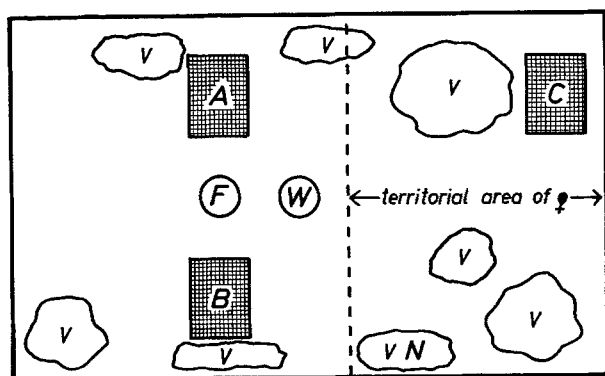


Fig. 1. Sketch of the habitat of our *Cossypha heuglini*. 'Territorial area': region wherein the ♀ spends 93% of its time. A) B) and C), places of cages for ♂ (= $m1$) and ♂ (= $m2$). W, water; F, food; N, nest; V, dense vegetation (coffee tree a.o.). Dimension of the room in meters: 5 \times 3 \times 2.5.

¹ T. HOOKER and B. I. HOOKER (LADE), in *Bird Vocalization* (Ed. R. A. HINDE; Cambridge University Press, 1969), p. 185.

² D. VON HELVERSEN and W. WICKLER, *Z. Tierpsychol.* 29, 301 (1971).

³ W. H. THORPE, *Behaviour Suppl.* 18 (1972).

⁴ D. TODT, *J. Ornith.* 111, 332 (1970).

⁵ W. WICKLER, *Z. Tierpsychol.* 30, 464 (1972).

⁶ D. TODT, in Vorbereitung.

⁷ T. FARKAS, *Ibis* 111, 281 (1969).

⁸ D. TODT, *Behaviour* 38, 146 (1971).

declined more rapidly than that one of the other birds. 25 min after the start of the experiment, and about 15 min after the females retirement, we stimulated the female to approach the cages of the males. This was arranged by feeding the female with insect larvae at the room position F (Figure 1). In consequence of this approach, the vocal activity of all the birds increased again. The differences between the individual activities, however, increased also (top of Figure 2). The timing of the duet contributions of the female and *m1* was much less coordinated than under normal conditions. This was perhaps an effect resulting from the high excitement of the birds (corresponding observations are published for shrikes¹). According to the results, we have to assume that the female recognized the *m1* male as its mate, inspite of the reduced vocal coordination. The higher vocal activity of *m1* may be

affected by the behaviour of the female, which, when being outside of its territorial area, preferred to sit and sing on the cage of *m1*; this was independent of the alternative cage position A or B (Figure 1). The different course of the vocal activity of *m2* and *m1* may also be affected by mutual stimulations of the males.

Experiments 2 and 3. The cages with the males were brought into the females rooms simultaneously but were deposited differently; one was installed inside, the other outside the females territorial area (Figure 1, position C and A). Similar to the findings of experiment 1, the vocal activity of the birds increased to a maximum value (100%) immediately after the start of the exposure of the 2 males to the female. However, the vocal activity of one of the males declined sooner and more rapidly than was observed in experiment 1. This decline occurred only in the activity of that one of the males which was deposited outside of the female's preferred sitting place. Unlike its behaviour in experiment 1, the female now left its territorial area only for moments (10–30 sec) and only during the first 4 min. 25 min after the start of the experiments 2 and 3, we arranged a new approach of the female to the male deposited at room position A. Again this was arranged by feeding the bird at the room position F. The approach lasted for 20 to 30 sec. In consequence of it, the vocal activities of the birds increased again and also with different characteristics (Figure 2, medium and bottom). Further approaches of the female to the room position A and F (experimentally released more than 40 min after the start of the experiments) affected the vocal activities only of the female and of that male which was deposited at room position C. After this, the male deposited outside the females territorial area remained silent and retreated to a sheltered corner of its cage. All the effects described here were found independent of the social and vocal relations between the female and the male kept at room position A (respectively C). According to our results, we have to assume that the vocal behaviour of each one of the birds observed was affected by the behaviour of the other two birds. In addition, the behaviour of the female depended on territorial conditions. In other words, the female preferred to sit and sing close to the bird which was inside of its territorial area, regardless of whether this was its recognized mate (see experiment 1) or its new vocal partner (*m2*), whose song was not coordinated to its duet contributions! This observation demonstrates that territorial conditions have a striking relevance for the maintenance of antiphonal duetting and pair contact.

Zusammenfassung. Im Wahlversuch bevorzugten die Weibchen des tropischen Paarsängers *Cossypha heuglini* H. nicht das eigene Männchen, sondern denjenigen der ihnen bekannten Gesangspartner, der sich innerhalb ihres Territoriums aufhielt. Dies zeigt, dass Bedingungen des Territoriums verhaltensbestimmender sein können als manche soziale Signalgrößen (hier koordiniertes Duettieren).

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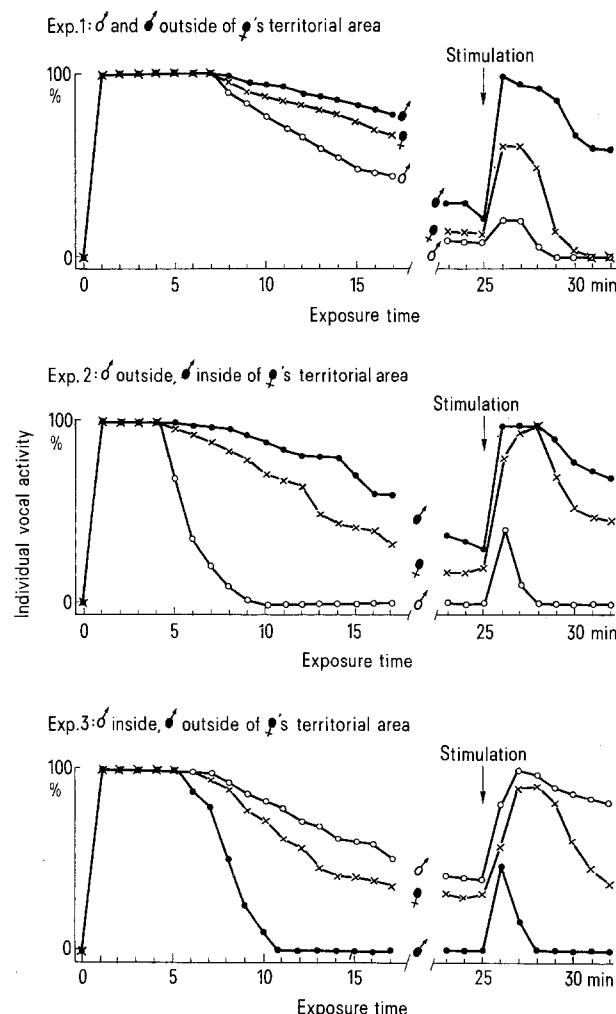


Fig. 2. Changes in the vocal activities of 3 *Cossyphas*. The activity is measured in the frequency of vocal patterns (which were uttered as parts of the duet contribution within 1 min) normalized according to the highest frequency observed for the particular individual (100%). Experiment 1: both the males outside the females territorial area. Experiment 2: only bird *m2* (male song partner of the female not mated to it) outside the territorial area. Experiment 3: only bird *m1* (the mate of the female) outside of the territorial area. Immediately after the birds *m1* (= ♂; ●—●—) and *m2* (= ♂; ○—○—) were exposed to the female (= ♀; —x—x—) their vocal activities increased to a maximum value. Later on, the changes in these activities differed both individually and in dependence on a set of various factors (see text).

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