

COMPARATIVE INVESTIGATIONS INTO THE REPRODUCTION BEHAVIOUR OF MONOGAMOUS, POLYGAMOUS AND UNMATED GREAT BUSTARD POPULATIONS IN SOUTH-EASTERN HUNGARY

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Introduction

The pattern of great bustard (*Otis t. tarda* L.) populations in Central Europe has been largely transformed by one-time hunting and due to effects produced by intensive cultural practices. The cult of hunting-trophies involved a decrease in the number of cocks while the mechanized cultural practices using plenty of chemicals are causing depopulation of the progeny each year. The unnatural population pattern developed due to such damages not only involved quantitative decrease and genetic debility but also disturbed the primary pattern of sexual relations.

According to early European and Asian literature primordially *Otis t. tarda* L. is monogamous (bibliography in: STERBETZ, 1973). Recent diagnoses, on the other hand, mention polygamy and „unmated” sexual relations (bibliography DORNBUSCH—KLAFS—WINKLER in: GLUTZ, 1973). At present, it is these abnormal forms that are frequent, monogamy can be noticed only in case of a natural or an almost natural sex ratio.

Consequences of the behaviour displayed in the reproduction period also manifest themselves in the effectiveness of reproduction, therefore, it is necessary to get to know these problems from the aspect of the practice of nature conservation.

Material and method

For such reasons ten populations were studied by the author in South-Eastern Hungary in the period from 1959 to 1972 and the existence of all three sexual types has been verified (STERBETZ, 1971, 1973). Further aim set by the author was to more thoroughly get to know these behaviour patterns in populations that could be watched continuously.

In counties Békés and Csongrád nine great bustard populations were studied by the author from 1976 to 1979 for monogamous, polygamous and unmated sexual behaviour. Location of the respective populations is presented on the sketch map attached, the pattern evolved, on tables. Legends:

adultus hím = cock taking part in reproduction,

juv. hím = non-rutting cockerel,

tyúk = female participating in reproduction,

juv. vagy szex? = non-reproducing bird of uncertain age and sex.

Table 2.
2. táblázat

1. Pitvaros – Királyhegyes

Year Év	Adult ♂	Juv. ♂	♀	Sex?	Sum total Összesen
1941					200
1969	8	—	23	—	31
1976	8	2	15	—	25
1977	2	1	14	—	17
1978	2	2	5	2	11
1979	3	2	10	—	15

Table 3.
3. táblázat

2. Cserebökény

Year Év	Adult ♂	Juv. ♂	♀	Sex?	Sum total Összesen
1941					150
1977	4	6	18	—	28
1979	9	6	29	—	44

Table 4.
4. táblázat

3. Székkutas

Year Év	Adult ♂	Juv. ♂	♀	Sex?	Sum total Összesen
1941					50
1969	2	1	5	2	10
1976	2	—	2	—	4
1977	2	—	1	—	3
1978	2	—	4	2	8
1979	—	—	—	—	—

Table 5.
5. táblázat

4. Csabacsúd

Year Év	Adult ♂	Juv. ♂	♀	Sex?	Sum total Összesen
1941					300
1946					70
1947					40
1969	—	9	13	—	22
1971	4	5	5	13	26
1972	6	2	8	2	18
1973	4	2	7	1	14
1974	6	2	10	6	24
1975	10	2	13	9	34
1976	5	1	4	10	20
1977	5	10	11	2	28
1978	7	9	12	7	35
1979	9	8	14	5	36

Table 6.
6. táblázat

5. Nagyszénás

Year Év	Adult ♂	Juv. ♂	♀	Sex?	Sum total Összesen
1941					300
1946					30
1953					40
1961					15
1966					54
1967					50
1969	30	5	40	—	75
1971					75
1972					63
1973					60
1974					60
1975					95
1976	10	12	30	10	62
1977	12	15	32	2	61
1978	14	13	35	6	78
1979	14	6	32	10	62

Table 7.
7. táblázat

6. Kardoskút

Year Év	Adult ♂	Juv. ♂	♀	Sex?	Sum total Összesen
1941					50
1961					10
1967	3	1	10	1	15
1968	4	1	5	4	14
1969	3	2	5	4	14
1971	3	3	6	—	12
1972	2	1	7	2	12
1973	2	—	3	3	8
1974	2	—	3	3	8
1975	3	2	5	2	12
1976	1	1	2	—	4
1977	1	2	2	1	6
1978	1	2	2	2	7
1979	1	1	3	2	7

Table 8.
8. táblázat

7. Békéssámson

Year Év	Adult ♂	Juv. ♂	♀	Sex?	Sum total Összesen
1941					100
1961					33
1969					15
1971	2	2	4	8	16
1972	2	—	2	4	8
1973	2	—	2	4	8
1974	2	—	2	1	5
1975	2	1	3	2	8
1976	2	1	3	—	6
1977	2	2	4	2	10
1978	2	2	5	2	11
1979	2	—	3	3	8

Table 9.
9. táblázat

8. Kaszaper – Tótkomlós

Year Év	Adult ♂	Juv. ♂	♀	Sex?	Sum total Összesen
1941					50
1961					10
1966	10	—	15	5	30
1967	5	2	15	8	30
1969	13	2	16	3	34
1971	12	2	10	1	25
1972	13	—	10	2	25
1973	11	1	7	1	20
1974	10	—	10	1	21
1975	6	2	10	11	29
1976	7	3	12	15	37
1977	8	5	14	25	52
1978	9	4	11	20	44
1979	10	5	16	22	53

Table 10.
10. táblázat

9. Pusztaföldvár – Orosháza

Year Év	Adult ♂	Juv. ♂	♀	Sex?	Sum total Összesen
1941					50
1961					10
1966	7	3	11	5	26
1967	5	2	12	11	30
1968	5	1	13	10	29
1969	5	2	14	8	29
1971	5	2	10	18	35
1972	4	—	9	5	18
1973	4	2	10	22	38
1974	6	6	13	5	30
1975	7	2	15	4	28
1976	7	3	20	6	36
1977	10	4	21	11	46
1978	12	5	23	10	50
1979	14	6	25	12	57

Mean values were calculated in view of plotting graphs of the population patterns. The sexual types watched each year in the various populations are also displayed on a Table. Tenfold, twentyfold and fortyfold telescopes were used for the examinations and a 400 mm teleobjective for proving. The author's investigations covered the following:

- choice, occupation and protection of the rutting sites,
- comparison of monogamous, polygamous and unmated cocks for sexual behaviour,
- behaviour of cocks not participating in reproduction,
- behaviour of hens with the three sexual types,
- relation of the sexes after fecundation.

Table 11.
11. táblázat

Sexual appearance – Szexuális forma

Nr.	Populáció	1976			1977			1978			1979		
		mg.	pg.	um.	mg.	pg.	um.	mg.	pg.	um.	mg.	pg.	um.
1.	Pitvaros, Királyhegyes			+			+			+			+
2.	Cserebökény	+		+	+		+	+		+	+		+
3.	Székkutas	+			+			+					
4.	Csabacsúd	+	+		+	+		+	+		+	+	
5.	Nagyszénás	+	+	+	+	+	+	+	+	+	+	+	+
6.	Kardoskút	+			+			+			+		
7.	Békéssámson	+			+	+		+	+		+	+	
8.	Kaszaper, Tótkomlós	+	+		+	+		+	+		+	+	
9.	Pusztaföldvár, Orosháza	+	+	+	+	+	+	+	+	+	+	+	+

mg. = monogamia.
pg. = polygamia.
um. = unmated = pár nélküli.

Results

1. Choice and occupation of the rutting site

As regards the great bustard populations in Eastern Hungary rutting grounds chosen on wide-spread natural steppe vegetation being adjacent to cereal or lucerne fields can be observed as a definite tendency. Adjoining

belts of steppe and cultivated vegetation alternately penetrating into each other are the most attractive here. Birds can always find here plant stands of various thickness and height suitable for the rutting ceremony, for hinding by day, later on for nesting. Plenty of food is an important factor, alike, since at the time of rutting, birds are moving on a small area, while their food requirement is higher. By day, they can spend less time on feeding. The undisturbed character of the area is of primary importance in comparison to all of the requirements mentioned. Should a cock in search of a rutting site or possessing already one be chased away from his territory by a rival bird or some other stress effect, it will not participate that year anymore in reproduction.

At the time of investigations populations strong in numbers (2, 4, 5, 8, 9) were staying all the year round on areas of 4 to 5000 ha extension and were choosing their rutting grounds in spring inside these. Dwarf populations of a few birds (1, 3, 6, 7), on the other hand, joined late in autumn the big populations to be found next to them. Thus great bustards in Pitvaros and Békés-sámson were wintering with the population in Kaszaper, birds from Szék-kutas and Kardoskút, with the pack in Pusztaföldvár, at about 20 to 40 km distance from their summer habitation. Early in March they returned to the territories possessed by them in the period of reproduction.

Late in winter, on the first frostless days old cocks begin changing their behaviour. During the warmer midday hours they are making from day to day more frequently aggressive commanding movements as characteristic of the later rutting. Time and again, they are flying to the rutting grounds. Final parting to the old males occurs early in March, while the hens and the young leave the hibernaculum only 10 to 15 days later. Young birds of one to two years of age are leaving last.

Marking out of the rutting grounds is performed by the monogamous, polygamous and unmated males alike but occupation thereof is achieved in different ways.

Cocks of all three sexual types repeatedly flutter round their territory to-be and the place thus marked out will be the scene of their later sexual relations. This morning and late afternoon activity aimed at marking out the territory is repeated over five to six days, then ends suddenly without transition. Monogamous and polygamous males usually occupy their rutting grounds quicker than unmated birds.

The rutting site — the same as for the majority of other birds — is firstly a psychological reality for the great bustard, likewise, isolation inside the species being its most important function. The preserve requirement suddenly appears with onset of the sexual cycle.

In a particular way, territory guarding by the monogamous and polygamous cocks only serves elimination of sexual rivalry. The bird occupying the preserve is indifferent to approaches by other animals. He also tolerates another great bustard cock as long as it does not mean sexual rivalry. Species mates of male sex may stay undisturbed in the immediate vicinity of the cock occupying his rutting preserve as long as their behaviour does not overstep the limits of the state of rest. Should, however, a foreign cock tip up its tail — this being the first sign of rutting or some other excitement — the preserve owner will attack him immediately. A high-pitched great bustard cock spreads its quill-feathers fan-wise then folds them again and flat-

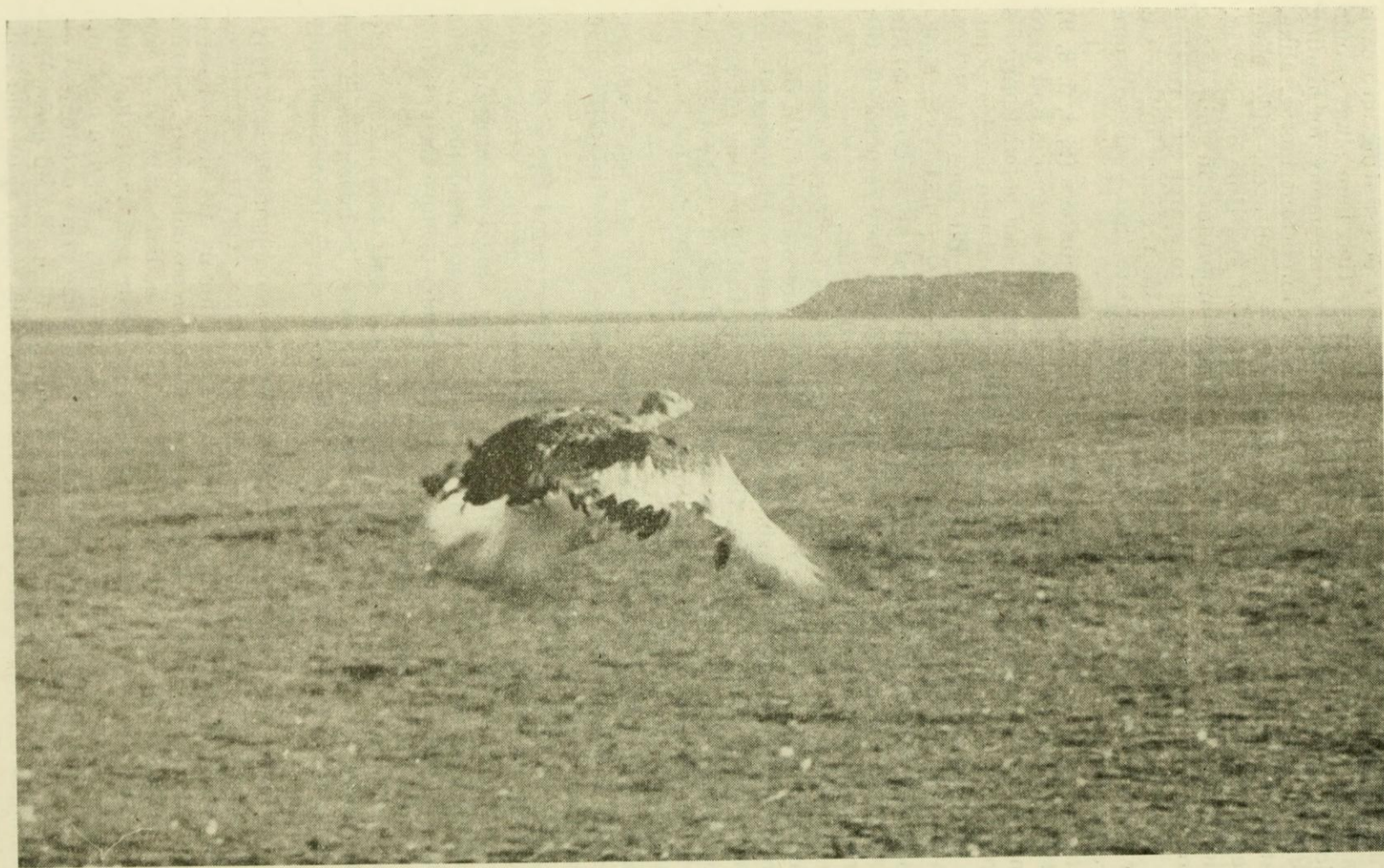


Figure 4. Great bustard cock marking his rutting preserve by fluttering it at Csabacsúd in March 1977.
4. ábra. Dürdőrevirjét röpülve kijelölő túzokkakas Csabacsúdon, 1977 márciusában (Fotó: Dr. I. Sterbetz)

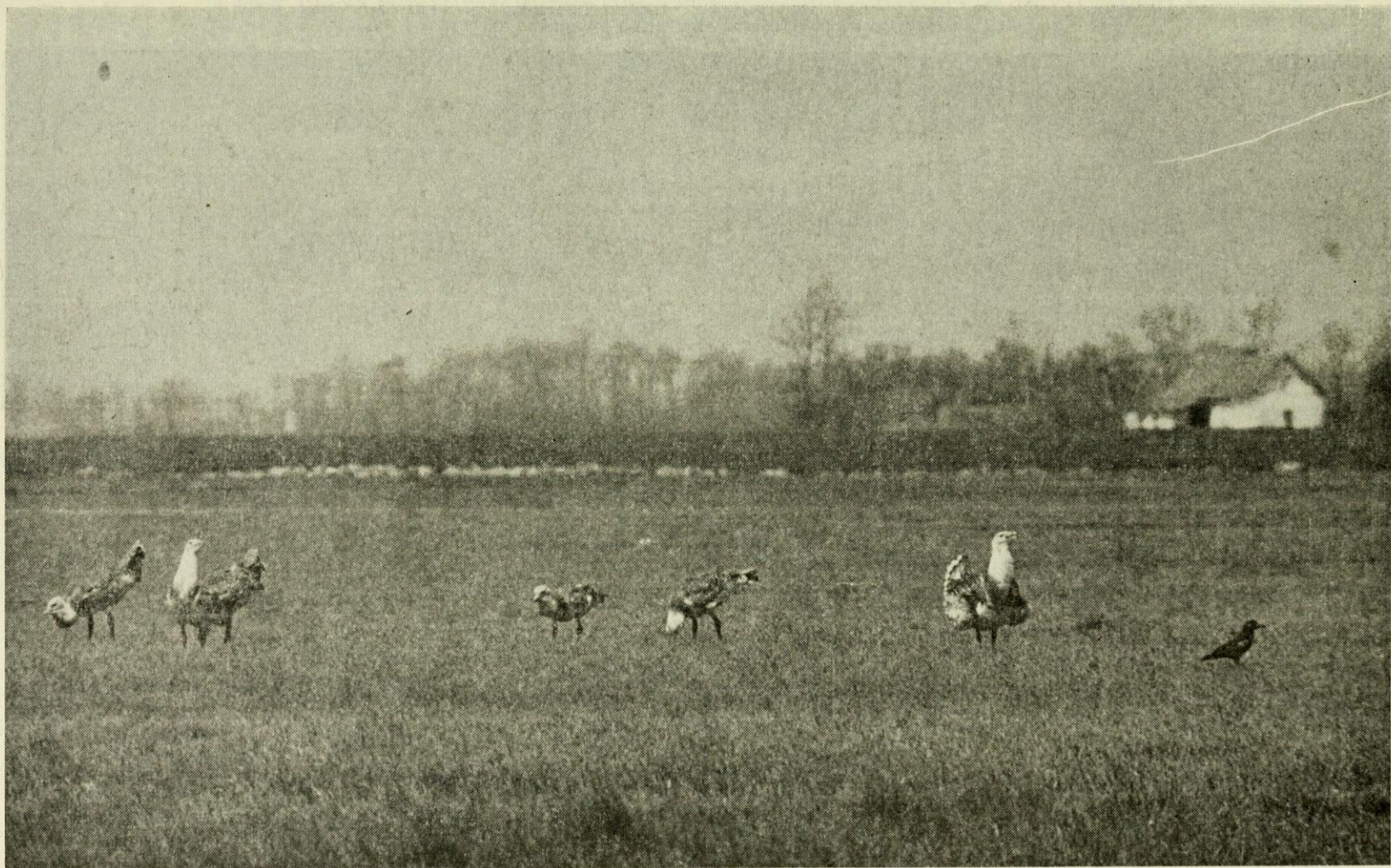


Figure 5. Old great bustard cock standing on right margin of picture tolerates non-commanding males inside his rutting preserve
5. ábra. A kép jobb szélén álló öreg túzokkakas dürgőrevirjén belül megtűri a nem imponáló hímeket is (Fotó: Dr. I. Sterbetz)



Figure 6. At time of rutting cockerels are roaming in a feeding community
6. ábra. Dürgés idején fiatal kakasok táplálkozó közösségben kóborolnak (Fotó: Dr. I. Sterbetz)

tens them on his back. At such times, his snow-white lower quill-feathers are shinning far. It is to this signal that the preserve owner reacts.

The marked and occupied preserve provides undisturbed mating for the owner. As long as the preserve borders are not definitely recognized, other monogamous or polygamous cocks often try to expropriate it. The preserve fight may end with severe injuries or even death of one of the partners. On sites with a great number of monogamous cocks living in one population (Csabacsúd, Nagyszénás) preserve fights are frequent. With polygamy, fights occur less frequently and were never observed by the author with the unmated type rutting in packs. Generally, the farther the sexual ratio of a population from natural 1 : 1 the less active the preserve defense will be.

2. Rutting by the three sexual types

The great bustard cock is capable of reproduction from its fifth to sixth year on (GEWALT, 1959, 1963, 1966). His rutting display is taking place when having got hormonally suitable for it, having taken possession of a rutting preserve, with one or more female birds staying nearby, finally when excited by the sight of sexual rivalry or some other sex effect.

The sexual behaviour of the cock ready for mating at first manifests itself in an aggressiveness anxious for the partner, then gradually takes on a commanding character and on such level has the only aim of arousing in the hen the mood for copulating. Details of the sequence and daily rhythm of rutting movements are omitted here since these are well known from literature (Summary in: DORNBUSCH—KLAFS—WINKLER in: GLUTZ, 1973).

All three sexual types agree in that it is the preserve owner cock that is visited by one or more hens.

In the case of monogamy, as soon as a hen nearing the cock gets inside the preserve boundaries she becomes possession of the cock who is ruling over her. He does not let his partner go over to the preserve of foreign cocks (observations at Kardoskút, Csabacsúd, Cserbökény and Székkutas). On the 19th April 1976, a cock being in full rutting at Békéssámson repeatedly tried mating with his hen, unsuccessfully. After repeated futile efforts he expelled his indifferent partner from the preserve. Next day, this cock was rutting again in the company of a hen but whether his previous-day mate has returned or he acquired a new hen could not be stated.

As regards polygamy, the cock has domination over a harem consisting of two-three-four hens, likewise, as the monogamous males. The hens' readiness for mating may establish an order of rank among the females. As observed by the author at Pusztaföldvár on the 2nd May 1978 in a four-member harem of a cock where repeated approaches of two active hens apparently excluded the possibility of fecundating the two other females latter being more difficult to excite.

With the unmated type the cocks rutting in groups do not dominate anymore the hens gathering round them, probably due to their numerical superiority. Relationship of the sexes is restricted here to the minutes of copulation. The fertilized hen is driven out from beside the cock by the next nearing female. Approaches by an excess number of hens exclude the possibility of remaining together for a longer period here by the partners.

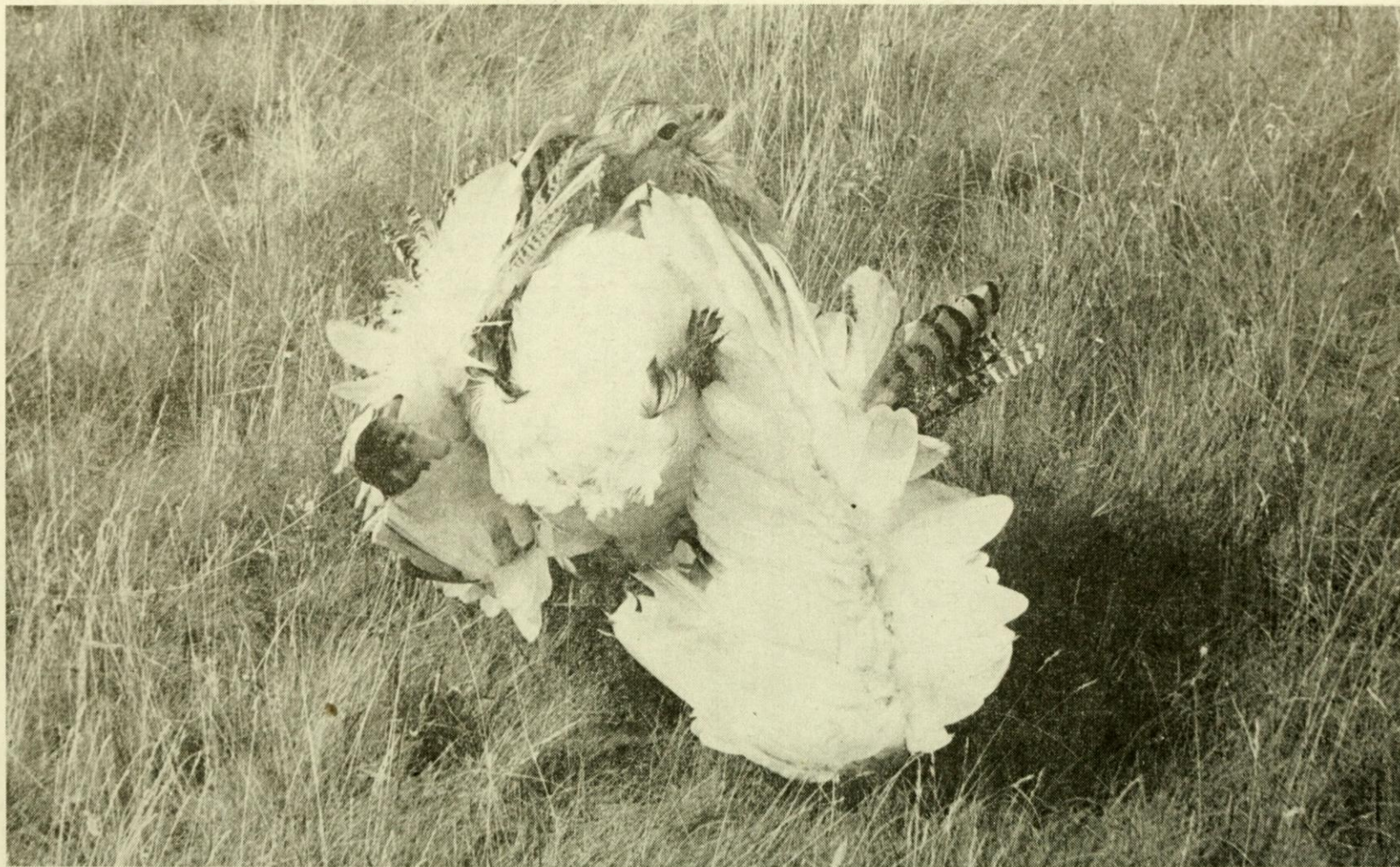


Figure 7. On its 200×300 m enclosure three-year-old semi-wild great bustard cock was excited to rutting by alarming closeness of observers
7. ábra. 200×300 m-es, elkerített élőhelyén a hároméves, félvad tűzokkakast dürgésre ingerelte a megfigyelők nyugtalanító közelsége
(Fotó: Dr. I. Sterbetz)

Pure monogamy in the populations examined was recorded by the author only at Kardoskút (No. 6) and in 1976—77 at Székkutas (No. 3). For the rest of the populations two or three sexual types were detectable at the same time. It should be emphasized that in such cases monogamous and polygamous cocks were staying always more distant from the unmated males rutting in groups and more intensively guarded their marked rutting territories.

It has been verified in several cases that excitement of non-sexual character may also induce rutting and even heighten it to the highest level in the great bustard cock. This phenomenon is independent already from the pattern of populations, from the age and hormonal state of cocks and also from the season. At Csabacsúd (No. 4), in November 1973, in a great bustard pack frightened by a sheep dog, one of the cocks was rutting for a few minutes as intensively as at the time of spring mating (STERBETZ, 1975). Cocks two to three years of age raised semi-wild at the great bustard rearing station in Dévaványa were rutting for some minutes when alarmed by the appearance of foreign persons on their 200 × 300 m enclosure. Whether resulting from sexual or other excitement rutting always means such tension as can be led back to the state of rest only by substitute activity. Walking with turned up tail, preening, waving of half-open wings, swinging of the trunk back and forth, dust bath, pecking and stacking to and from of blades of grass, moreover two to three minutes sleeping by the bird falling prone were observed by the author.

3. Behavior of non-rutting young and old cocks

No manifestations referring to their later sexual types were noticed by the author in the behaviour of sexually immature cockerels. These birds forming smaller feeding communities were staying in packs in the environs of rutting grounds or inside them. The community of cockerel packs disintegrates only after the reproduction period when the social relations of all great bustards without regard to age and sex are disturbed by moulting.

At Csabacsúd (No. 4) author had an opportunity to observe the spring behaviour of a male having grown too old and become inactive. Author kept watching here since 1965 a very big old cock that did not mark out a rutting preserve for himself in the last eight years, was not rutting and did not join the feeding community of young males either. He remained alone from the disintegration of the winter great bustard packs until autumn flocking. Omitting aggressive forms of expression he was staying unhurt on territories of both monogamous and polygamous active males.

4. Behavior of the hen at the time of rutting with the three sexual forms

Sexual interest of the hen is aroused by the cock when latter is making commanding movements. At Csabacsúd (No. 4) it was observed by the author on the 25th April 1979 that a hen shunned a cock wanting to copulate without rutting. On the same site, it was found on several occasions that „play rutting” by cockerels of no full sexual value was ignored by the hens. The more showy the rutting of old cocks the sooner the hen gets excited. Hens need more excitement than males for mating to come about. At Kardos-

kút (No. 6) in 1976 a stronger cock expelled the monogamous owner from an unsuitably occupied rutting ground. The expelled male tried in vain to return first peacefully then aggressively. After the failure he roamed in the company of his hen in the environs of his earlier preserve but after loss of the rutting ground he discontinued rutting. After two days the hen left the male. This year there was no nesting here.

As regards grouped rutting by unmated cocks, as well known, females try to associate now with one now with another cock and make efforts to precede their rivals in mating. Under such circumstances the more spectacularly commanding cocks are getting at more hens but too frequent copulation is probably one of the reasons of the frequent infertility of eggs. Therefore, among cocks rutting in groups there are often males to be found rutting steadily but unable to accept the approaches of hens flocking round them.

5. Relationship of cocks and hens in the post-fecundation period

The sexual relations of the various types still difficult to look over in the hours of rutting is more clearly differentiating during the post-copulation period.

After fecundation the hen leaves the rutting preserve and retires to her nesting site. As regards the populations in Eastern Hungary usually there is no large distance, as a rule only a few hundred metres, between the rutting and nesting grounds. The hen is receding into larger distance only when forced by the state of the field vegetation.

In the case of monogamy the partners remain together also after mating. The cock follows the hen retiring to her nesting site, is keeping guard nearby, and the more active males vigorously defend their hatching mate. This behaviour was described by CHERNEL (1904) as being of general validity. NAGY (in: FODOR—NAGY—STERBETZ, 1971) at Zsadány, in May 1938 mentions a case when the cock guarding the hatching hen attacked a nearing horseman. Such a nest protecting scene was observed by the author at Kardoskút (No. 6) on the 15th May 1978. Here a cock staying at about 40 to 50 m distance from the nest approached to 20 m a woman gathering flowers of camomile (*Matricaria chamomilla*), then jumping up a few times tried to force her to leave with outstretched neck and hovering wings. This behaviour pattern said to be frequent in earlier observations and in literature occurs but rarely at present as a consequence of the unnatural population patterns developed. The monogamous cock following his mate to the nesting ground is rutting still for a few days while guarding the hatching hen. It was observed by the author at Csabacsúd (No. 4) that the cock guarding his nesting mate returned to his rutting preserve, was rutting there for several hours, then after sunset returned near his hatching hen. As retards monogamous types, the community of partners disintegrates late in the nestling rearing period probably when cocks start summer moulting (STERBETZ, 1976).

Polygamous cocks do not show uniform behaviour. E.g. at Pusztaföldvár (No. 9) in May 1977 a cock having a harem of four hens after rutting retired with a single female to her nesting ground. Thereafter, he did not care anymore for the other three hens of the harem. At Csabacsúd (No. 4), on the other hand, author found in 1977 that after withdrawal of the hens to their

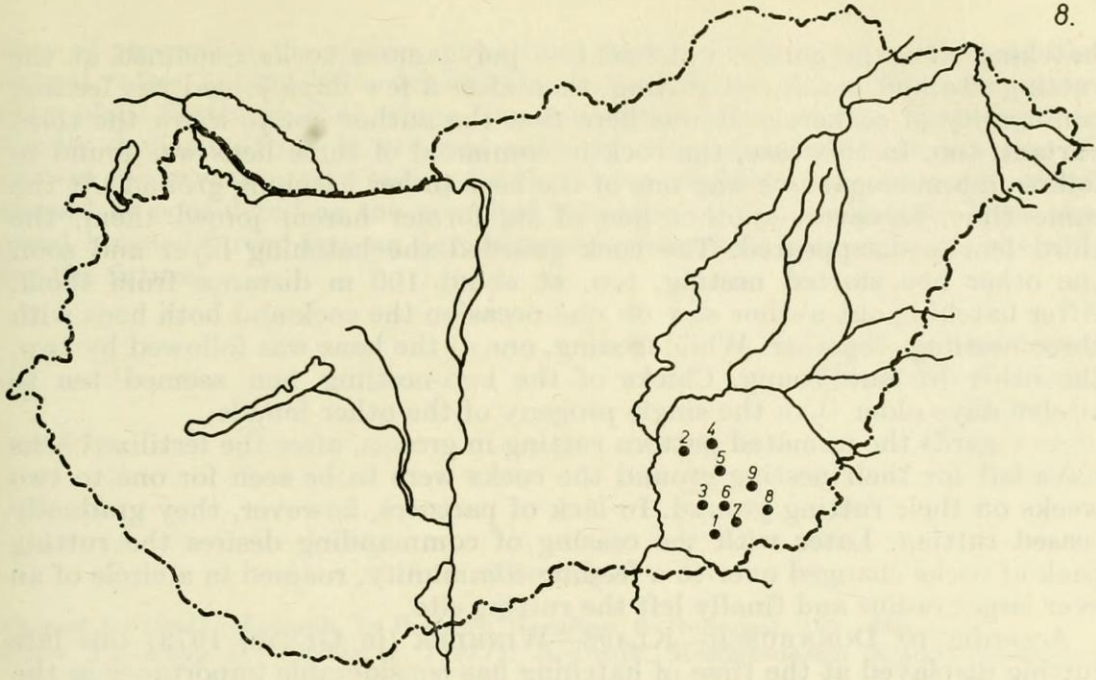


Figure 8. Location of populations examined
8. ábra. A vizsgált populációk előfordulása

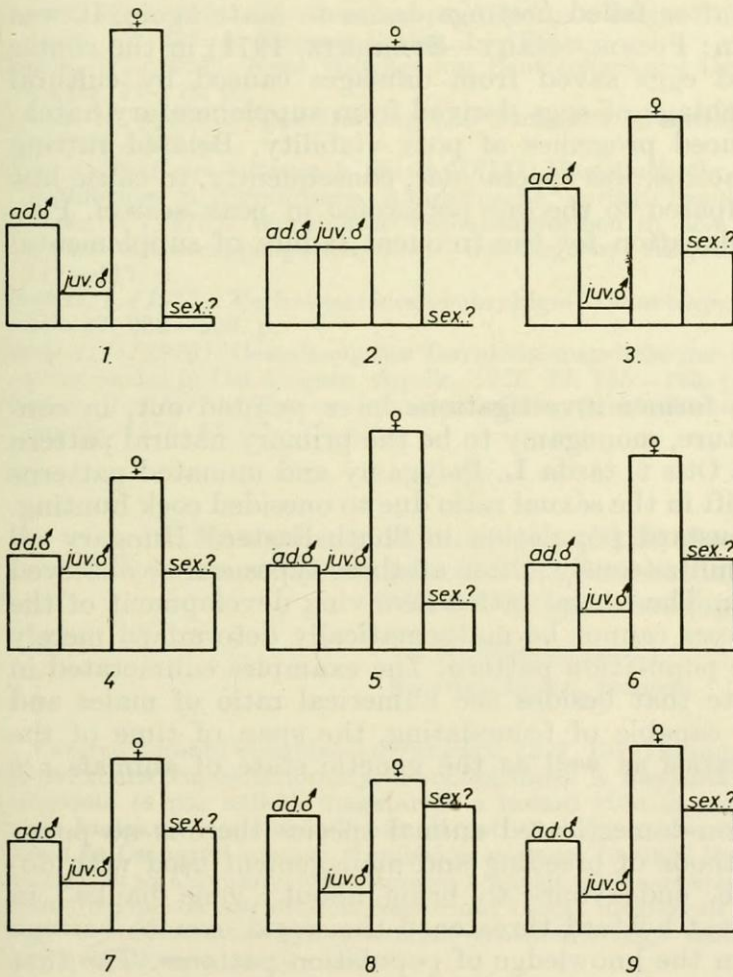


Figure 9. Mean values of population pattern (%)
9. ábra. A populációstruktúra átlagértékei (%)

hatching sites the earlier watched two polygamous cocks remained at the rutting site and continued rutting, then after a few days joined the feeding community of cockerels. It was here that the author got to know the third variant, too. In this case, the cock in command of three hens was found to follow in a monogamous way one of the hens to her hatching ground. At the same time, however, another hen of its former harem joined them, the third female disappeared. The cock guarded the hatching layer and soon the other hen started nesting, too, at about 100 m distance from them. After hatching out author saw on one occasion the cock and both hens with three nestlings together. While feeding, one of the hens was followed by two, the other by one young. Chicks of the two-nestling hen seemed ten to twelve days older than the single progeny of the other female.

As regards the unmated pattern rutting in groups, after the fertilized hens have left for their nesting ground the cocks were to be seen for one to two weeks on their rutting ground. In lack of partners, however, they gradually ceased rutting. Later with the ceasing of commanding desires the rutting pack of cocks changed over to a feeding community, roamed in a circle of an ever larger radius and finally left the rutting site.

According to DORNBUSCH—KLAFS—WINKLER (in GLUTZ, 1973) this late rutting displayed at the time of hatching has considerable importance in the fecundation of hens that after failed nestings desire to mate again. It was demonstrated by Fodor (in: FODOR—NAGY—STERBETZ, 1971) in the course of hatching great bustard eggs saved from damages caused by cultural practices that a high percentage of eggs derived from supplementary hatching were infertile or produced progenies of poor viability. Belated rutting was found to be rather inactive, less spectacular, consequently, to cause but moderate excitement compared to the one performed in peak season. Probably, this is also an explanation for the frequent failure of supplemental hatchings.

6. Conclusions

Results of the author's former investigations have pointed out, in conformity with earlier literature, monogamy to be the primary natural pattern of sexual relations for the *Otis t. tarda* L. Polygamy and unmated patterns have been induced by a shift in the sexual ratio due to onesided cock hunting.

As regards the great bustard population in South-Eastern Hungary all three variants do exist, simultaneously. Often all three types can be observed within a single population. The sexual ratios involving development of the various — abnormal — types cannot be mathematically determined merely by the composition of the population pattern. The examples enumerated in the study seem to indicate that besides the numerical ratio of males and females being in the age capable of fecundating, the span of time of the prevailing unfavourable ratios as well as the genetic state of animals are determinants alike.

For populations of a non-domesticated animal species there is no possibility of applying the methods of breeding and management used with domestic animals. Therefore, endeavours to bring about „gene banks” in support of the ill-fated great bustard threatened the world over to become extinct should be based on the knowledge of population patterns. The first

step of preserving the species, the closed season, enables regeneration of the sexual ratios having been deteriorated earlier. In all probability, this may take place firstly at sites where the primary 1:1 sexual ratio or polygamy hardly deviating from it, are met with. In view of an effective practice of nature conservation, providing for the living conditions of such populations should be considered as the principal aim since without a genetic basis the great bustard forced into an agricultural environment cannot be maintained for the future.

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Monogám, poligám és pár nélküli túzokpopulációk szaporodási magatartásának összehasonlító vizsgálata Délkelet-Magyarországon

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A szerző korábbi vizsgálatai (STERBETZ, 1971, 1973) kimutatták, hogy a túzok természetes szexuális kapcsolatformája a monogámia. A napjainkban már majdnem általános poligámia és pár nélküli magatartás a hosszú időn át tartó, egyoldalú kakasvadászattal kialakult, természetellenes állapot. A dolgozatban az 1976–1979. évekből kilenc Békés és Csongrád megyei populáción végzett, további ilyen tárgyú vizsgálatait ismerteti, és az állományok szerkezetét a közölt táblázatokban mutatja be. Leírja az egyes szexuális típusok szaporodási életformái között megfigyelt eltéréseket, és rámutat arra, hogy a túzokmentés gyakorlatának eredményessége csak genetikailag megalapozott, életképes állományoktól várható.