The Structure of Social Behaviour in *Theropithecus gelada*

FERNANDO ALVAREZ and CARMEN CÓNSUL
Estación Biológica de Doñana, C.S.I.C.

ABSTRACT. Through the use of principal components analysis of the correlation matrix between excentricity quotients of intra- and inter-individual transitions between pairs of the 22 most frequent behaviour elements of male and female gelada baboons observed in captivity, the total variance could be described in terms of a low number of causal factors. In intra-individual sequences the five factors requested of the analysis explain 74 per cent of the total variance. The following intra-individual groupings were found: (I) "autostimulation", (II) "intensive social" versus "groom", (III) "male sexual", (IV) "attack" versus "sexual presentation", and (V) "greeting" versus "threat". In inter-individual transitions, the five factors explain 68 per cent of the variance. The following communicative sets were found: (1) "female-sexual releasing", (2) "greeting and approaching releasing" versus "groom releasing", (3) "austostimulation releasing" versus "male-sexual releasing", (4) "fight releasing", and (5) "conflict". Mimetic induction of same acts or acts within one particular intra-individual set was frequent.

INTRODUCTION

There has been general re'uctance in ethological studies against the use of higher level categories such as aggression, leadership, dominance, and so on, if these are not backed by empirical observation or testing.

This general principle, forming part of the core of ethological theory, does not prevent the recognizing and studying of those complex categories, which should be treated with a minimum of subjectivity.

The search for organizing or causal factors of behaviour has often been undertaken by means of the study of temporal relationships (i.e., behavioural sequences) among behaviour elements (patterns or items of behaviour, units of the ethogram).

Following the pioneer study of WIEPKEMA (1961) and some others on non-primate vertebrates, work of this sort on primates has been undertaken on rhesus monkeys (ALTMANN, 1965), chimpanzees (VAN HOOFF, 1973), human children (BLURTON JONES, 1972), and squirrel monkeys (MAURUS & PRUSCHA, 1973). These studies have proved the existence of objective higher level categories for these species. These we tried to isolate in the case of the gelada baboon.

After several reports have become available of studies done for this particular species in natural state (CROOK, 1966; DUNBAR & DUNBAR, 1974) and in captivity (MATTHEWS, 1956; BRAMBLETT, 1970; SPIVAK, 1971; ALVAREZ & CÓNSUL, 1971; FEDIGAN, 1972; ALVAREZ, 1973; KUMMER, 1974; EMORY, 1975a, b; BERNSTEIN, 1975), its social organization and behaviour is quite well understood, and even the anatomical basis for peculiar patterns of behaviour is known (OSMAN HILL, 1969).

An overall structural study of individual and communicative processes appears to

be much needed to help in the understanding of the body of knowledge accumulated on this interesting animal, a fact that we pursued through the use of principal components analysis of transitions of behavioural units.

METHODS

As a first step previous to the quantitative treatment of the observations, we concentrated on the descriptions of the elements of the ethogram. For this purpose, observations were made on 17 geladas (adults and juveniles of both sexes) in various conditions of captivity.

The elements of behaviour were described on the basis of sketches, written notes, still photographs and frame by frame analysis of 16 mm motion pictures.

Once the most frequent elements of the behaviour catalogue were described we engaged in the recording of the intra- and interindividual sequential order of occurrence.

These observations were done at the Delta Primate Center (Louisiana, U.S.A.) and are based on four male and six female adults, wild trapped and living in a 100 × 400 ft enclosure with grass and trees and no roof.

When sequence recording was made only two of the adult males and some or all of the females plus some juveniles were occupying the cage.

The animals readily distributed themselves into two one-male groups, which were taken as reference for the observations (KUMMER, 1974).

The data on intraindividual sequences were collected so that the 248 hours spent in active observation were equally distributed among all subjects.

The intraindividual sequential order was recorded by talking into a microphone, where the occurrence of each element and the end of 60 seconds periods were registered. Subsequently these data were transcribed to written form and the transitions between the 22 most frequent elements (occurring at least 30 times) were located in a 22-dimensional matrix, where for each element of behaviour, the number of times it was both preceded and followed by each of the other elements could be readily observed.

Two acts were considered to be in sequence (and therefore, their transition recorded) if one followed the other and both were registered in the same period. No transition was noted of one element with itself.

In the event of two elements occurring simultaneously the transition of each one into the other was entered in the matrix once. If an element preceded the combination of other two items occurring simultaneously, the transition was recorded between the preceding element and each one of the other two elements.

The interindividual sequences were recorded by concentrating each of the two observers on one subject of male-male, female-female and male-female pairs, taking care that the 124 hours of recording were equally distributed among these pairs of individual subjects, with the reservation that female-female and male-female pairs included only animals within the same social unit.

Each of the observers concentrated on each of the members of the pair, the recordings of the behaviour elements were made immediately after their occurrence and

both went into the same magnetic tape of a Wolensak recorder. A sound timer made a noise every 60 seconds and was recorded directly.

The differences in speed of recording were adjusted by the concentrating of both observers (previous to formal observations) at the same time on one individual and recording into the same magnetic tape, one observer inside a room looking into the cage and the other outside, so that the listening of the other's observations would not influence the recording. When inter-observer agreement appeared to be sufficient the formal observations were started.

The cross-individual recordings were also transcribed to written form, taking care that the sequential order of the starting of occurrences was maintained, as well as the ending of the periods.

The inter-individual transitions between each pair of the 22 most frequent elements (the same ones considered in intra-individual sequences) were located in a 22-dimensional matrix, where the number of times each element was preceded and followed by each of the other elements could be readily observed.

Two acts were also considered to be in sequence (and their transition recorded) if they were registered in the same period.

In this part of the study we considered that each element could be succeeded by itself, since in this case the performance by one animal is followed by the same behaviour element in the other.

RESULTS

Description of Behaviour Elements

A short description is provided for the patterns of behaviour used in this study, for more detail see Spivak (1971) and Alvarez and Cónsul (1971), see Figure 1.

Approaching. The animal directs its locomotion toward the other member of the pair under observation.

If the performer went toward a group of animals and neither of them could be said to be the receptor of this behaviour, approaching was not recorded.

Attacking. The subject jumps toward the other member of the pair. The mouth is open and the teeth and gums are bared and directed against the receiver.

Autogrooming. The animal inspects its fur, parting the hair with one or both hands and removes particles with hand or mouth.

Barking. Intense sound, the only one in the geladas repertoire that we can call a bark.

Contact calling. Low frequency grunt. It is the sound most frequently produced by the geladas.

Fighting. Attacks with mouth completely open and upper lip curled over the nose. The gnashing of the teeth is directed particularly to the sides of the neck and shoulders. The receptor tries to interpose its teeth to the teeth of the opponent. These rapid attacks and open mouth displays in front of each other is, for the purpose of this study, what is called fighting.

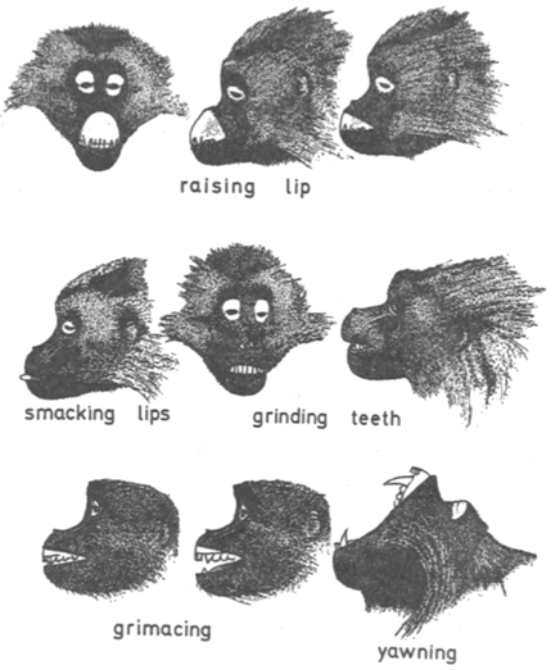

Fig. 1. Some of the behaviour elements recorded.

Gasping. The air goes in and out rapidly through the open mouth producing a noise, to which a low intensity vocalization is added, matched by the entrance and exit of the air through the air passages.

Genital inspection. The performer approaches its muzzle to the anogenital or pubic areas of the receiver.

Grimacing. The lips are retracted backwards while the teeth are shown. The mouth can be closed (upper and lower teeth together) or slightly open or even chatter rapidly against each other.

Grinding of teeth. The mouth is opened and closed, the large canines of the upper and lower jaw of males come into lateral contact, producing a sound and sharpening the edges at the same time.

Females do not have such large canines, so when they perform the same movements the cheek teeth come into contact, producing a chattering sound.

Grooming. The performer inspects the fur of a partner, parts its hair with both hands and takes particles from the hair both with its fingers or directly with the tongue.

Groom-presenting. The performer keeps still looking away from a partner, who is near him, and approaches a part of his body, very often exposing areas of its fur which it cannot reach (armpits, groin, nape, etc).

Mounting. The animal is behind his partner and rests the open hands on the receiver's hindquarters or embraces it from behind, keeping seated or going bipedal, grasping or not the partner's heel with one foot.

Mount-presenting. The subject orients its rump toward a partner and keeps the tail out of the way, exposing the anogenital area.

Moving away. By walking, running, jumping, etc., the animal increases the distance from a partner from whom it was no more than one meter apart.

If it were initially near more than one individual, this activity would not be recorded.

Pelvic thrusting. Forward and backward pelvic movements against the anogenital area of a partner. It was usually accompanied by penis intromission.

Raising lip. The upper lip is raised in various degrees, showing only teeth, or teeth and gums or even, by raising the lip and flipping and turning it over the nose, show the internal side of the lip and upper gums.

Rubbing nose. The subject brushes its nose with the cupped wrist brought quickly close to the nostrils.

Scratching. Inward movement of forearm, the fingernails scratching its own fur.

Sexual calling. Intermittently produced soft sound (hu hu hu), always accompanied by a slight upward tilting of the muzzle.

Smacking lips. The teeth and lips are intermittently parted and brought together, allowing the end of the tongue to come in and out. A vocalization is sometimes added to the motor pattern.

Yawning. The muzzle is raised while the mouth is opened and the teeth are displayed. Sometimes a sound (similar to that on humans in the same context) is added to the motor pattern.

Certain behaviour elements, such as eyebrow raising, staring, looking elsewhere, and looking at, were not registered, as its recording frequently depended on the orientation of the subject with respect to the observer, so that very often they occurred and were not seen.

Other elements of the ethogram occurred in low frequencies and are not dealt with here. These are looking around, head protruding, protective threat, alert posture, genital display, striking of tongue, masturbation, embracing, body shaking, brushing ground, playbiting, and some others.

Intra-Individual Sequences

The matrix of 11,956 transitions between each of the 22 described elements was the starting point for the analysis of correlations between the patterns of transition frequencies shown by each element, those presenting very similar patterns will be considered as sharing a high degree of causal factors.

Since our criterion for common causality is based in temporal proximity, that is, the frequency with which every two elements occur as neighbours, the original before-after transition matrix was transformed into a symmetrical matrix by adding up symmetrical cells.

In the matrix of observed transition frequencies (o) the expected value for each cell (e) in case of random sequence (all acts independent of each other) was calculated by dividing the product of marginal totals by the sum total. In order to diminish random variation in the case of small expected values, the quotient $(o-e)/\sqrt{e}$ was calculated for each cell of the matrix. This excentricity quotient, successfully used by VAN HOOFF (1973) appears to be a better index than o/e, used by WIEPKEMA (1961).

Since transitions of each element with itself were not recorded, the descending diagonal of the original matrix contained no figures. Since the conclusions on causal factors will be based on the values of the excentricity quotients and each element depends, by definition, on the same causal factors as itself, we wrote the highest value of the respective rows in these empty cells of the descending diagonal of the matrix of excentricity values.

Then the correlations among the pairs of elements was calculated (Pearson r) and the analysis of principal components of the correlation matrix was performed, followed by varimax rotation.

The components analysis will provide us with the number of factors accounting for the data on intra-individual transitional sequences, as well as the loadings of each behaviour element on each factor.

The results are presented in Table 1 and Figure 2, where for each of the 22 items the loadings on the five factors requested of the analysis are presented, the portion of the total variance explained by these five components being 74 per cent, leaving 26 per cent to be explained by the remaining 17 components.

Table 1. Intra-individual sequences. Component loadings and portion of variance explained by each factor.*

	Components				
Behaviour elements	I	II	III	IV	V
1 Rubbing nose	*−.907*	−.161	.180	−.005	.189
2 Autogrooming	*−.905*	.123	.131	−.114	.143
3 Scratching	*−.864*	.178	.261	.065	.179
4 Groom-presenting	.135	*.722*	.281	.161	.349
5 Grooming	−.015	*.688*	.292	.151	−.264
6 Moving away	−.011	*−.889*	.243	.084	.041
7 Approaching	−.017	*−.840*	.106	.204	.056
8 Barking	.156	*−.790*	.161	−.055	−.004
9 Grimacing	.307	*−.611*	.236	−.069	−.014
10 Contact calling	−.251	−.431	.014	.244	.327
11 Pelvic thrusting	.194	.105	*−.953*	−.021	−.054
12 Gasping	.141	.044	*−.944*	−.005	.048
13 Mounting	.294	.163	*−.679*	−.098	*−.491*
14 Sexual calling	.240	−.091	.165	*.791*	.145
15 Mount-presenting	.199	−.359	.210	*.760*	.101
16 Fighting	.351	−.292	.189	*−.643*	.176
17 Attacking	.341	−.326	.205	*−.601*	.145
18 Yawning	.117	*.525*	.272	−.158	*.635*
19 Grinding teeth	.114	.165	.132	−.276	*.546*
20 Raising lip	.257	−.055	.133	−.172	*−.796*
21 Smacking lips	.275	.304	−.105	−.044	*−.766*
22 Genital inspection	.341	.340	.021	−.092	*−.584*
Proportion of variance	23.1%	20.1%	11.1%	10.2%	9.3%

* Elements contributing most to each component are in *italics*.

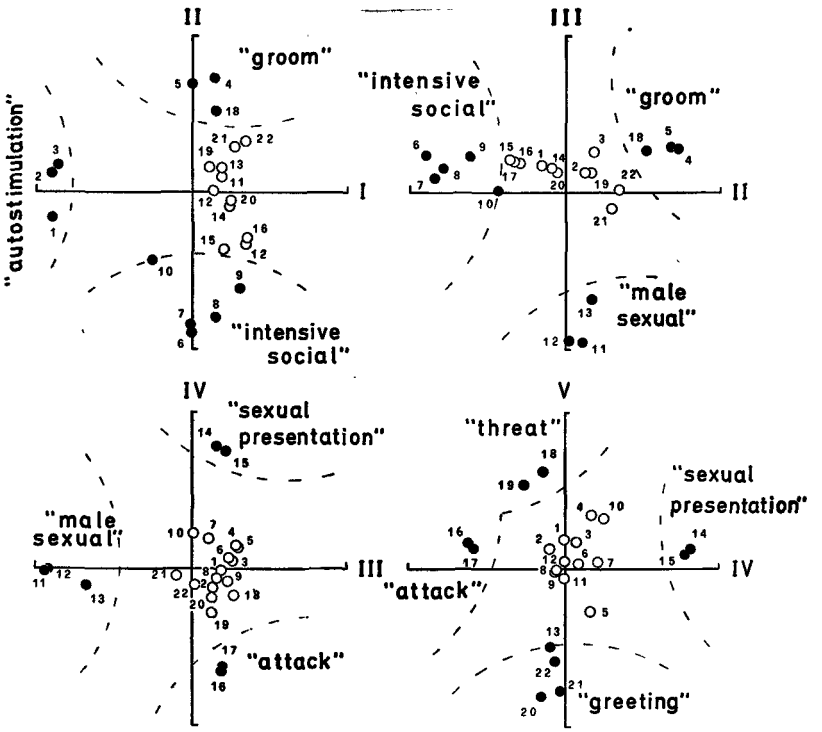

Fig. 2. Intra-individual sequences. Plots of behaviour elements loadings on the plane defined by pairs of principal components. Black dots represent elements contributing most to the components.

By considering the elements with high loadings (over 0.5) we could identify the factors hereby colloquially labelled: (I) "autostimulation", (II) "intensive social" versus "groom", (III) "male sexual", (IV) "attack" versus "sexual presentation", and (V) "greeting" versus "threat".

The first component ("autostimulation") had high loadings for *nose rubbing, autogrooming,* and *scratching.*

The component "intensive social" *vs.* "groom" presents highest loadings for *approaching, moving away, barking, grimacing, contact calling* (negative) and *grooming, groom-presenting* and *yawning* (positive). These two sets of behaviour elements exclude each other, in accordance with the tension reducing function that grooming activities represent, serving as a behavioural sink which avoids other kinds of interactions.

The "male sexual" component presents highest loadings for *mounting, pelvic thrusting,* and *gasping,* that is, overt sexual activities.

The component termed "attack" *vs* "sexual presentation" shows the highest loadings for *attacking* and *fighting* (negative) and *sexual calling* and *mount-presenting* (positive), the exclusion between these two sets of activities reflecting the tendency shown by geladas to use sexual presentation to express affinity and to reduce aggression.

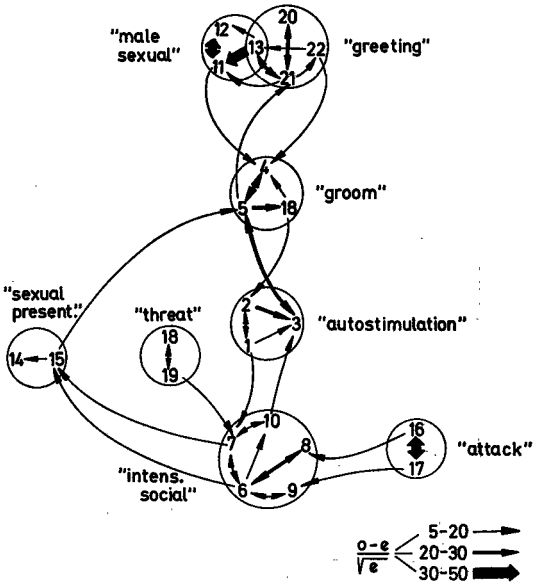

Fig. 3. Intra-individual sequences. Flow chart of excentricity quotients between transitions of behaviour elements. Groups within circles are sets obtained by principal components analysis.

The last component ("greeting" *vs* "threat") also has highest loadings for two opposite sets of activities: *raising lip, smacking lips, genital inspection* and *mounting* (negative), and *grinding of teeth* and *yawning* (positive).

The elements *mounting* and *yawning* present high loadings on two components each ("male sexual" and "greeting" for *mounting*, "groom" and "threat" for *yawning*).

At this point it seems that we could get a still better understanding of the structure of individual behaviour by considering also the transitions of each element with all the others. In order to assess the relative importance of each transition (independently of high or low absolute frequencies) we obtained the excentricity quotients for every cell of the before-after transition matrix.

The highest values of this quotients between pairs of behaviour elements is shown in Figure 3, where the latter are also grouped according to the results of principal components analysis.

As can be observed in this figure, there is a strong tendency for the transitions to occur between the elements of the same principal components groups; some of these groups and some elements within them serving as intermediaries, and others as dead ends of the chain.

It also appears to be of interest that the sets we called "autostimulation", "sexual presentation", and "intensive social" are linking incompatible groups (opposite ends of components II and IV, respectively). Besides, except in the case of *mount-presenting*, they are different elements within the sets those connecting with the mutually exclusive groups.

INTER-INDIVIDUAL SEQUENCES

The matrix of 6,975 inter-individual transitions was used to determine the communicative function of each behaviour element, as well as the structure of the communication process.

If the excentricity value for each transition measures the degree to which the observed frequency departs from random, high enough values would indicate a facilitating or triggering function of the preceding over the following elements. For the purpose of establishing these relationships we considered only quotients greater than 5.

Again, as in intra-individual sequences, and for statistical reasons, when *e* was less than 5 a minimum value of 5 was used as expected frequency.

The results as to the triggering function for each element appears in Table 2, with the responses ranked according to the degree in which their frequency departed from the random expected value.

The structure of the communication process was approached by the principal

Table 2. Inter-individual sequences. Responses triggered in the recipient animals by each behaviour element.

Signals	Responses Excentricity quotients of transitions			
Behaviour elements	35.1–45	25.1–35	15.1–25	5–15
1 Rubbing nose				Rubbing nose
2 Autogrooming				Autogrooming Scratching Rubbing nose
3 Scratching				Scratching Rubbing nose
4 Groom-presenting	Grooming			
5 Grooming		Yawning	Groom-presenting	
6 Moving away		Approaching		
7 Approaching				Moving away Smacking lips Raising lip
8 Barking				Barking
9 Grimacing				
10 Contact calling		Contact calling		
11 Pelvic thrusting				Sexual calling
12 Gasping				Sexual calling
13 Mounting				
14 Sexual calling				
15 Mount-presenting	Mounting		Genital inspection	Pelvic thrusting
16 Fighting				
17 Attacking				
18 Yawning				Grinding teeth Grooming
19 Grinding teeth			Grinding teeth	
20 Raising lip				Mount-presenting
21 Smacking lips			Mount-presenting	Smacking lips
22 Genital inspection				

components analysis of the correlation matrix between distributions of responses for each behaviour element. Those showing a similar pattern of responses presenting a strong positive correlation.

Thus, correlations (Pearson r) were obtained between distributions of excentricity quotients [$q = (o-e)/\sqrt{e}$]. The rotation used was varimax.

The resulting loadings of each behaviour element on the five factors requested of the analysis are presented in Table 3 and Figure 4.

The total variance explained by the five factors was 68 per cent.

We could now determine the factors defined by the elements presenting high loadings on them, which, according to the usual responses, we labelled in the following way: (1) "female-sexual releasing", (2) "greeting and approach releasing" versus "groom releasing", (3) "autostimulation releasing" versus "male sexual releasing", (4) "fight releasing", and (5) "conflict".

The elements showing highest loadings on the first component (*genital inspection* and the elements of the intra-individual "male sexual" set: *mounting, gasping*, and *pelvic thrusting*) appear to trigger only *sexual calling* in the recipients, an item of the intra-individual "sexual presentation" set performed only by females, apparently more often at the height of estrus, an activity that has no direct connection with other patterns but *mount-presenting* (see Figure 3).

The second component showed highest loadings on its positive end for *moving away* and *raising lip*, elements which seem to elicit *approaching* and *mount-presenting*. In the negative side of the same component the elements *groom-presenting, yawning,*

Table 3. Inter-individual sequences. Component loadings and portion of variance explained by each factor.*

Behaviour element	Components 1	2	3	4	5
22 Genital inspection	−*.986*	−.008	.001	.006	.002
13 Mounting	−*.985*	.015	.008	.003	.000
12 Gasping	−*.972*	.005	−.070	.017	.004
11 Pelvic thrusting	−*.897*	−.018	−.069	.035	−.014
6 Moving away	.266	*.780*	−.183	−.083	.189
20 Raising lip	.044	*.779*	−.307	−.079	.323
4 Groom-presenting	.077	−*.854*	−.201	.002	−.009
18 Yawning	.149	−*.770*	−.297	−.029	.075
5 Grooming	.023	−*.548*	.002	.042	.082
21 Smacking lips	−.252	.459	−.150	−.146	*.605*
7 Approaching	.095	.412	.178	−.033	−.462
3 Scratching	.126	.021	*.941*	.106	−.126
2 Autogrooming	.071	.040	*.864*	.111	−.086
1 Rubbing nose	.271	.251	*.767*	.156	−.039
15 Mount-presenting	.154	.243	−*.579*	.194	−.153
16 Fighting	.048	.104	−.033	−*.962*	−.082
17 Attacking	.074	.086	−.077	−*.918*	.087
9 Grimacing	.168	.322	−.277	.044	*.798*
19 Grinding teeth	.111	−.120	.249	−.019	*.729*
14 Sexual calling	.095	.070	−.174	.211	−.210
8 Barking	.075	.348	−.263	−.285	−.041
10 Contact calling	.064	−.031	−.238	.178	−.099
Proportion of variance	19.0%	18.0%	14.3%	8.6%	7.8%

* Elements contributing most to each component are *in italics*.

latter (its loading on the "groom" set is rather high), being used more often than anything else as greeting and, given the sexual implications of this set as well as its frequent connections with the "male sexual" grouping, it would be expected (as actually happened) that this item would trigger *mount-presenting* in the recipient animals.

Finally, the evidence about elicitation by certain behaviour elements of several acts of the same intra-individual grouping set in the recipient (often of the same set as the triggering units) suggests more a communication of general moods rather than act to act effect.

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Authors' Present Address: FERNANDO ALVAREZ and CARMEN CÓNSUL, *Instituto de Aclimatación de Almería, C. S. I. C., General Segura 1, Almería, Spain.*