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Social Organization and Demography in the Rock Agama, *Stellio caucasius*

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Abstract. -We studied the social organization and demography of the rock agama *Stellio caucasius* in a natural population, located in Gobustan (eastern Azerbaijan, approximately 60 km south of Baku) and in an introduced population in the small Karadag Range near Krasnovodsk (western Turkmenistan). We found that these populations are highly stable with low turnover. This appears to be the result of delayed reproduction, longevity and a sedentary life style. Population growth is relatively slow due to high juvenile mortality and low immigration rates from adjacent subpopulations. The age structure of all subpopulations studied was dominated by older age classes. Rock agamas exhibit those natural history and population characteristic of a K selected species.

Key words: Agamidae, age, Azerbaijan, density dependence, K-strategy, Lacertilia, ontogenetic trajectories, polygyny, population dynamics, social behavior, spacing, *Stellio caucasius*, survivorship, mortality, territoriality, translocation, Turkmenistan.

FIG. 1. Adult (10+ years old) male *Stellio caucasius* perched on basking site (left); adult female *S. caucasius* (right).

Introduction

Long-term mark and recapture studies of natural populations have become important in recent decades due to their great power in demonstrating population parameters. These investigations permit the testing of hypotheses concerning the mechanisms governing population parameters. The ability to follow particular individuals through time reveals the scale of behavioral heterogeneity within the local population. It also allows the examination of these population parameters as a function of age or changing social status.

This approach has already gained firm position in the population studies of birds and mammals, but it has only recently been broadly employed in reptile studies.

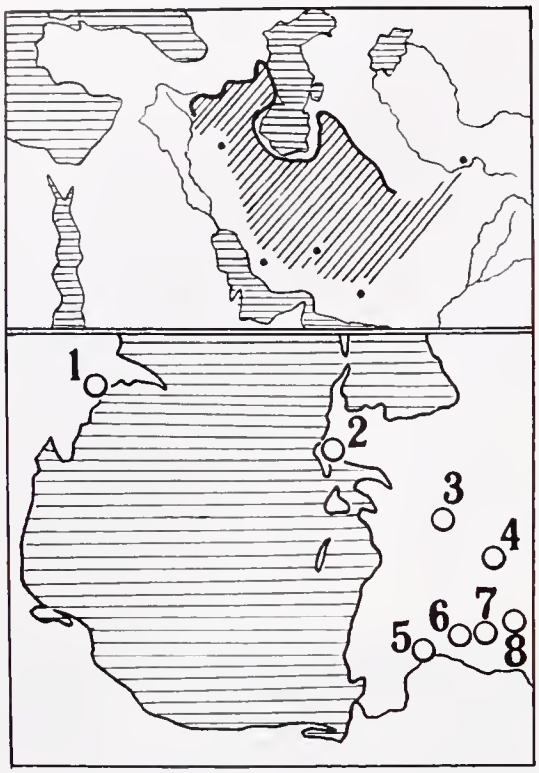

FIG. 2. Regional distribution (cross hatched area) of *Stellio caucasius* (upper plate). Specific study sites in Azerbaijan and the Turkmen Republic: 1) Gobustan; 2) Krasnovodsk; 3) Bol'shoi Balkhan Range; 4) Kyurendag Range; 5) lower Sumbar River; 6) Parkhai Gorge; 7) Kalaligez; 8) Aidere (lower plate).

Although this method is used in modern herpetology rather frequently, it is oriented mainly toward answering the questions of traditional population ecology (dynamics of numbers and sex-age composition of local populations, modes of spacing in the context of resource utilization by communities and species, etc.). In behavioral ecology, and particularly with respect to the fates of particular individuals and their social relationships, the reptiles in general and lizards in particular remain poorly studied (for review see Semenov, 1989).

The rock agama, *Stellio caucasius*, is an ideal subject for the study of behavioral aspects of population organization in reptiles that are K strategists. This is a long-lived lizard attaining an age of ten or more years (Zykova and Panov, 1991). Many populations are characterized by high and very high density. Most individuals demonstrate strong home area fidelity. Adults live in small social groups in which the lizards form long lasting pair bonds (Panov and Zykova, 1985; 1989).

This paper examines the social interactions within local settlements of rock agamas and analyzes the role of social behavior as a regulator of demographic processes.

Methods and Materials

Rock agamas are large lizards with an overall length of up to 30 cm. and weighing up to 160 gm. Males are on average larger than females and have a heavier build. General background color is a mixture of gray, brown and olive with a darker, dull spotted pattern on the back and sides. During the breeding season males differ from females by having black on the breast, contrasting with pale or pinkish-gray on the throat (Fig. 1). In males, there is light gray epidermal holocrine gland in the center of the blackish-gray belly. These lizards are typical inhabitants of stony landscapes, although some populations have become adapted to the life on the steep slopes of clay canyons or even at the margins of the sandy desert (Ananyeva and Ataev 1984; Panov, Zykova, Glauzer and Vasil'ev, 1987).

The bulk of data presented here was obtained during a comparative study of two populations of rock agama: a natural population, located in Gobustan (eastern Azerbaijan, approximately 60 km south of Baku) and in an introduced population in the small Karadag Range near Krasnovodsk (western Turkmenia) where rock agamas were known to be absent earlier (Fig. 2). In the second area, on 17 May 1985, we introduced into an abandoned quarry 13 adult males, 19 adult females, 13 two year old lizards and 25 juveniles born in the preceding year. All these animals were caught in the Blocky Balkan Range situated some 160 km from the introduction site. The latter lies in view of Krasnovodsk Plateau known to be a part of rock agama

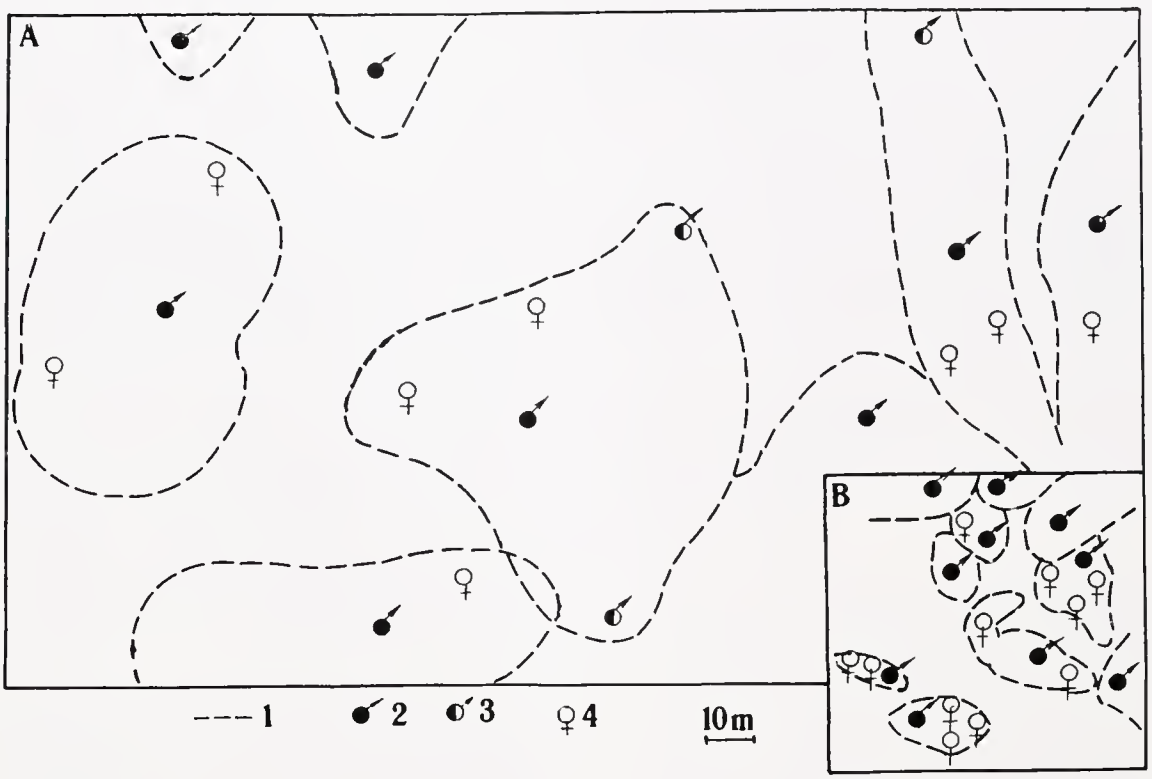

FIG. 3. Territory structure in Gobustan (A) and Aidere (B): 1) territory boundaries; 2) breeding males; 3) subordinate males; 4) females.

breeding range (Ataev, 1985). The introduction site is similar to the dry semidesert habitats of rock agamas found in Gobustan. The predominately stony surface is covered by very sparse grasses, but trees and bushes, in contrast with Gobustan, are wholly absent. The experimental plot was situated in a broad, dry valley with steep slopes broken by narrow ravines and rifts. The numerous cavities and cracks under and between the stones provided abundant temporary and permanent shelters for the lizards. Prior to release all introduced agamas were marked by toe clipping.

In Gobustan, on the natural plot of 0.65 hectares, capturing, marking and observations were conducted in April 1987 and 1988; in spring of 1986 and 1989 we performed censuses and selective capture of lizards. In Krasnovodsk, on the introduced population, field work was carried out 24 April - 6 May 1986, 22 - 25 March and 30 April - 18 May 1987, 26 April - 17 May 1988, 5 - 10 April and 28 April - 23 May 1989, 15 - 25 May and 10 -11 September 1990 (total of 103 days). Some observations were made during short visits in the summer and fall from 1985 to 1989.

Important additional data were obtained during the course of field studies conducted on two marked populations in western Kopetdag near Kara-Kala settlement (Sjunt-Khasardag State Reserve). An observational plot in Parkhai Gorge was inspected in the spring months of 1986 and 1989 and in September - October 1986 - 1988; a population in the Kalaligez area was investigated in the fall of 1984 - 1987 (total of 25 days).

In all of the above study plots we carried out total censuses of lizards in the areas under study. Most of the agamas observed on the plots were captured. They were measured with a ruler and calipers according to standard procedures, weighed and

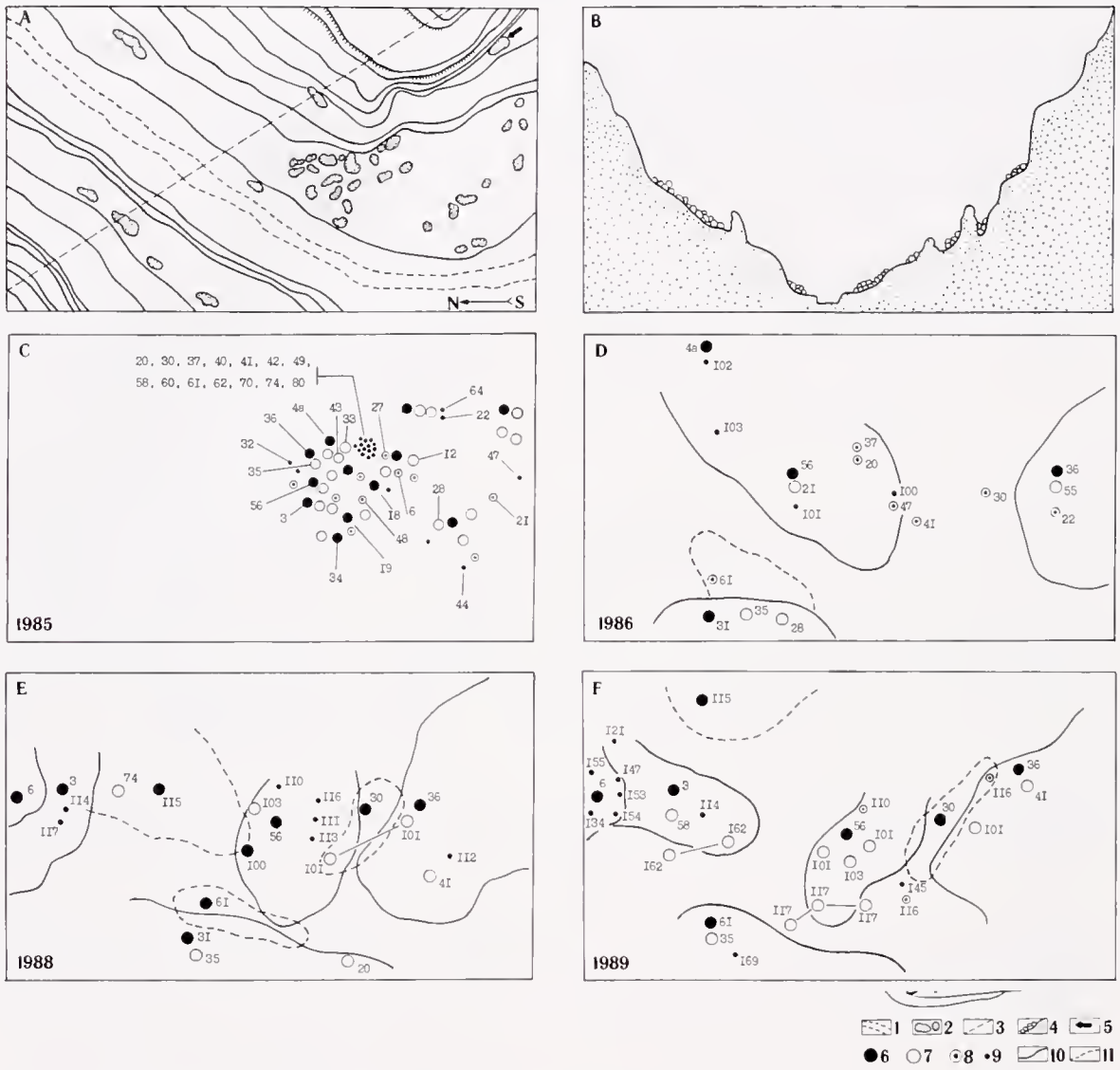

FIG. 4. Krasnovodsk experimental study plot. A. Map of study site. B. Cross-section of the study . C. Distribution of rock agamas in 1985. D. Distribution of rock agamas in 1986. E. Distribution of rock agamas in 1988. F. Distribution of rock agamas in 1989. 1. Dry creek bed. 2. Large rocks and boulders. 3. Cross-section illustrated in Fig. 4B. 4. Talus. 5. Communal winter shelter. 6. Adult male. 7. Adult female. 8. Second-year lizard. 9. Yearling. 10. Territory boundary. 11. Subordinate male home range boundary. Numbers refer to individual lizards.

photographed. Animals caught for the first time were marked by toe clipping. Prior to release all agamas received individual color marks made with dye. The locations of all individuals on the plots were mapped.

The ages of agamas were estimated using standardized size criteria (Zykova and Panov, 1991). We assumed that the age of individuals corresponds to the number of winter hibernations. So, the ages of agamas captured in spring will be slightly overestimated. Our "yearlings" in May are actually about 10 months old; "two year old" lizards in May are approximately a year and 10 months old, etc.

Altogether 426 agamas were captured and marked, 144 of them were observed a total of 273 times during subsequent years.

Results and Discussion

Spacing Patterns in Rock Agama Settlements

The baseline of spacing pattern of a whole social organization in Rock Agama is a mosaic of mutually exclusive territories owned by mature adult males. Mature females have either mutually exclusive or overlapping home ranges situated within territories of those males with which the given female is tied by the family bonds. The adult female, as a rule, does not leave the territory of "her" male. Therefore, the territory of adult breeding male, if there is female(s) living in it (which is not necessarily the case) in the same time the territory of pair or a family group defended as a whole by the breeding male only.

The home ranges of immature lizards one and two years of age may lie both within the territory of the family group or outside in the neutral zones separating such territories. The home range of an immature male during the first years of life within an adult male territory, shifts to the periphery of this territory as the immature male becomes older. In contrast, the home range of an immature female adjacent to that of an adult male shifts with time toward the male's territory.

In saturated habitats all suitable space is shared among adult males, so that neighboring territories have common boundaries. The size of territories in such saturated habitats depends on the substrate and local food abundance (Fig. 3). In barren habitats of Gobustan with low microrelief (absence of talus mounds, in particular) the size of adult male territories was found to vary from 100 to 210 m^2 (140.0 15.8 m^2 on average). In the middle altitudes of the Western Kopetdag Mountains (Canyon Ai-Dere, see Fig. 3B) where the climate is more humid and the vegetation is rich and diverse and the substrate includes jumbles of fallen rocks and boulders, the size of territories was found to range from 28 to 136 m^2 (94.0 $\pm$ 16.3 m^2 on average), for details see Panov and Zykova (1985).

Formation of Territorial Structure

We followed the establishment of territorial structure in the course of our long-term observations on the Krasnovodsk introduced population. Here 13 male "founders" were released into an area that would have supported a population of a density comparable to that in natural colonies of rock agamas. Males were released into deep holes and crevices which seemed to us to be similar to hollows normally used by rock agamas as their permanent dens.

However, contrary to our expectations, the majority of introduced males left the area where they had been released, and moved away at distances ranging from 60 to 500 m. Only three males remained in proximity to the release site by the next spring. At that time the territory of only one male (N 56) overlapped the release site. The boundaries of two other males (NN 36 and 31) territories were 60 and 100 m respectively from the release site (Fig. 4 c, d).

The process of territory establishment adjacent to the release site is shown in Fig. 4 c-f. During 1986, the year following introduction, adult male territories were large and had no common boundaries (Fig. 4d). Since male rock agamas do not patrol the borders of their territories (as, for example, males of steppe agama, *Trapelus sanguinolentus*, do (see Panov and Zykova, 1986), it is difficult to locate precisely the boundary between territories and, therefore to estimate exactly the real territory size. The greatest territory diameter was estimated in 1986 on the experimental plot as 140 m, with the width of the neutral zones separating neighboring territories as some 20-60m. The small, indistinctly demarcated home ranges of three immature lizards (males NN 30 and 61, and female N 41, all less than two years old) were situated in these neutral zones (Fig. 4e). Other immatures approximately two years old established their home ranges within the territories of mature males, as well as four

lizards born already in place of introduction in preceding year.

In 1988, the third year after introduction, most of the area that in 1987 was neutral zone was shared among relatively young males of about four years of age (NN 30 and 61) and three years of age (N 115 already born on the introduction site). Although these males apparently had attained maturity, they seemed to be bachelors at that time. Three year old male N 115 and four year old female N 74 were repeatedly seen in 1988 in close proximity (10-15 m) to each other, but we did not witness immediate contacts between them.

In 1989, the fourth year after introduction, slight changes in territorial structure were observed (Fig. 4e). There was some tendency toward clumping of territories toward each other, possibly because of the increasing density of lizards. Male N 61 (about five years old) left his adolescent bachelor home range and occupied the territory of deceased male N 31 and established a bond with his former mate, a female of eight or nine years of age. The corpse of male N 31 indicated that he had died between June 1988 and April 1989. Relatively young male N 115 occupied the territory of five to six year old male N 4a after he disappeared. Female N 74 moved into the territory of 10 to 11 year old male N 3.

Dynamics of Space Utilization Within a Home Area

During the hot periods of the year, each individual had at least one permanent den and one to several observational posts (used also as basking sites) where it spent considerable time, except during periods of foraging. In individuals about one year old or younger the den and basking site were the same or immediately adjacent. Usually the shelter was situated under a boulder or rock on which the lizard basked. Foraging activities of juveniles and yearlings take place within a radius of several meters of the individual dens. Many subadults of both sexes and some adult females behave in a similar way, although during foraging they often move greater distances from the den, up to several tens of meters.

During the day adult males range more widely. The several posts of a male are connected by a network of relatively permanent pathways. The territory is utilized unevenly with some points located along the pathways receiving regular use while others, situated at some distance from the pathways being visited only occasionally or not used at all during a given season.

This pattern of territorial use can result in changes in territorial boundaries. For example, by comparing the positions "c", "d", and "e" in Fig. 4, one can see that in 1988 the border of the territory of male N 36 shifted 30-40 m eastward from its position in 1986. Such shifts are possible in non-saturated habitats only. In established rock agama settlements with dense populations the boundaries remain constant from year to year.

In relatively sparse Krasnovodsk population the cases of mutual intrusions by neighboring males into neutral zones separated their territories and even into peripheral parts of these territories themselves are possible. The above said does not hold in respect to male-"pretenders", or "satellites". Their home ranges may broadly overlap the peripheral parts of two or more territories of adult "resident" males (see, for example, home ranges of male-pretenders NN 30 and 61 in Fig. 4). In saturated habitats home ranges of satellites are practically always situated within the territories of resident males.

By the winter the agamas leave their summer home areas and migrate to communal hibernation shelters. Migrations begin when air temperatures are relatively high (25^0 C and above). Communal winter dens may be situated up to 500 m from an individual's home area. On 23 March 1987 on the Krasnovodsk experimental plot, when only a few agamas had returned to their summer areas from the communal hibernation shelter (daily temperatures ranged from 2^0 C to 16.5^0 C) we found in that shelter males NN 21, 27, 36, 61,

females NN 22 and 58 (ages from two to seven years) and subadult male N 105. Summer residences of these lizards are shown in Fig. 4, home areas of others were located 100 - 500 m from the communal winter den.

Individual Ontogenetic Trajectories

An ontogenetic trajectory is defined as a sequence of changes in social status and of social roles of an individual during its life (Wiley 1981). In rock agamas social behavior and social status of individuals of both sexes appear to be similar during the first two years of their lives. But thereafter ontogenetic trajectories of males and females become progressively divergent.

It is not known if lizards remain in the vicinity of their birth place during their lives. Among those juveniles (n=61) that were captured on the two plots in the western Kopetdag at the end of September and the beginning of October (i.e. at the age of two to three months), only five (8.2%) were observed near the places of their first capture (within a radius of 25 m) in next year. The proportion of such recaptures on one of the two plots was as high as 25%, while on another plot none of 41 juveniles caught during preceding fall was observed later on. Unfortunately of all those juveniles that were captured during the first months of their lives, it remains unknown whether they remained near their birthplaces or if they dispersed by the time of capturing (dispersion of juveniles just after hatching has been described for *Anolis aeneus* ; Stamps, 1988).

More definitive results were obtained from recaptures of those first year lizards that were initially captured soon after their first winter hibernation, in April and May. Of those lizards 64.5% (20 of 31) were observed regularly within a radius of 10 to 50 m from the place of their first capture, in some cases over a period of several years. First year animals initially occupy small home ranges of about 10 m in diameter both outside the territories of adult males (5 males and 5 females in Krasnovodsk population in 1985) and within such territories (4 males and 5 females). When the home ranges of first year lizards were immediately adjacent their interactions appeared to be agonistic. In some cases between adjacent home ranges a well defined boundary was established and both neighbors displayed pronounced territorial behavior toward each other. In other cases the home ranges overlapped and a stable rank order was formed so that one lizard appeared to dominate the other in the overlap zone.

Generally, the mature members of the settlement behave indifferently toward yearlings. However, in periods of high sexual activity adults may chase the yearlings short distances.

After the second winter the young agamas returned from communal den to their original summer home area where they knew the topography of the place and their foraging routes became longer and pioneering of new feeding places and new temporary shelters began. Apparent differences between social behaviors of young males and females began to emerge only after their third winter, at an age of more than 30 months.

Male Ontogenetic Trajectories

Males participate in reproduction only after they have acquired a territory. Males continue to reproduce until the end of their lives. For example, on the Krasnovodsk plot male N 3 in 1989 at an age of approximately 12 years had a large territory that included four adult females of different ages and two immature females. In addition the same year we observed interactions between this male and immature female N 161 in the border zone between his territory and that of male N 61.

If, on the given territory, the only one female lives, in the case of her disappearance a holder of territory becomes a widower. He however, subsequently does not try to search for females outside his territory. In Gobustan, such case of widowhood was observed in about 6 years old male. A more young male, evidently, may also turn out to be a widower.

TABLE 1. Composition and age structure of family groups of the experimental introduced population at Krasnovodsk and the natural population at Gobustan.

	Krasnovodsk					Gobustan			
Year	1986	1987	1988	1989	1990		1986	1987	1988
Individual	Age in years					Present (+)/Absent (-)			
♂ N 36	5*	6	7	8	9	♂ N 41	+	+	+
♀ N 55	4-5*	-	-	-	-	♀ N 38	+	+	_
♀ N 22	2	3	-	-	-	♀ N 45	+	+	+
♀ N 41	2	3	4	5	6	♀ N 66		2	-
♀ N 119	-	-	1	2	3	♂ N 42	+	+	+
Juv N 148	-	-	-	1	2	♀ N 51		+	-
♂ N 56	6*	7	8	9	10	♂ N 52		+	+
♀ N 101	1	2	3	4	5	♀ N 47		+	+
♀ N 103	1	2	3	4	-	♀ N 48		-	+
♀ N 117	-	-	-	2	?	♀ N 81		2	3
Juv N 110	-	-	1	2	-	Juv N 90		-	+
♂ N 6	3	4	5	6	7	♂ N 56		+	+
♀ N 121	-	-	1	2	3	♀ N 49		+	+
♀ N 154	-	-	-	2-3	-	♀ N 50		+	+
Juv N 157	-	-	-	1	-	♂ N 63		+	+
♂ N 30	2	3	4	5	-	♀ N 64		+	+
♂ N 37	-	-	-	5	6	♀ N 65		+	+
♀ N 116	-	-	1	2	3	♂ N V		+	+
Juv N 145	-	-	-	1	2	♀ N 40	+	+	+
♂ N 18	7	8	-	-	-	♀ N 44		-	+
♂ N 27	-	-	5	6	7	♀ N 87		2	3
♀ N 43	-	4*	5	6	-	Juv N 80		-	+
♀ N 80	-	3	4	5	6				
♀ N 107	-	2	3	4	5				
♀ N 106	-	1	2	3	4				
Juv N 144	-	-	-	1	-				
Juv N 158	-	-	-	1	2				
Juv N 159	-	-	-	1	-				

* = minimum estimated age.

Female Ontogenetic Trajectories

Female rock agamas are able to reproduce at about three years of age. By this age to be a successful breeder, a female should establish a stable bond with a male territory holder and obtain constant shelters within his territory. For a female that had a juvenile home area within a male's territory the process of assimilation into a family group and establishment of a bond with the male is very direct. An example of this was female N103 who was observed for the first time in 1986 as a first year juvenile living on the territory of male N 56 where she continued to stay at least until 1989 (see Fig. 4d-f and Table 1A).

Females that had juvenile home areas on the periphery of an adult male's territory, in the home range of a non-territorial satellite male, or in a neutral zones where sexually active males were totally absent usually left and attempted to establish a bond with a territory holding male. This process of selection of a male and territory may take several years and involve short stays in the areas of several males. For example, female N 101, originally having frequented the territory of male N 56,

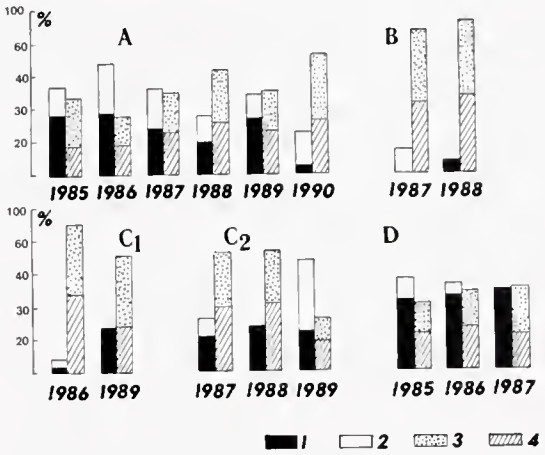

FIG. 5. Population structure of study populations. A. Krasnovodsk. B. Gobustan. C_1. Parkhai Gorge (spring). C_2. Parkhai Gorge (fall). D. Kalaligez. 1. Yearlings. 2. Second-year lizards. 3. Adult males. 4. Adult females.

subsequently over a period of 3 years (1988-1990) was resident of the neutral area visited at different time by two adult territorial males (NN 56 and 36). Female N 74 resided at ages of a little less than 4 years temporal home range of 3 year old male N 115 in next year moved on to territory of male N 3 (Fig. 4 e,f) who
became a permanent target for her courtship displays.

It is useful to describe shortly a peculiar courtship behavior of females addressed by them towards males, which we regard as a very important mechanism contributing to establishment and maintenance of personal bonds between mating partners. At sight of a male young female moves to him and at once tries to climb onto his back. A male, as a rule, during first minutes of contact tolerates these actions of female who is crawling over him in different directions and makes insistent attempts to crawl under him. After that male behaves as if he is inclined to retire, while a female pursues him and repeats her actions. Such a behavior is quite characteristic of females younger age classes, even of those lesser than 2 years old. The behavior retains in older puberal females, although, contrary to expectation, it almost never occurs prior to actual sexual interactions, i.e. copulations. Once a female has selected a male she begins to co-habit his shelters. Where there are several females on a territory usually the oldest female cohabits with the male.

The home ranges of adult females overlap broadly, especially if the territory is large. However, some older females exhibit territorial behavior in the vicinity of their shelters, basking sites and foraging areas when approached by other older female.

Females leave the territory of their family groups only for egg laying and to migrate to communal winter shelters. We did not observe emigration or dispersal of females. Over the five year study of the Krasnovodsk population the time of residence of adult females introduced in 1985 ranged from one to five years (mean = 2.5 ± 0.6, n=6).

Family Groups

The mode of sexual relations in rock agama settlement may be defined as a territorial facultative polygyny. As many as four females may establish bonds with a territorial male. In the natural Gobustan population there were 1.73 females per male on territories. In the introduced Krasnovodsk population the average number of females per male was increasing as population structure matured. Over the duration of our study the average number of females within the family groups was 1.33 (1988), 1.86 (1989) and 2.43 (1990).

The term "family group" is not quite precise since each female enters into such a unit independently from other females. Any personal or functional bonds between female members appear to be absent. Only relations between the territorial male and each of the females may be regarded as bonds.

The stability of such breeding units is determined primarily by an association its

TABLE 3. Survival of rock agamas introduced as adults in the Krasnovodsk experimental plot in May 1985. The number of lizards alive is presented; the number is parentheses is the per cent surviving since the previous year.

Year	1985	1986	1987	1988	1989	1990
Males	13 (100)	8 (61.5)	7 (87.5)	6 (85.7)	5 (83.3)	4 (80.0)
Females	19 (100)	6 (31.6)	4 (66.7)	3 (75.0)	3 (100)	1 (33.3)
Total	32 (100)	14 (43.8)	11(78.6)	9 (81.8)	8 (88.9)	5 (62.5)

TABLE 2. Life table of a cohort of rock agama yearlings introduced into the experimental population at Krasnovodsk.

Age x	Frequency f_x	Survival l_x	Mortality d_x	Mortality Rate q_x	Survival Rate p_x
1	25	1.000	0.280	0.280	0.720
2	18	0.720	0.120	0.167	0.833
3	15	0.600	0.120	0.200	0.800
4	12	0.480	0.080	0.167	0.833
5	10	0.400	0.080	0.200	0.800
6	8	0.320			

$l_x = \frac{f_{xi}}{f_{xl}}$; $d_x = l_{xi} - l_{xi+1}$; $q_x = \frac{d_x}{l_x}$; $p_x = 1 - q_x$ (Caughley, 1977)

TABLE 5. Sex ratios in different rock agama populations (n).

	Year					
Location	1985	1986	1987	1988	1989	1990
Gobustan (spring)	-	-	1:1.1 (31)	1:0.9 (33)	-	-
Western Kopetdag						
Parkhai Gorge						
spring	-	1:0.9 (21)	-	-	1:1.6 (13)	-
fall	-	-	1:0.7 (10)	1:0.8 (16)	1:0.7 (10)	-
Kalaligez (fall)	1:1 (12)	1:0.8 (18)	1:1.2 (11)	-	-	-
Krasnovodsk (spring)	-	1:0.8 (20)	1.1 (30)	1.1 (40)	1:0.9 (47)	1:1.2 (41)

Grand sex ratio for all localities summed = 1:0.98 (393).

member to certain shelters and to its home range (or territory) as a whole. All this seemingly explains why females accept so readily a new male partner after the death of a previous mate. For example, male N 36 established bonds with a single adult female and two immature females (all from the initial cohort of lizards simultaneously introduced to the study plot) immediately upon introduction (Table 1). Subsequently, upon the deaths of these females replacement females were recruited from those subsequently born in the colony.

Population Dynamics

Rock agamas are long lived and predominately sedentary. Populations are characterized by stable membership with recruitment as the primary source of new members. Emigration and immigration are of minor importance. Each of these factors were examined in the Krasnovodsk population.

The general picture of changes in the relative proportions of immatures, matures and sex ratio is shown in Fig. 5. It is necessary to repeat that in 1985 the original colonizing cohort was composed primarily of immatures, this may have resulted from capture sampling error. In 1986 the proportion of immatures to adults was similar but in 1987 and 1988 the ratio of immatures to adults was nearly equal. Since 1988 adults have predominated. Comparison with natural populations (Fig. 5) shows that adults predominate though relative proportions may vary significantly among areas and years. Sex ratio, males to females, is generally equal (Fig. 5; Table 5).

Recruitment

Surveys of juveniles were conducted during the spring (Fig. 5) since few lizards were active during the hottest weather in summer and early fall. Differences in the numbers of over wintering juveniles may be attributable to embryonic mortality or hatchling mortality in the first months after emergence or over the first winter.

Post Hatching Mortality and Survivorship

The survivorship of 25 juveniles introduced into the Krasnovodsk experimental plot are presented in Table 2. We assumed that those lizards that disappeared, that is, those not recaptured, had died. Of the initial 25 hatchlings, 15 (10 females, five males) survived to sexual maturity (three years) and of this cohort four males (80%) and four females (40%) survived six years, to the end of the study. The annual survival rate (p_x) ranged from 0.72 to 0.83.

We believe the high survivorship of lizards in the Krasnovodsk experimental plot during the first three years of life are comparable to natural populations. We tested this by comparing survivorship in a cohort of 20 hatchlings, hatched in 1986, 1987, and 1988, that were first captured in 1987, 1988 and 1989 as yearlings. Among these lizards 15 (75%) survived to two years and 13 (65%) to three years of age. Of those surviving to three years were three males and 10 females.

Since the duration of this study was approximately half the life span of a rock agama, survivorship in animals older than six years is based on indirect evidence. We estimated the age, based on standardized size criteria (Zykova and Panov 1991) of adult lizards captured for introduction onto the Krasnovodsk experimental plot. Such age estimates are at best imprecise but the adults in this group ranged from three to 11 years with 78% being four to six years old (Table 3).

The maximum rate of disappearance (which we attribute to mortality, not emigration) occurs in the first year (Table 3) after introduction. From the second year after introduction adult male survivorship is nearly constant and comparable to survivorship during the first six years of life (Table 2). The more variable mortality rates for females may be due to small sample size.

We combined cohorts of lizards of four, five and six years of age and calculated survivorship and estimated survivorship to the 9-11 year age class (Table 4).

In general, survivorship in rock agamas after the first winter following hatching is relatively constant until the eighth year. After the eighth year mortality increases. The maximum estimated age of for males was 12-14 years (n=4) and for females it was 9-10 years (n=2).

Sex Ratio

Although the rock agama social system is territorial polygyny, the sex ratio among adults does not differ significantly from even one (Table 5). This relationship was found at several localities throughout the range and for all localities taken together.

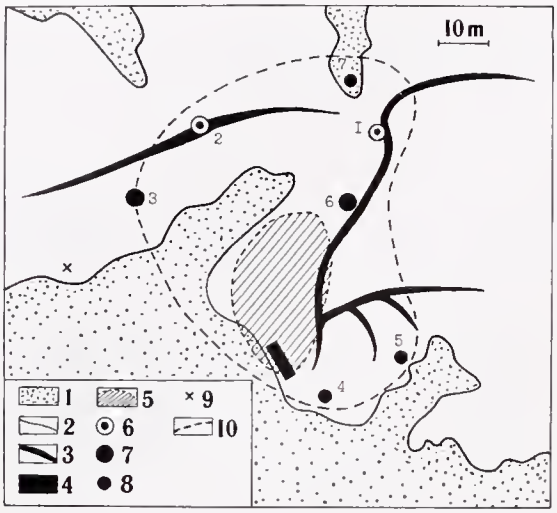

FIG. 6. Expansion of the introduced colony at Krasnovodsk from 1985 to 1990. 1. Unsuitable habitat. 2. Boundary of unsuitable habitat. 3. Principal ridges. 4. Initial introduction site. 5. Principal study area under regular observation. 6. Subpopulation established by an introduced adult male. 7. Subpopulation established by an introduced immature male. 8. Subpopulation established by offspring of introduced lizards. 9. Single sighting of rock agama. 10. Boundary of populated area in 1990.

Movement and Dispersion

Rock agamas display a high level of home area fidelity. Juveniles that were marked after their first winter were found to remain within 50 m of that location up to two years or until sexually mature (at two to three years of age). Some data on the capture of juveniles before their first winter suggests that home site fidelity may extend from the age of three or four months to the end of life. Four of six juveniles (66%) marked in October 1988 in the Parkhai Gorge (Western Kopetdag) were found in the same place the next spring. The maximum movement of immature lizards was not greater than 300 m. A juvenile male first captured in October 1985 before his first winter was recaptured in 1987, 200 m from the first capture location. He was recaptured in the spring of 1988 as a mature male with a territory 250 m from the previous capture location and 100 m from the initial capture point 31 months before.

As the population increases, new areas will be pioneered, mainly by young dispersing lizards. Given the sedentary habits of these agamas we would expect such expansion to be relatively slow. Such an expansion occurred in the introduced population at Krasnovodsk (Fig. 6). From 1985 to 1990 the initial introduced population occupying an area of approximately 300 m^2 dispersed into adjacent areas of approximately 25 ha. Of the seven subpopulations formed during this period two (Fig. 6, points 1 and 2) were founded by introduced mature adult lizards after the initial introduction. Two other subpopulations (Fig. 6, points 3 and 6) were founded by lizards that were immature when introduced. Finally, three subpopulations were established by the offspring of the original introduced lizards. In 1988 (the fourth year after introduction) there were 33 individuals (13 adult males, 14 mature females and 10 immatures) in these seven subpopulations.

Individual lizards were observed to leave their home areas only for collective winter shelter. Females may leave their home areas looking for places appropriate for egg laying (Danieljan and Grigorjan 1975; Ananyeva and Danieljan 1987).

Conclusions

As it can be seen, the characteristic features of Rock Agama social organization and demography are high stability of breeding individuals' contingent and low population turnover. This is evident consequence of sedentary way of life characteristic for males of all age classes, longevity of these lizards, and postponed onset of breeding in early lifetime of young agamas.

The latter may be especially applied to males. Although they are capable to reproduce already at the age of a little under three years (after their third wintering), most of them begin to breed, actually, only at the age of four or five

years. How it may be seen, a male attains the status of a breeder only after he had taken possession of territory of his own. So each maturing male faces with obvious difficulties since many features of species' social organization of settlement (high density together with strong territoriality of males retaining control over his home area until his death) lead to deficiency of vacancies which might be used by young male-recruits. Temporary exclusion of part of mature (non-territorial) males from process of reproduction may, in principle, decrease the whole reproductive potential of the local population.

Besides such social regulators of population growth, rapid increase of population size is retarded also by rather slow recruitment of new deme members. Although breeding productivity of Rock Agama is relatively high (from seven to ten eggs per mature female during breeding season-- see Ataev, 1985), only a small number of new-born agamas die. Even if these losses (especially the latter figure) is overestimated, the analysis of demographic structure of all demes under study shows the numerical preponderance of mature individuals over immature ones. This is in good agreement with the general conclusion about the low rate of population growth in Rock Agama. Another argument in favor of this conclusion is a quite slow expansion of growing population into new, early unoccupied areas.

To conclude, it may be stated that Rock Agama give us a good example of lizard species practicing a typical K-strategy. It was to be expected providing large size of individuals and the ecological peculiarity of the species-- in particular, its pronounced omnivorousness with prevalence in diet (at least in respect to biomass) of diverse plant objects. It is noteworthy that in Rock Agama, like in many species of higher vertebrates (birds and mammals) practicing K-strategy, among deme members there are considerable number of mature male being excluded from reproduction by density-dependent social factors.

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