

INTERRELATIONS BETWEEN SEXES IN *Lacerta saxicola*

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INTRODUCTION

Mating systems are considered as a result of the interdependent development of behavioral reproductive strategies of sexes (Davies, 1992; Govaty and Buschhaus, 1998). However, there exists no generally accepted hypothesis on the origin and evolution of these strategies. Investigations of intersexual social behavior of reptiles may be useful for solution of this problem. Rather advanced intersexual relations of reptiles are known (Bull, 1994; Tsellarius and Tsellarius, 1996; Panov and Zykova, 1999). However, detailed long-term observations on intersexual relations of reptiles are very scarce.

MATERIAL AND METHOD

In the article at hand we have briefly reported the results of our seven-year observations of a group of individuals of *Lacerta saxicola* in the deciduous forest of the Navagir mountains, in Northern Caucasus. Observed was the group of the lizards inhabiting a little clearing arisen as a result of a fall of two trees. All the members of the settlement were marked with personal color mark and their age was known. In total, more than 600 contacts between marked males and females have been described and analyzed. A detailed description of the studied region, the observation and the data handling technique have been published (Tsellarius and Tsellarius, 2001; 2005a; 2005b; Tsellarius and Tsellarius, 2002). In order to appreciate correctly the process of social life in the settlement it must be taken into account that age of *Lacerta saxicola* may attain probably 15 years. At present, the age of settled individuals, those constituting “backbone” of the settlement, amounts from 5 to 12 years.

RESULTS

Intersexual Behavior

Having examined intersexual behavior of lizards, we differentiate three main kinds of behavior of males. 1. Indifference. Male does not express visibly an interest in female. 2. Amicable communication. Curving the neck,

male touches by nose female's sacrum, back and nape, crawls over her, sometimes slightly bites her tail or neck. Male regularly and for a long time lies over female or near her, putting his legs on her back. Some of these actions are included in the courtship also, but we differentiate those as a particular set of behavioral acts since they are rather often performed without any connection with copulation and occur not during mating period only, but throughout the activity season with approximately equal frequency. 3. Aggression towards female. In all instances, it is the redirected aggression of non-ritualized nature. It has been rather rarely observed exclusively either in the course of, or immediately after the border conflict between territorial males, from one of the contestants.

In females, there are four kinds of non-sexual behavior. The first (1. Indifference) and the second (2. Amicable communication) are almost entirely similar to those of males. 3. Rejection of a bodily contact. Female dodges, but usually does not take to flight. This action may be accompanied by peculiar displays, that is rotation of forelegs, which is connected, in the event of maximum expression, with bending up the forepart of body. 4. Aggression towards male. Ritualized threat has been observed from time to time towards only unfamiliar non-territorial males. Females well recognizes settled males of the settlement personally. Direct vigorous non ritualized attack with strong bites was observed as a response to forced copulation only.

In the studied region we have observed three patterns of copulation. 1. Amicable copulation. Male takes a female by jaws by the sacrum and massages it, and at the same time often more or less vigorously scratches the base of tail with foreleg. Then he bends the hind part of body under female and inserts a hemipenis. The female usually appears to be rather indifferent or slightly bites the male, and never takes to flight after copulation. The copulation may be preceded and/or followed by amicable communication. 2. Initiation. It differs from amicable copulation mainly in that at the beginning the male firmly takes the female by the tip of tail and follows her at such a way for some time, before to take her by the sacrum. The scratching of female's tail base always takes place and it is always vigorous. During the massage, sometimes during coitus, female tries to tear herself away and may strongly bite the male. Amicable communication after copulation has never been observed. However, the female usually remains near

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the male. This pattern took place mainly in those instances when a territorial male mated a virgin or an unfamiliar young female. 3. Rape. A male rushes to the female, his behavior resembling an attack, and immediately seizes her by the side or the sacrum, and copulates with her after brief vigorous massage in spite of the violent resistance of female. The scratching may be absent. In the case of rape, a male pays no attention to any displays of female. After mating, female either takes to flight or attacks the male, cruelly bites and chases him. Strength of the massage is very different in different patterns of mating. In females undergone the initiation or the rape, on a sacrum and on a base of tail the bruises arise, which are distinctly observable even at a distance, with binoculars. There were no bruises after amicable copulation.

Intersexual Relationships

There are several quantitative indices found rather useful for analysis of dyad non sexual interrelations.

1. Degree of intimacy, $INT = (C_b - C_w)/(C_b + C_w)$, where C_b is amount of interactions, which include bodily contacts, C_w is amount of interactions without bodily contacts.
2. Degree of female's initiative, $FI = (I_f - I_m)/(I_f + I_m)$, where I_f is amount of bodily contacts on female's initiative and I_m is amount of bodily contacts on initiative of male.
3. Degree of female's amicability, $FA = (A_f - N_f)/(A_f + N_f)$, where A_f is amount of interactions in which female carries out behavior of amicable communication, N_f female is indifferent or rejects a bodily contact. All indices vary from -1 to $+1$. In observed settlement, in the case of long-term dyad interrelations, the absolute value of any index amounts to either about zero or more than 0.4. It permits to operate with only three values: positive, zero and negative. Six kinds of long term non sexual interrelations are most usual here (Table 1).

Different kinds of interrelations are the successive stages of progress of relationship between female and settled male. Female's switch to settled life follows a reaching of sexual maturity and takes place usually after third hibernation. Female-newsettler initially finds herself among unknown or unfamiliar males, and female's rela-

tions with all neighboring males are initially hostile. The males, from time to time, try to enter into amicable contact with encountered female, but female avoids any interactions with males. Hence, saying hostility we mean the hostile behavior of female, but not of male. The latter is characterized by mixed indifferent-amicable behavior. In this case, a copulation is always forced. Female actually has no possibility to select a sexual partner.

Almost simultaneously with forming of structure of her own home range, which may overlap territories of several males, female may begin to ingratiate herself with one of the males having the resident status. Ingratiating female does not look for meetings with the male. In any encounter, however, she takes an initiative for amicable communication. Female does not ingratiate herself with more than one resident at a time. In a certain case, however, she may switch from one subject to another. After 7 – 15 days of female's ingratiating, the resident includes her basking centers in his system of patrol routes (Tsellarius and Tsellarius, 2005a) and interrelations become amicable. From this point, female usually stops to take the initiatives in amicable communication, she begins to avoid, if possible, a bodily contact, but may amicably respond to male's initiatives.

Interrelations with other "overlapped" residents become amicable too, however on initiative of males (casual ingratiating, see Table 1), and this process takes 3 – 4 months. In this case, a male, from time to time, takes attempts to enter into amicable contact, and female, little by little, begins to take no avoidance and next begins to amicably respond to initiatives of the male. It appears that there occurs nothing but a habit. It is rather usual, that female-newsettler does not ingratiate herself with any resident; and amicable interrelations will be established in such opportunistic manner. It is significant that, however, amicable relations are established not with all residents. Interrelations with some individuals remain hostile for unlimitedly long time for unknown reason.

In almost all instances the relations with poachers were kept hostile. These relations may turn into amicability after only the poacher becomes resident. However,

TABLE 1. Characteristics of Different Kinds of Dyad Interrelations between Males and Females

Kind of interrelations	INT	FI	FA	Period of occurrence
Hostility	–	–	–	All the season
Female's ingratiating*	+	+	+	Before and/or after mating period
Male's casual ingratiating*	–	–	0	Before and/or after mating period
Male's obstinate ingratiating	0	–	0	All the season
Amicability	+	–	+	All the season
Partnerships	+	0	+	All the season

* During mating period, a reverting to the previous kind of interrelations (see below) usually takes place on female's initiative.

there are rare exceptions to this rule. We observed the incident of arising of amicable relations between an old female and a poacher. These rare exceptions are very significant since they are showing that there exists no insuperable impediment to amicability to any male.

Amicability is characterized by high frequency of interactions with bodily contacts and by amicable response of female to male's initiatives. The initiatives, however, are taken by male mainly. Amicable lizards may forage and bask about one another for a long time, but without bodily touch. Amicable relations may be continued for an indefinitely long time. A number of amicable partners are not limited both in males and in females. In the event that relations are amicable, female has an ability to suppress importunity of the male by means of either to assume posture of mate rejection or to crawl repeatedly over the male's back. It always leads to stopping the importunity of the male. Therefore, a forced copulation takes place, actually, in situation when female persistently refuses amicability with the male.

A partnership is the next stage after amicability. The conversion of the amicability into partnership, however, is not inevitable. There are approximately 80% of adult females, which have never had partnership status. Sometimes, a partnership is a result of male's initiatives (obstinate ingratiating). It demands hard efforts for a long time. The male persistently follows preferred female during two, three years. After all, the female surrenders, as it were. Much more often, however, the partnership is a result of female's efforts. Female begins to form partnership making efforts to enter into bodily contact in every encounter with amicable resident. The male begins to visit her basking centers more and more frequently. As a result, formed are the centers of male's activity in basking centers of that female (Tsellarius and Tsellarius, 2005b). Having converted amicability into partnership, female always kept a fidelity to the resident selected as an object of ingratiating, unlike conversion of hostility into amicability. Basking centers of female are disposed over the territories of several males. Usually, but not always, selected is the resi-

dent, in whose territory the majority of basking centers of given female have been formed.

When partnership relations have been established, partners spend much time together. The animals lie in bodily contact for a long time, crawl over one another, frequently return to the partner. Just the recumbent posture in mutual embrace is the specific difference between amicable and partnership pairs. A partnership can last for many years. In all observed pairs these relations last up to the death of one of the partners. It is important, that both kinds of intimate relations, amicability and partnership, are intense during all the year and are not restricted within the mating period only.

Actually, any female may be forced from time to time. The female, however, which has partnership status, is significantly more rarely forced (Table 2). The attempts to rape are broken off with aggression of her partner towards violator. Protection is very effective just because of the male spends much time in female's basking centers (Tsellarius and Tsellarius, 2005a, b) and intensively patrols them. During mating period, however, female copulates not only with the partner, but permits copulation with several amicable males.

DISCUSSION

One of the current ideas of the evolution of intersexual relations is that sexual aggression is the peculiar strategy of males. It is believed that this strategy to force females to resort to the protection of a certain male and to pay copulation for this protection (Govaty and Buschhaus, 1998). It is evident, however, that the sexual aggression of males of *Lacerta saxicola* is a result of social fastidiousness of female. In other words, a sexual aggression is an inevitable side effect of social fastidiousness of females. Another side effect is that females are forced to use various behavioral devices in order to compensate for the consequences of their fastidiousness. As a result, the situation is rather paradoxical. Really, establishing an amicability or, especially, a partnership, female choose not a sexual partner, but a male, which can be used as a protector, and which can be rejected as a sexual partner. Per se, she creates the surroundings in which she qualifies for freedom in choosing of a sexual partner. The reason that female does not establish these interrelations with each neighbor is unknown.

Poorly corresponds with current conceptions of behavioral ecology is the fact also, that there simultaneously exist two ways of forming of pairs, on initiative of male and on initiative of female. However, a more interesting

TABLE 2. Frequency of the Unsuccessful Attempts at Rape in Different Surroundings

Relations between female and the owner of the territory where attempt took place	Total number of observed attempts	Rate of attempts being unsuccessful because of aggression of territory owner, %
Hostility*	24	45.8
Amicability	37	78.4
Partnership	33	100

* Attempts of territory owner, which are successful in 58.6% of cases ($n = 29$), are not taken into consideration.

fact, in our point of view, is the motivation of male's behavior. The majority of evolutionary conceptions either explicitly or implicitly suggest that the evolution of male's behavior leads, first of all, towards acquisition of access to copulation, preferably to exclusive access (Wilson, 1975; Emlen and Oring, 1977). In the case of the *Lacerta saxicola* male, however, it is evident that a possibility to communicate with female is much more attractive than copulation in itself. Accordingly, female pays not a copulation, but communication for defense and for freedom in choosing of sexual partner.

Just owing to these eccentric, with relation to reproductive success, predilections of the males there is a possibility of reconciliation of the conflicting objectives of the sexes. In female's point of view, the main and rather complicated problem is that territories – and, consequently, resources — are randomly distributed among males. The poacher establish a residence either in initially empty space or on a place, which is emptied since death of previous owner. At a later time, redistribution of territories does not happen (Tsellarius and Tsellarius, 2004). A combination of good quality of territory and of its owner is a rare random event. As a result, female has no possibility to obtain simultaneously good ecological conditions and good sexual partner. Female has a possibility to slip out the situation just owing to the amicable communication, which is, in male's point of view, the most attractive resource for all year round. The resident pays protection for communication and renounces a copulation to some extent.

As a result, both the males and the females have a possibility to convert their main motivations into behavior. In other words, everybody is highly pleased. This harmony, however, has no connection with breeder fitness and offspring viability by no means. It is quite possible that situation cannot be interpreted in such terms as a cost, a benefit and reproductive success. It must be taken into account that behavior of animal is a realization of certain psychic state, that is motivation. A fitness cannot be the motivation in any case. It is beyond any doubt that the issue demands further investigation. Anyway, however, the situation appears to be essentially more complex than some socio-biological conceptions suggest.

REFERENCES

- Bull C. M.** (1994), "Population dynamics and pair fidelity in sleepy lizards," in: Vitt L. J. and Pianka E. R. (eds.), *Lizard Ecology*, Princeton Univ. Press, pp. 159 – 174, 335 – 387.
- Davies N. B.** (1992), "Mating systems," in: Krebs J. R. and Davies N. B. (eds.), *Behavioral Ecology: An Evolutionary Approach*, Blackwell Sci. Publ., Oxford, pp. 263 – 294.
- Emlen S. T. and Oring L. W.** (1977), "Ecology, sexual selection, and the evolution of mating systems," *Science*, **197**, 215 – 223.
- Govaty P. A. and Buschhaus N.** (1998), "Ultimate causation of aggressive and forced copulation in birds: female resistance, the CODE hypothesis, and social monogamy," *Am. Zoologist*, **38**, 207 – 225.
- Panov E. N. and Zykova L. Yu.** (1999), "Social behavior and communication in rock agama *Laudakia caucasica*," *Russ. J. Herpetol.*, **6**(3), 215 – 230.
- Tsellarius A. Yu. and Tsellarius E. Yu.** (1996), "Courtship and mating in *Varanus griseus* of Western Kyzylkum," *Russ. J. Herpetol.*, **3**(2), 122 – 129.
- Tsellarius A. Yu. and Tsellarius E. Yu.** (2001), "Alteration of spacing pattern of population of *Lacerta saxicola* in broad-leaved forests of Navagir mountain ridge," *Zool. Zh.*, **80**, 1 – 8 [in Russian].
- Tsellarius A. Yu. and Tsellarius E. Yu.** (2005a), "An access to the females as a resource of male's territory in *Lacerta saxicola*," Ananjeva N. and Tsinenko O. (eds.), *Herpetologia Petropolitana. Proc. of the 12th Ord. Gen. Meeting of the Soc. Eur. Herpetol.*, August 12 – 16, 2003, St. Petersburg, pp. 222 – 225 [this issue].
- Tsellarius A. Yu. and Tsellarius E. Yu.** (2005b), "Formation and defense of the individual space in males of *Lacerta saxicola*. 1: Home range," *Zool. Zh.*, **84**, in press [in Russian].
- Tsellarius E. Yu. and Tsellarius A. Yu.** (2002), "Age change and probable function of the signaling coloration in males of *Lacerta saxicola*," *Zool. Zh.*, **81**, 970 – 977 [in Russian].
- Tsellarius E. Yu. and Tsellarius A. Yu.** (2005), "Formation and defense of the individual space in males of *Lacerta saxicola*. 2: Territory and territorial relations," *Zool. Zh.*, **84**, in press [in Russian].
- Wilson E. O.** (1975), *Sociobiology: The New Synthesis*, Harvard Univ. Press, Cambridge.