

AN ACCESS TO THE FEMALES AS A RESOURCE OF MALE'S TERRITORY IN *Lacerta saxicola*

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INTRODUCTION

Recent ideas of social interrelations of animals, territoriality included, are mainly based on the results of investigations of social insects, birds and mammals. These animals are characterized by great postnatal parental investment. Many features of mating systems and systems of resource monopolization are considered as direct results of optimization of this investment (Emlen and Oring, 1977; Davies, 1992). Amphibians and reptiles do not have such investment. However, social structure of their communities may have characteristics closely resemble social interrelations in birds and mammals. It is probable that a detailed analysis of formation of social structure of reptiles would be useful for solution of some problems of behavioral ecology.

MATERIAL AND METHOD

Since 1996, we have been observing a settlement of bisexual *Lacerta saxicola* in one of canyons of the Navagir mountains, in Northern Caucasus. The settlement is located in a little clearing in a dense hornbeam-beech forest. Such clearings that arise as a result of a fall of one or two trees are the most favorable habitat to *Lacerta saxicola* in studied region (Tsellarius and Tsellarius, 2001). The space under forest canopy outside the clearings is sparsely populated, and the majority of encountered individuals were the wanderers.

The observed settlement included 19 to 25 individuals in different years, sex ratio was nearly 1:1. Every spring, all settled members of the settlement were captured and measured, the color mark was renewed if required. The same operations were performed with the wanderers which visited the territory of the settlement. In every lizard we amputated in certain pattern up to three phalanges of fingers. It is a permanent mark, which permits to recognize the individual during all its life and, additionally, amputated phalanges are used to determine the age of lizards by bone layers. Every day, if the weather was favorable for activity of the lizards, the territory of the settlement was under surveillance during one to five hours. Recorded

were the movements over the space and the behavior of lizards during encounters with conspecifics. In total, by now, we have marked nearly two hundred lizards, and the overall duration of observations being more than 450 h. As an index of diversity of females in home range of a certain male we use the polydominance index ($1 \leq S_\lambda \leq 8$) (Pesenko, 1982). An intensity of a male patrolling was estimated as a ratio of the frequency of registration of patrolling to that of any other activities (Tsellarius and Tsellarius, 2005). The index named "aggression level" presents a stage of stereotyped agonistic behavioral pattern to which this pattern has been reduced in the average (Tsellarius and Tsellarius, 2004a). Detailed description of the observing technique and the data handling were published earlier (Tsellarius and Tsellarius, 2001, 2002).

RESULTS

Space Use in Males

During one or two years after a hatching the males of *Lacerta saxicola* wander over the vast space, that is up to 0.5 km². A switch to the settled mode of life occurs, as a rule, soon after reaching sexual maturity, i.e., after a second hibernation. Having settled, the male usually keeps fidelity to the selected site during all the life, i.e., up to 5 – 15 years. In the initial period of settled life the male does not display any aggression towards conspecifics, i.e., he has a non-territorial status. He uses the space of home range more or less evenly, there are neither area of concentrated use (the core area, in *sensu*: Samuel et al., 1985) nor centers of activity. In this stage of life male's home range is on average 118 ± 24.1 m² ($n = 5$) and broadly overlaps both the home ranges of the coevals and those of the territorial males. We term the males of such stage the poachers. The period of poacherism lasts 2 – 3 years, sometimes up to 5 years, certain individuals probably can be stuck in this status for all the life (Tsellarius and Tsellarius, 2002). The males that passed into the next stage of ontogenetic trajectory — that is territorial stage — were named the residents. The home range of resident is less than poacher's home range (75 ± 34.2 m², $n = 12$, $t = 2.94$), and always has strongly pronounced internal structure. The main elements of the home range are: an area of concentrated use

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or core area; the centers of activity; the patrol routes. The residents, unlike poachers, display an aggression towards other males. The aggressive initiatives are localized within the bounds of the area of concentrated use, i.e., there exists a territory. Size of the territory is on average $20.3 \pm 3.06 \text{ m}^2$. The home ranges of residents may broadly overlap. The core areas, however, are completely separate in all instances. The structure of resident's home range is strongly determined by the individual space patterns of the females inhabiting his home range (Tsellarius and Tsellarius, 2005).

The centers of activity are the sites where a male spent the most part (60 – 70%) of activity time. There may be from 2 to 7 such sites per home range. Centers of activity of a male always coincide with the centers of basking of certain (not all) females (Tsellarius and Tsellarius, 2005). In the event that preferred female alters a disposition of her basking centers, the disposition of male's activity centers will be altered too. Connection between male's centers of activity and female's basking centers remains close during all the year and is not restricted by the mating period only.

Patrolling is the particular mode of movement over home range. Patrolling male moves quickly, in relatively straight line, with frequent short stops. Additionally, the patrolling includes almost whole set of the behavioral acts typical of situation with shortage of prognostic information (Tsellarius and Tsellarius, 2005). It is probable that motivation of patrolling is an information deprivation. An intensity of patrolling is closely connected with diversity of females in resident's home range ($r = 0.81$, $n = 12$) and has no connection with the frequency of visitation of home range by other males. Patrolling is the main kind of activity of the majority of residents over almost the entire season. A system of patrol routes usually includes all the basking centers of all the females within the core area. Actually, movements of a male over the home range are the patrol runs, which start and finish in the basking centers of females. The core area that contains male's activity centers and a patrol routes network is formed just owing to intensive patrolling. A frequency and duration of male's excursions beyond the borders of his core area negatively associated with the diversity of females inhabiting core area ($r = -0.84$, $n = 15$).

Access to Females

The residents display aggression towards both the individuals of their own status and the poachers. The poachers, however, are able to avoid contacts with residents and exploit the ecological resources of resident's home range without significant limitation. But they have no regular ac-

cess to basking centers of females, where females spend more than 70% of the time of activity, since these centers are intensively patrolled by residents. As a result, the poachers are deprived of a long communication with females. It is significant that limitation concerns exactly communication, while an access to copulation remains almost unlimited.

Social status of copulated females and a rate of successful attempts at copulation are significantly different in poachers and in residents. However, a total number of accomplished copulations (per individual) may be about equal in males of different status. In average, the poachers takes more attempts at copulations and more frequently takes attempts at rape.

Ontogenetic Formation of Territoriality

In all instances, an appearance of aggressiveness and, consequently, establishing of a territory and forming of initial structure of home range, coincides with event when poacher obtains an access to basking centers of females. The access was always obtained as a result of either re-disposition of basking centers of females in such a way that new centers arise beyond the borders of resident's territories, or death of one of residents controlling these centers. Thus, a residence is always formed in place unoccupied by territorial males. We have never observed an usurpation of other's territory, and, probably, it is fundamentally impossible.

Having obtained an access to the basking center of female, the poacher begins to visit it regularly. As a result, a center of activity of the male is formed here and an area of concentrated use surrounds it. At the same time the male begins to display aggression towards other males, initially only in response to aggression of neighbors. Consequently, all-round passive defense zone is formed around female's basking center. As yet we cannot term this zone a territory, since territoriality demands active defense of space (Burt, 1943). Soon after, however, the male begins to take the aggressive initiatives, and, accordingly, he obtains resident status. As a result, in studied site the long-term "ownerless" female's basking centers have never been recorded. All long-term basking centers were disposed within the bounds of defended territories of residents. It must be taken into account that penetration of one resident into another's territory has for an object, as a rule, the basking centers of females disposed in this territory (Tsellarius and Tsellarius, 2005a). This tendency, as well as connection of male's activity centers with basking centers of females, takes place during the entire season and is not restricted within the mating period only.

Thus, an agonistic behavior of male and, accordingly, forming of defended space within home range are induced by regular communication with female, but not by copulation in itself. A possibility to communicate with female is under control of forces of social nature, whereas sexual activity and the possibility of its accomplishment (copulation) are not significantly affected by social circumstances. The given picture well corresponds with experimental data obtained in captivity (Sakata et al., 2002). Just the striving to communication with female, but not to copulation, determines the space use pattern of a male. It is a possibility to communicate, but not to copulate, is, in male's point of view, that the main resource of his home range. In other words, in ordinary conditions amicable communication is more strongly motivated than any other activity.

Motivation of Aggression and Resource Defense

Here it would be appropriate to say some words about aggression in general. Unambiguously desired effect of any actions referred to the direct aggression is — in aggressor's point of view — the removal of the circumstances hindering in realization of certain activity and/or circumstances increasing uncertainty of situation. In other words, an aggression is the forcible change of circumstances, which results in a renewal of mental comfort (in *sensu*: Ovsianikov and Badridze, 1989). In the case of *Lacerta saxicola*, only few particular residents — and in only particular circumstances — display aggression towards the conspecifics which hinder (or may hinder) in communication with female (Tsellarius and Tsellarius, 2005a). In ordinary resident, in the event that intruder courts female, an aggression level, the frequency and distance of aggressive actions are the same as in other situations (Table 1). Only an attempt of forced copulation always provokes very vigorous reaction of resident and is usually crowned by severe fight with following chase of violator. It is probable, however, that resident takes a rape as nothing but some aggression in his territory, since this pattern of copulation starts with male's behavior resembling vigorous attack most of all (Tsellarius and Tsellarius, 2005a, 2005b).

There exists another peculiarity characterizing male's aggression. A formal display of threat towards intruder is

turned into the strict, direct and unambiguous one not in the situation when intruder attempts to court female, but when his behavior is either non-complementary to behavior of territory owner or it threatens to become non-complementary (Tsellarius and Tsellarius, 2005a). For example, intruder does not run away or does not take submissive pose in response to resident's formal threat. If a familiar intruder runs or submits, the resident does not attack or chase him, with the exception of some particular situations. In other words, an aggression is directed towards circumstances, which hinder (or may hinder) in realization of resident's preference to accomplish certain forms of social behavior (in *sensu*: Maslow, 1936). In the case of *Lacerta saxicola* males these forms are essential behavioral traits of male's status in a system of male/male (but not male/female) relationships. Thus, a male defends not a resource, but its own social status.

DISCUSSION

Territoriality is usually considered as one of the ways of defense of some resources (Wynne-Edwards, 1962; Ever, 1968). It is supposed that the main resource of territory is an access to copulation (Emlen and Oring, 1977; Davies, 1992; Martins, 1994; etc.). In other words, defending of certain space inhabited by females, the male tries to secure here a priority for his own gametes. This conception permits to create a rather consistent explanation of the origin and evolution of territoriality. The fact that male in some extent renounces the copulation for the sake of amicable communication with female (Tsellarius and Tsellarius, 2005ab) and that communication is the most attractive resource of his home range, it is poorly corresponds with current view of a background of territoriality. Moreover, there is another paradox. Although aggressiveness of a male is stimulated by female and an access to communication with female is — in male's point of view — of utmost value, male's aggression, as a rule, is not used for the defense of access to communication itself. Aggressive male provides females inhabiting his territory for protection against forced copulation and for freedom of choosing of the sexual partner, but territory owner does not inevitably

TABLE 1. Reactions of Residents to Intruders in the Borders of Core Area

Conditions of the contact	Number of observed contacts	Frequency of agonistic interactions, %	Distance of aggressive initiative is taken, m	Aggression level
Intruder is at a distance of more than 1 m from female and does not strive for contact with her	220	74.1	1.2 ± 0.67 (n = 33)	3.9 ± 0.92 (n = 81)
Intruder is about female or courts her	34	82.4	1.5 ± 0.60 (n = 5)	3.7 ± 1.12 (n = 21)

become a preferred sexual partner (Tsellarius and Tsellarius, 2005a, 2005b).

On the other hand, female gives an access to communication, as a rule, to aggressive males only (Tsellarius and Tsellarius, 2002). Thus, male's aggressiveness (= territoriality) provides him for an access to the desirable resource, but does not guarantee for exclusive use of female. Moreover, in certain circumstances territoriality may — to a rather great extent — complicate a life of the male since it restricts an access to ecological and social resources of the habitat. In *Lacerta saxicola*, in any case, conservative males — which for term of life are fastened to their territories — are found in undoubted disadvantage (Tsellarius and Tsellarius, 2005).

Such situation is not unique. Similar state is well known of many species and, generally, is rather typical (Carpenter, 1987). As for *Lacerta saxicola*, it is quite possible that territoriality is nothing but side effect of male's ability to defend female. In itself, the territory, may have no adaptive significance. In our point of view, a much more interesting question is not the question of the origin of territoriality and its influence on fitness, but what a profit is got by male from communications with female, why he so strongly seeks for communication even though it does not provide him for preference for copulation. Mentioned profit must be rather large in order to compensate for damage from side effects of aggression, the territoriality including. However, we must be ready for that comprehension of the situation — in the framework of such notions as a benefit, a cost, a fitness and so forth — will be found impossible, since we have dealt with a behavior that is realization of certain mental state, i.e., motivation. Thus distant and indirect after effect of behavior as a fitness cannot be motivation in any case.

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