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Social Relationships between Males and Females in Rock Lizard (*Darevskia brauneri*, Lacertidae). 2. Searching for an Area of Stable Residence, Criteria for Choice of Social Partner, and Factors of Friendly Integration of Dyads

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Abstract—Long-termed intersexual friendly relationships between males and females of the Brauner's lizard are characterized by high levels of spatial association and high frequency of affiliative behavior between partners (see report 1). In present article we consider changes in the frequency of affiliative behavior in males (*Am*) and females (*Af*) after the first appearance of female on the male's territory and conditions for the transition of lizard to stable residency (SR). Generally, *Am* becomes stable during the first days of initial period and does not change later. This fact suggests that in most instances male's choice criteria are some peculiarities of the female's exterior. In the initial period, *Af* is always low, however, gradually rises to the level of *Am* if *Am* is high. The main condition of female's SR is high *Am* of the owner of the territory where female establishes her comfort areas. Hence, social partner choice in female is based on male's behavior, and high *Am* triggers the formation of friendly interrelations. Significant correlation between social and sexual interrelations is absent. As can be judged by female's reactions to male's sexual behavior, his sexual activity is rather a factor of social disintegration. Structure of costs for social partner search is different in males and females, and these differences well harmonize with differences in gender strategies of partner choice. The social strategies are well interpreted in terms of the optimal foraging theory.

Keywords: friendly interrelations, affiliative behavior, social partner choice, search for partner, gender social strategies, lizards, *Darevskia brauneri*

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One of the most important components of the mating strategy is the choice of a partner, i.e., assessment of some or other of their qualities (choice criteria) and subsequent behavior aimed at gaining "possession" of the attractive partner. If potential partners are spatially dissipated, searching for the partner that would satisfy certain criteria becomes another important component. On one hand, there exists a well-developed theoretical basis, which explains the formation of the mating strategies and gender differences of these strategies (Trivers, 1972; Emlen and Oring, 1977). On the other hand, there are many field and experimental studies, which tested and concretized these theoretical notions (Tokarz, 1995; Martin and Lopez, 2000; Bleay and Sinervo, 2007; Kelso and Martins, 2008; Lancaster et al., 2009; and others).

A considerable part of studies in this field are aimed at investigation of the criteria for choosing the partner, mainly morphological criteria and much rarely behavioral ones. The studies concentrating on the search for the partner are extremely rare, although the strategies for the search and choice should be closely linked (Emlen, 1966; Real, 1990; Stamps et al., 2005). Most studies concentrate on sexual, not social, relationships and in most cases partner choice is studied in females, as the main male strategy is considered to be maximization of the number of partners (Trivers, 1972), which implies low selectivity. At the same time, alternative mating strategies are considered almost exclusively for males, although there are grounds to suppose that females are more flexible than males (Crews, 1998).

In the rock lizards *Darevskia brauneri* (Mehely 1909), stable intersexual friendly interrelations (A-relations) were found, which are characterized by a high frequency of occurrences of affiliative behavior, both males's and females's (Tsellarius et al., 2016). A-behavior is the specific behavioral ensembles, including physical contact without any sexual or agonistic context. The frequency of occurrences of affiliative behavior of an animal toward different individuals of the opposite sex is different and can be considered as an indicator of the social attractiveness of these individuals. Here we term "social partner" as an individual with a high social (affiliative) attractiveness. In the article at hand, we firstly consider the changes in the social behavior during the existence of dyads. These changes allow us to make some conclusions on the social partner selection criteria. Secondly, we study the relations between some kinds of social and sexual behavior in males and females of Brauner's lizards. And thirdly, we consider the scenarios of transition of lizards to stable residency which is a prerequisite for long-term spatial association between males and females.

STUDY AREA AND METHODS

The survey carried out in 1997–2006 on the southern flank of the Navagir ridge in the area between Anapa and Novorossiysk in a dense high hornbeam-beech forest. The study area was situated under the gap of forest canopy, about 30 m in diameter, inhabiting in different years by 18–28 adult Brauner's lizards. In the present article lizards are named by their individual numbers, the males assigned the "M" index and the females "F". The age of the individuals was determined by the amputated phalanx of one of the fingers using the skeletochronological method (Smirina, 1974; Tsellarius, A.Yu. and Tsellarius, E.Yu., 2002).

Movement trajectory of the individualy marked lizards, the location and duration of their stops, activity type, places, duration and characterization of contacts with conspecifics were recorded during the visual observations and plotted on a schematic map. The total duration of visual observations over the entire period of works was 1124 hours, that of video recording 28 h. In 2001–2002, at the end June – beginning July, the time budget of 6 territorial males and 5 adult settled females was studied. The total duration of the timekeeping was 9 h 7 min.

Here we term "home range" (HR) as an area of placement of all points where an individual was observed (registration points), which was contoured using the method of the convex polygon (Rose, 1982). Term "territory" designates the part of HR within which a conspecific of the same sex induces non-ritualized aggression of HR owner. The "comfort zone" is the area of concentration of registration points inside HR (Samuel and Green, 1988). The amount of resources whitin a territory (quality of the territory) was estimated by sight on a six-point scale (0–5), taking into account the key ecological conditions: the possibility of basking, abundance of refuges, and food accessibility.

The causes of non-return disappearance of an individual from the study area were determined with a sufficiently high degree of probability (Tsellarius, A.Yu. and Tsellarius, E.Yu., 2009). Two variants of disappearance were observed. In one case, the lizard began to make prolonged excursions outside its HR and comfort zones became indistinct, lizard periodically left HR for 1 to 3 days and then irreversibly. These changes developed from 10 days to 1.5 months, part of disappeared individuals were registered afterward, sometimes far beyond study area. The second variant – a sudden disappearance of the individual. None of the animals that disappeared suddenly were registered afterwards (Tsellarius, A.Yu. and Tsellarius, E.Yu., 2009). In this case we assumed the death of the individual and in the case of disappearance with a "preparation", its re-settlement.

Here, saying "dyad", we mean a territorial male and a female that had at least one comfort zone within the territory of that male. The affiliativeness of a male (*Am*) or a female (*Af*) implies the proportion of contacts (in %), in the course of which the affiliative behavior was recorded. Sexual activity of a male is a ratio of precopulative priming instances (in %) to the total number of contacts between the members of the dyad observed during the mating period. The attendance of a male territory by female (*AT*) is the ratio (in %) of female's registration points within the territory of the male to the total number of registration points of this female. More detailed descriptions of the study area, field research techniques and data processing were given in Tsellarius et al., 2016.

The calculations were performed in the Excel program. We used standard formulas and tables to calculate the statistical criteria and determine the level of confidence probability (Lakin, 1973; Sidorenko, 2001). To characterize the samplings, a median is given with a *lim* (in parenthesis). In the text and tables we used the following designations: U—Mann-Whitney criterion, φ^*—Fisher's F-test, r_{sp}—Spearman's rank correlation coefficient, k—the number of degrees of freedom, and P—the level of confidence probability. When ranking, the value variant was expressed in round numbers.

RESULTS

Changes in the Affiliativeness during the Life of a Dyad

When discussing the changes in the affiliativeness of an individual, it should be remembered that in this case, affiliativeness is the proportion of contacts, in which the individual represents respective behavior, not the frequency of A-reactions of an individual to the A-behavior of a conspecific. The reaction can vary greatly from rejection to responsive A-behavior or the motor reaction can be absent altogether: the lizard continues its current routine activity without paying attention to the behavior of the co-contactant. It should also be taken into account that when we describe various types of development of the events,

Table 1. Frequency of variants of long-term changes in the affiliativeness of dyad members*

Changes in affiliativeness	Number of dyads	%	Stable affiliative behavior, %		φ*	*P*
			male	female		
No changes	2	11.8	82.4	11.8	4.59	>0.99
Of only males	0	0.0				
Of only females	12	70.6				
Of both dyad members	3	17.6				

* The dyads were under observation since their formation and existed for at least two years.

we do not mean universal laws but a classification of scenarios observed in reality.

Males. No significant differences between the affiliativeness of a male (*Am*) calculated for the first month of the existence of a dyad and for the rest of the first season could be found in any of the cases. At the same time, the *Am* in different dyads proves to be different already in the first season ($\chi^2 = 29.12$, $k = 8$, $P > 0.999$), it could be both very low and quite high. A similar picture is observed when comparing the first and second years of the dyad existence. After the second year, *Am* either remained unchanged until the end of the existence of the dyad or rapidly increased by the 3rd–4th year. Hence, three scenarios of the change of *Am* were observed:

1. The *Am* value remained low over the entire period of the dyad existence.

2. During the first days *Am* rapidly increased and remained unchanged subsequently.

3. The events developed according to the first or second scenario, then *Am* increased and stabilized at a higher level, i.e., two episodes of stabilization of *Am* were observed with an interval of 3–4 years.

A stable *Am* (1st and 2nd scenarios) was observed in the most events (Table 1).

Females. During the first 2–5 weeks of male/female acquaintance, rejection reactions towards males prevailed in female behavior, the affiliativeness (*Af*) was low or affiliative behavior absent altogether. If *Af* increased, in most cases it became noticeable no earlier than in the second month of the existence of the dyad. On the whole, 4 scenarios of the change of affiliativeness can be distinguished:

1. The *Af* value remained low during the entire period of the dyad existence.

2. No earlier than a month after the existence of the dyad, *Af* started to increase gradually, the growth stopped only in the next season or even a season after the start of it's rising, after which *Af* stabilized at a more or less high level (Fig. 1).

3. For several years, the events developed according to the first scenario, however, then *Af* increased very rapidly and stabilized at a higher level.

4. For 1–3 months, *Af* was low, then increased abruptly on a period 3 to 7 days, then returned to the low level and remained at the same level until the end of the existence of the dyad.

The main difference in the changes of affiliativeness of females, compared to males, is that the increase in *Af*, if it starts, starts after a sufficiently long acquaintance with the male. In most cases, the increase occurs very slowly and *Af* stabilizes only in the 2nd or 3rd season of the existence of the dyad (Fig. 1). A stable affiliativeness that formed at the very first stage of the existence of the dyad and remained until its breakup is always, without exceptions, a low affiliativeness (scenario 1). Such dyads didn't exist for more than one year in most cases (details below). In addition, changes of affiliativeness in males always mean its stable increase, whereas in females increase of *Af* was observed with a subsequent decrease. In general, a stable *Af* is found comparatively rarely (Table 1).

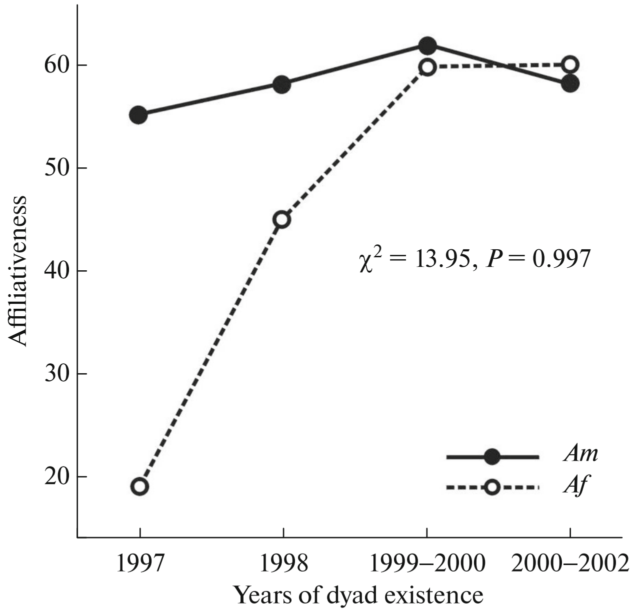

Fig. 1. Changes in the affiliativeness of male (*Am*) and female (*Af*) for a period of existence of the M11/20 + F8/2 dyad.

Table 2. Affiliativeness of males (*Am*) corresponding to different scenarios of changes in the affiliativeness of females (*Af*)

Scenarios of changes in *Af*	*Am*	*n*	*U*	*P*
1, 4. Steadily low or increasing and then decreasing	7 (4–39)	13	4.0	0.99
2, 3. Increasing and remaining high	50 (18–60)	6		

Correlation between Male's and Female's Affiliativeness

With the only exception, the stable increase of the affiliativeness of a female (*Af*) occurred against the background of a high or middle affiliativeness of the male (*Am*) (Table 2). As a rule, at low *Am*, no stable increase in *Af* was observed and it remained at a low level (scenario 1). In tote, the correlation between *Am* and *Af* was high ($r_{sp} = 0.82$, $n = 35$, $P > 0.99$). Taking into account that *Am* usually formed in the first days of the existence of the dyad and that the growth of *Af*, if it started, began no earlier than the second month, it must be assumed that *Af* depends on *Am*, and not vice versa. In other words, if male's affiliativeness is high, *Af* begins to "catch up" with *Am* (Fig. 1). Only in two dyads out of nineteen, a different picture was observed. In the dyad M2/6 + F10, the affiliativeness of the female remained low, despite the relatively high *Am* (38.9, Table 4). In the dyad M11/20 + F5, a spontaneous rise of *Af* occurred (scenario 3) with a subsequent increase in *Am* (Table 3). We discuss these cases below. As for the transient rises of *Af* (scenario 4), they were observed only in subadult females toward males with a low affiliativeness, often toward two or three neighboring males in sequence. No significant change in *Am* occurred in this case.

Affiliative Selectivity

Males. Social attractiveness of the same female could be different among males (Table 4). Since the affiliativeness of a female usually depended on that of a male, the male's selectivity degree could be estimated from the frequence of appearance of friendly relations (A-relations), i.e., relations with high level of affiliativeness of both partners. As A-relations are long-term, at any moment of time they were recording for a lot of stable residents (A. Tsellarius et al., 2016). However, appearances per se were relatively rarely observed. Of the 23 dyads under observation since the first week of their existence, A-relations appeared in only five (13.0%). When considering males individually, in the M2/6 male, for example, the A-relations with a female did not appear within seven years (1997–2003), though it had access to 11 permanent female residents during this period; M16 had no A-relations for two years after the death of its A-partner, though it had access to five females.

Females. As follows from the data presented above, in most cases *Af* depended on *Am*, not vice versa. This suggests that high *Am* is the main criterion for choosing a social partner for a female; i.e., the choice of female is predetermined by the choice of male. This is the prevailing trend. However, females apparently also have a choice that is not associated with the male's affiliative behavior and not necessarily realized in a steady increase in *Af*—let's term it latent selectivity. The existence of this selectivity is indicated by isolated instances of increase in *Af* (scenarios 3 and 4) under conditions of low male affiliativeness. For example, F23 was regularly in contact with five males (Fig. 2) with equally low *Am* (0–4). The female's affiliativeness increased toward only three of them (M4, M2/6, and M11/20); the "rejected" males (Fig. 2) were more accessible than two of the three "selected" ones (M2/6 and M11/20), whose home ranges were located on the other bank of the stream, where F23 had no comfort zones (Fig. 2). In another case, with a spontaneous increase in the affiliativeness of F5 toward M11/20 (Table 3), there were two equally available males, M11/20 and M2/6 for it; the affiliativeness of the selected M11/20 was significantly lower than that of the discarded M2/6 (11.4 and 28.8, respectively; $\varphi^* = 2.03$; $P = 0.96$).

In addition, in some cases, the increase of *Af* could be blocked by the high sexual-exploratory activity of male. This can be illustrated by the development of relations in the M2/6 + F10 dyad; they emerged at the end of May 1998 and were characterized by an unusually high frequency of behavior of the male toward the

Table 3. Changes in the affiliative behavior of partners in the M11/20 + F5 dyad

Sex and statistics	Period of observations		
	1998–2000	early 2001	late 2001
Male's affiliativeness (*Am*)	11.4	17.6	52.4
Female's affiliativeness (*Af*)	20.0	52.9	61.9
n	35	17	21
φ^*	1.00	2.22	0.62
P	0.68	0.97	0.47

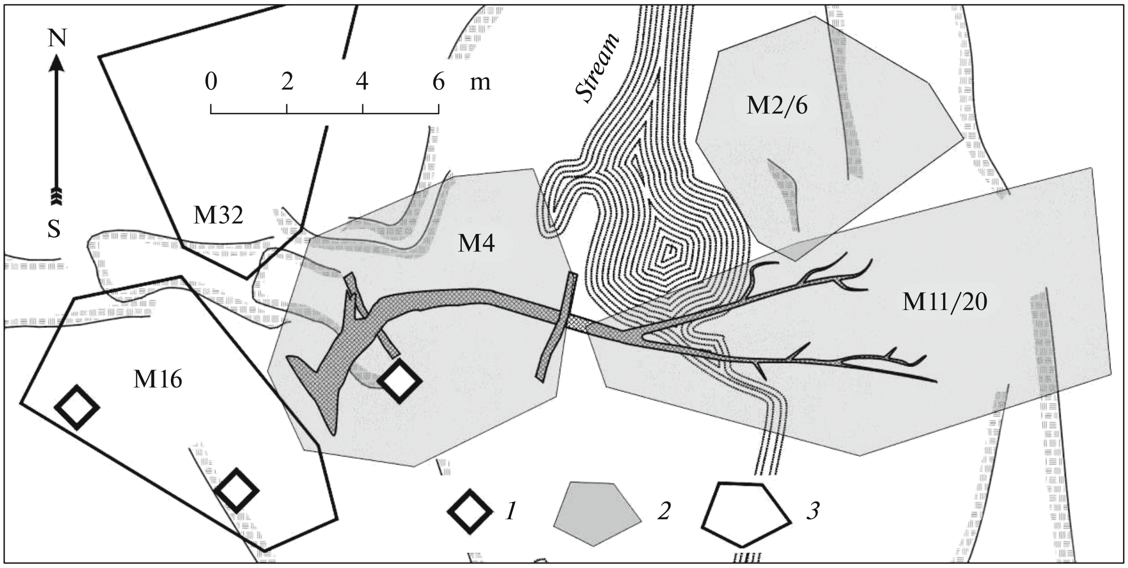

Fig. 2. Arrangement of comfort zones of the F23 female and male territories which she attended: (*1*) female's comfort zones; (*2*) territories of males toward which spontaneous temporary rises of female's affiliativeness were observed; and (*3*) territory of males toward which the affiliativeness remained low.

given female throughout the three months of its existence, 44.4%, while for M2/6 this value in general did not differ from that of other males except for contacts with F10 and was 22.7% ($n_1 + n_2 = 18 + 97$, $\varphi^* = 1.82$, $P = 0.93$). The male's affiliative behavior was also high (38.9), however, there was no significant increase in *Af* in this dyad; the female shunned the male, moved to the territory of M27 at the end of the season, and did not appear thereafter on the territory of M2/6 at all. Thus, the criterion of the female social choice is not only the affiliative behavior, but also the frequency of the sexually orientated activity of the male.

Relationship between Social and Sexual Attractiveness

The male's sexual activity toward the female did not show any reliable correlation with the affiliativeness of male ($r_{sp} = 0.27$) or female ($r_{sp} = 0.20$), nor with male's attendance of places with the highest female occurrence ($r_{sp} = 0.20$). The male's sexual activity could be equal to zero at any kind of social relationship (A. Tsellarius et al., 2016).

In Brauner's lizard female, we have never recorded the behavior aimed on achievement of copulation, except reflex arching of tail base, which was observed in any copulation, irrespective of kind of social interrelations and type of precopulative priming (A. Tsellarius et al., 2016). However, sexual attractiveness of male should be estimated from the frequency of female's rejecting behavior. The reaction of females to the sexual-exploratory behavior of males proved to be mostly rejecting, the differences in the rejection dergree at friendly interrelations (74% R-reactions, $n = 19$) and unfriendly ones (88%; $n = 49$) being small and statistically insignificant ($\varphi^* = 1.34$; $P < 0.85$). The female response to the initial stage of precopulative priming was rejecting in 100% of cases at any type of interrelation and any priming scenario and commonly included elements of aggressive behavior, the only difference being that with friendly relations the female resisted less vigorously.

Choice of Place for Residence and Spatial Integration of Dyads

As mentioned in the section on research methods, from the peculiarities of the behavior of an individual in the period preceding its irreversibly disappearance, we can determine, with high degree of confidence, whether the reason for this was death or migration beyond the region of observation (Tsellarius, A.Yu. and Tsellarius, E.Yu., 2009). The period of existence of individual home ranges that disappeared due to

Table 4. Differences in the affiliativeness of males (*Am*) toward the same female in the first two years of dyad existence

Female	Males	*Am*	*n*	φ*	*P*
F10	M2/6	38.9	18	2.93	0.99
	M4	6.8	44		
F8/2	M11/20	58.2	55	2.78	0.99
	M4	22.2	18		
F18/3	M4	20.6	68	2.63	0.99
	M90/40	3.3	30		

Table 5. Duration of existence (in seasons) of home ranges* with different causes for the disappearance of owners

Sex of individual region owner	Reason for disappearance		$n_1 + n_2$	U	P
	relocation	death			
Females	1 (1–2)	5 (1–7)	10 + 6	7.0	0.99
Males	1 (1–2)	8 (5–10)	3 + 6	0.0	0.95

* Data used for only those home ranges that were under observation since their appearance till disappearance.

Table 6. Age (number of hibernations) of males and females to the moment of formation of temporary and permanent home ranges

Sex of home range owners	Age at the moment of formation of HRs		$n_1 + n_2$	U	P
	temporary	permanent			
Females	3 (2–6)	5 (2–7)	10 + 8	17.0	0.95
Males	2 (2–2)	3 (2–4)	3 + 7	4.5	<0.95

relocation was significantly less than that of home ranges, which owners died (Table 5). Thus, the HRs can be conventionally divided into temporary home ranges that disappeared as a result of relocation and permanent ones that existed for more than two years and disappeared as a result of the death of their owners. Accordingly, we can speak of temporary and permanent residents.

The age at which the Brauner's lizard switches from vagrancy to temporary residence generally coincides with the age of sexual maturity, the differences between males and females are not signicicant. A transition to permanent residence for males mostly occurs earlier than for females (Table 6, $U = 9.0$, $P = 0.99$). In observed instances, the center of origin of male's territory was the female comfort zone, which was free, i.e., located outside the existing territories (Tsellarius, A.Yu. and Tsellarius, E.Yu., 2006). The permanent HR and the territory could form either simultaneously (the nonterritorial male "found" an available female's CZ) or some time after settling in a HR when a free female CZ appeared within the HR. The boundaries of the territory changed insignificantly for the rest of the male life (Fig. 3). The male could have any interrela-

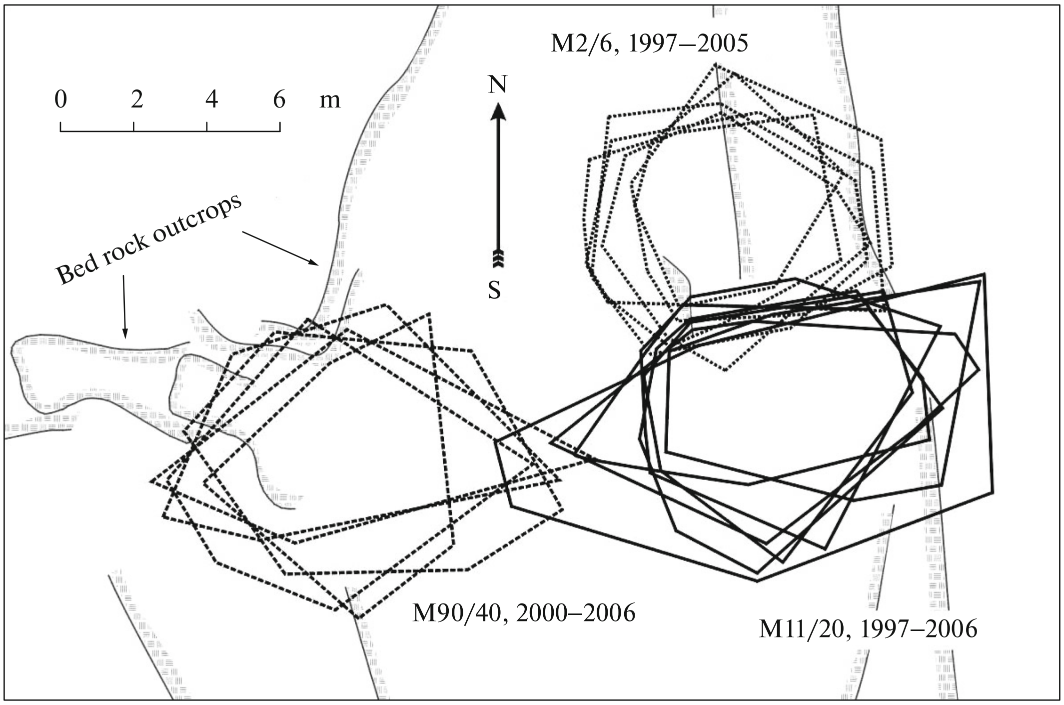

Fig. 3. Variation of the boundaries of territories throughout the life of males (only some part of individuals are represented).

Table 7. Territorial males of the central part of the study area, quality of their territories, and number of females having comfort zones on the male territory in different periods of observation

Name of place in which the territory is situated	Period of observation					
	1997–1998			2001–2002		
	owner of territory	quality of territory	number of females	owner of territory	quality of territory	number of females
Morning flank*	M16	2	4–2	M22/07	2	2
Rock*	M32	4	3–2	M17	5	7
Snag*	M4	5	6	M90/40	2	3–2
Cliff*	M27	3	3–?	M108	1	?
Mossy stones	M11/20	1	1	M11/20	4	3
Mound	M2/6	3	5	M2/6	4	4
Evening flank	M13/07	3	4	M13/07	3	2
Southern flank**	–	2	0	M119	2	2
Path**	–	0	0	M28	2	?
Total number of territories	7			9		
Quality average	2.6			2.8		

The quality of the territory was evaluated in units of the six-point scale.
"?" No exact data.
* Territories whose owner changed as a result of the death of the previous owner.
** Before 2000 these sites were not part of any male territory.

tions with the female around whose CZ the territory formed; subsequent disappearance of this female (which happened often) did not affect the existence of the already existing territory.

The environmental quality of the space occupied by observed lizards' settlement was rather low on average (Table 7), however, the quality of its parts significantly varied; accordingly, the environmental quality of the territories also varied and could change in the course of the male lifetime (Table 7) as a result of changes in the trees' crown shape, landslides, and transfer of leaf-litter, boulders and brushwood by stormwater floods, etc. Thus, the male's choice of place for permanent residence occurs at an early stage of his ontogenetic trajectory; the choice is related with accidental concurrence; in the sequel, a quality of the territory is changed by the processes beyond male's control.

Unlike in males, the age of females when they formed permanent HRs was significantly greater than in the case of temporary HRs (Table 6). Having reached sexual maturity, the female evidently begins to strive for stable residence, but changes the position of the HR, once or more times, before she would finally settle, and we have never observed the attempts to settle down at the same place twice. In all observed instances of transition of a female to stable residence, after a while she had a friendly interrelation established with one or two males whose territories included her comfort zones. At the same time, none of the temporarily settled females had these interrelations.

For a female that appeared in the settlement for the first time or visited it occasionally for a short time (designated as "random" females in Table 8), the attractiveness of the male's territory was primarily determined by the environmental conditions, not by the behavior of its owner (Table 8). If a female stayed on the settlement area, in the first year correlation observed both between the territory attendance (*TA*) and its quality, and also between the *TA* and the affiliativeness of territory owner (*Am*). In the second year of dyad existence and later, the correlation between the *TA* and the quality of the territory disappears, however, it remains high between *TA* and *Am* (Table 8). In fact, if the social attractiveness of the female (*Am*) was low for the territory owner, the attendance decreases; if the social attractiveness is high, the attendance remains at the same level or increases regardless of the quality of the territory. It is important to bear in mind that high affiliativeness of a male is a condition of female transition to stable residence, but this does not mean that stable comfort zones cannot appear on the territories of neighboring males with low affiliativeness. Female commonly used several territories simultaneously (Tsellarius et al., 2016); however, in areas with low *Am* of owners she spent significantly less time.

It should also be noted that formation of dyads, i.e., formation of female's stable comfort zones on the ter-

Table 8. Rank correlation between the territory attendance by a female (*TA*), the quality of territory, and the affiliativeness of its owner (*Am*) at different stages of dyad existence

Correlation	"Casual" females ($n = 21$)		Stable dyads, period of existence			
			first year ($n = 17$)		second year and later ($n = 9$)	
	r_{sp}	P	r_{sp}	P	r_{sp}	P
TA and quality	0.60	0.99	0.52	0.95	0.01	<0.50
TA and *Am*	0.11	<0.50	0.70	0.99	0.70	0.95

Table 9. Percentage of time spent by the territorial males and resident females on various forms of locomotor activity

Type of activity*	Fraction of time (%) spent by		U	P
	males ($n = 6$)	females ($n = 5$)		
Patrolling	16 (14–28)	0 (0–0)	0.0	0.99
Intrasexual conflicts	3 (1–4)	0 (0–1)	0.0	0.99
Intersexual contacts	6 (4–12)	2 (1–5)	2.0	0.99
Intensive foraging	4 (3–4)	10 (4–26)	1.5	0.99
Other	3 (2–7)	6 (2–9)	8.0	<0.6
Total	34 (28–47)	18 (8–37)	5.0	0.95

* Exploratory responses, threat displays, dashes for prey, movements to distances of less than 20 cm during basking, and some other short-term locomotion episodes have been excluded from consideration.

ritory of males occurs only beyond the timing of mating period (Fig. 4), when the total frequency of sexual and sexual-exploratory behavior of males is much lower than in the mating season (Tsellarius et al., 2016). Probably, high sexual activity of a male can reduce the attendance of its territory by a female regardless of his affiliative behavior (see also the Affiliative Selectivity section).

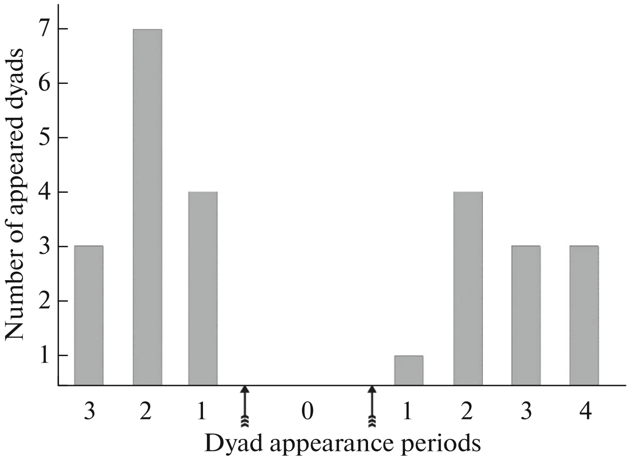

Fig. 4. Appearances of new dyads in different periods of the activity season ($n = 23$). Abscissa (left to right): (3–1) decades before the start of the mating period; (0) mating period; and (1–4) decades after the end of the mating period; the arrows indicate the start and the end of the mating season.

Time Budget for Females and Males

The time which males spent on locomotion is approximately twice as much that in females (Table 9). The differences between males and females are not only in the amount of locomotor activity, but also in its structure. The activity of males is mainly the patrolling of the territory (specific movement accompanied with olfactory marking and including brief stoppages with assumption displays; Tsellarius, A.Yu. and Tsellarius, E.Yu., 2005) and social interaction, whereas for females the motor activity is primarily associated with active search for food (Table 9).

DISCUSSION

According to our data, the social partner choice is not accidental for Brauner's lizards and the criteria of this choice are different for males and females. The male's affiliativeness (*Am*) mostly formed "at a glance" against the background of always identically rejecting behavior of all females in the early period of dyad existence. The male's affiliativeness is almost the same during and beyond the mating periods, and high *Am* is not necessarily combined with the presence of sexual intercourse (Tsellarius et al., 2016). Therefore, it may be suggested that the affiliative (social) attractiveness of a female is not related to its receptivity, nor its behavioral characteristics. Obviously, when choosing a female partner, a male primarily responds to the "exterior" of the female, i.e., to its color, proportions, motility, or some symptoms of the total physiological state. The fact that the attractivity of the female is not equal for different males suggests that the same set of external signs is evaluated by males differently. In other words, the selection criteria are not the same for different males.

The female affilativeness (*Af*) is primarily determined by the ”amicability” of male; i.e., the behavior of the partner is the main criterion for social partner selection; unlike the males, the selection criterion is the same for all individuals. The attractiveness of “amicable” males for female lizards was also reported for *Sceloporus graciosus* (Kelso and Martins, 2008). The relatively long period in which a female forms its attitude to a male is probably determined by the fact that evaluation of the frequency of manifestations of certain forms of male behavior requires a rather long period of time (Wachtmeister and Enquist, 1999). In general, feasible selectivity of females is low unlike that of males.

An increase in the *Af* level to the *Am* level takes some time and requires regular contacts with a male; consequently, stable residence of partners is not only a property of a friendly dyad, but also an essential condition for its appearance. The transition of a female to stable residence and high attendance of male territory are also closely associated with the high *Am*. Hence, in the observed settlement of Brauner’s lizards, the formation of friendly interrelations was triggered by the social attractiveness of a female for a male, that expressed as high *Am* towards female.

It is rather widely believed that long-term social bonds between males and females are largely determined by the reproductive (including sexual) strategies (Emlen and Oring, 1977; Gowaty and Buschhaus, 1998; Ulrich and Christophe, 2003; et al.). In this case, however, there is no correlation between the social and sexual attractiveness of a female, and the presence of a long-term friendly interrelations are not necessarily coupled with sexual intercourse.

Moreover, according to our data, firstly, the female response to sexual and sexual-exploratory behavior of male is mostly rejecting in any kind of interrelation (see the “Correlation between the Social and Sexual Attractiveness” section). Secondly, in the mating season when the frequency of sexual and sexual-exploratory behavior of males are higher than in the beyond this period (Tsellarius et al., 2016), dyads (with any type of relationship) never formed (Fig. 4). Thirdly, an increase in the affiliativeness of a female can be probably blocked by the high level of sexual-exploratory behavior of the male. All this suggests that the male’s sexual activity is more likely to prevent the formation of friendly relations and leads to disintegration of dyads; i.e., this is a social disintegration factor.

Regarding the observed ways of relationship formation, we should take into account the existence of latent selectivity of females and the fact that female’s affiliative persistence can increase its attractiveness to males (dyad M11/20 + F5, Table 3). This suggests that the described partner selection strategies and, accordingly, the prevailing dyad integration pattern may be optional (Zamudio and Sinervo, 2003); i.e., they may depend on the current social and environmental conditions. This assumption corresponds well with the ascertained correlation between the partner choice strategies and the structure of the costs for formation of friendly relations in males and females (see below).

For male, an active search is almost absent; he chooses a social partner from among females that occasionally settle on his territory. At the same time, the initiation of A-relations with a female is initially determined by male’s territoriality; nonterritorial males have no such relations due to absence of access to female comfort zones (Tsellarius, A.Yu. and Tsellarius, E.Yu., 2006). A territorial male spends much time on patroling, territorial conflicts, and intersexual contacts (Table 9). Therefore, the male’s main costs are not searching for a partner, but its attraction and retention.

A female is actively searching for a territory with favorable conditions; a high level of affiliativeness (*Am*) of the owner of the territory is the main condition for female transition to stable residence. Since high *Am* in this case inevitably leads to the establishing of A-relations, we can say that the female is inherently looking for conditions in which it can form A-relations with a male. The search takes more than two years (Table 6), and the female successively forms several temporary home ranges, and never making attempts to settle at the same place twice. Such abode search strategy of females is probably typical of many lizard species (Evans, 1951). The efforts spent by a female on maintaining an affiliative relation with a male are relatively low (Table 9), the main efforts being the search for an object.

The partner search strategy of females in terms of the optimal foraging theory belongs to the *searcher* category; the male search strategy is that of *pursuer* (Emlen, 1966; MacArthur and Pianka, 1966). The *pursuer* strategy under the conditions of abundance of potential “preys” leads to the formation of high selectivity (MacArthur and Pianka, 1966), as was just observed for males in our case. The *searcher* strategy under the conditions of patchy environment, combined with successive visiting of spots (settlements) without repetition, rare accessible objects, and large search time are the circumstances that make the searcher choose the first suitable variant (Stamps et al., 2005), which is just observed in females. Because these strategies are largely determined by the amount and spatial distribution of the resources, for different environmental conditions we can expect other search strategies, different ways of friendly integration of dyads, or no such integration at all.

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REFERENCES

Bleay, C. and Sinervo, B., Discrete genetic variation in mate choice and a condition-dependent preference function in the side-blotched lizard: Implications for the formation and maintenance of coadapted gene complexes, *Behav. Ecol.,* 2007, vol. 18, no. 2, pp. 318–323.

Crews, D., On the organization on individual differences in sexual behaviour, *Am. Zool.,* 1998, vol. 38, no. 1, pp. 118–132.

Emlen, J.M., The role of time and energy in food preference, *Am. Nat.,* 1998, vol. 100, no. 916, pp. 611–617.

Emlen, S.T. and Oring, L.W., Ecology, sexual selection, and the evolution of mating systems, *Science,* 1977, vol. 197, no. 4300, pp. 215–223.

Evans, L.T., Field study of the social behavior of the black lizard, *Ctenosaura pectinata, Am. Mus. Novit.,* 1951, no. 1493, pp. 1–26.

Gowaty, P.A. and Buschhaus, N., Ultimate causation of aggressive and forced copulation in birds: Female resistance, the code hypothesis, and social monogamy, *Am. Zool.,* 1998, vol. 38, no. 1, pp. 207–225.

Kelso, E.C. and Martins, E.P., Effects of two courtship display components on female reproductive behavior and physiology in the sagebrush lizard, *Anim. Behav.,* 2008, vol. 75, no. 2, pp. 639–646.

Lakin, G.F, *Biometriya (Biometry)*, Moscow: Vysshaya Shkola, 1973.

Lancaster, L.T., Hipsley, Ch.A., and Sinervo, B., Female choice for optimal combinations of multiple male display traits increases offspring survival, *Behav. Ecol.,* 2009, vol. 20, no. 5, pp. 993–999.

Martin, J. and Lopez, P., Chemoreception, symmetry and mate choice in lizards, *Proc. Roy. Soc. B,* 2000, pp. 1265–1269.

MacArthur, R.H. and Pianka, E.R., On optimal use of a patchy environment, *Am. Nat.,* 1966, vol. 100, no. 916, pp. 603–609.

Real, L., Search theory and mate choice: 1. Models of single sex determination, *Am. Nat.,* 1990, vol. 136, no. 3, pp. 376–404.

Rose, B., Lizard home ranges: Methodology and functions, *J. Herpetol.,* 1982, vol. 16, no. 2, pp. 353–269.

Samuel, M.D. and Green, R.E., A revised test procedure for identifying core areas within the home range, *J. Anim. Ecol.,* 1988, vol. 57, no. 3, pp. 1067–1068.

Sidorenko, E.V., *Metody matematicheskoi obrabotki v psikhologii* (Methods of Mathematical Data Processing in Psychology), St. Petersburg: Rech', 2001.

Smirina, E.M., Prospects in determining the age of reptiles by bone layers. *Zool. Zh.,* 1974, vol. 53, no. 1, pp. 111–117.

Stamps, J.A., Krishnan, V.V., and Reid, M.L., Search costs and habitat selection by dispersers, *Ecology,* 2005, vol. 86, no. 2, pp. 510–518.

Tokarz, R.R., Mate choice in lizards: A review, *Herpetol. Monogr.,* 1995, vol. 9, pp. 17–40.

Trivers, R.L., Parental investment and sexual selection, in *Sexual Selection and the Descent of Man,* Campbell, V., Ed., Chicago: Aldine, 1972, pp. 136–179.

Tsellarius, E.Yu. and Tsellarius, A.Yu., Age-related changes and probable significance of signal coloration in male rock lizards from the Navagir Range, *Zool. Zh.,* 2002, vol. 81, no. 8, pp. 970–977.

Tsellarius, A.Yu. and Tsellarius, E.Yu., Formation and defense of individual space in male rock lizards: 1. Home range, *Zool. Zh.,* 2005, vol. 84, no. 9, pp. 1123–1135.

Tsellarius, A.Yu. and Tsellarius, E.Yu., Formation and defense of individual space in male rock lizards: 2. Home range and territorial relationships, *Zool. Zh.,* 2006, vol. 85, no. 1, pp. 73–83.

Tsellarius, A.Yu. and Tsellarius, E.Yu., Life span and factors of mortality in the rock lizard *Darevskia brauneri* according to the results of long-term observations on the Navagir Range, *Zool. Zh.,* 2009, vol. 88, no. 10, pp. 1276–1280.

Tsellarius, A.Yu., Tsellarius, E.Yu., and Galoyan, E.A., Social relationships between males and females in the rock lizards *Darevskia brauneri* (Lacertidae). 1. Friendly monogyny in males and polyandry in females, *Zool. Zh.,* 2016, vol. 95, no. 7, pp. 1–12.

Ulrich, H.R. and Christophe, B., *Monogamy: Mating Strategies and Partnerships in Birds, Humans and Other Mammals,* Cambridge: Cambridge Univ. Press, 2003.

Wachtmeister, C-A. and Enquist, M., The evolution of female coyness: Trading time for information, *Ethology,* 1999, vol. 105, no. 4, pp. 983–992.

Zamudio, K.R. and Sinervo, B., Ecological and social contexts for the evolution of alternative mating strategies, in *Lizard Social Behavior,* Fox, S.F., McCoy, J.K., and Baird, T.A., Eds., Baltimore: Johns Hopkins Univ. Press, 2003, pp. 83–106.

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