ISSN 1062-3590, Biology Bulletin, 2016, Vol. 43, No. 9, pp. 1099–1109. © Pleiades Publishing, Inc., 2016.
Original Russian Text © N.A. Zavyalov, S.A. Albov, L.A. Khlyap, 2016, published in Zoologicheskii Zhurnal, 2016, Vol. 95, No. 5, pp. 584–596.

Mobility of Settlements and Elements of the Biological Signaling Field of Beavers (*Castor fiber*) in the Basin of the Tadenka River (Prioksko-Terrasny Nature Reserve)

N. A. Zavyalov[a, *], S. A. Albov[b], and L. A. Khlyap[c]
[a]*Rdeysky State Nature Reserve, Holm, Novgorod oblast, 175271 Russia*
[b]*Prioksko-Terrasny Nature Biosphere Reserve, Danki, Moscow oblast, 142200 Russia*
[c]*Severtsov Institute of Ecology and Evolution, Russian Academy of Sciences, Moscow, 119071 Russia*
**e-mail: zavyalov_n@mail.ru*
Received March 3, 2015

Abstract—This study was performed in the basin of the Tadenka River (Prioksko-Terrasny Nature Reserve) in the years 2007–2012. We investigated the spatial dynamics of beaver settlements and the stability of various elements of the biological signaling field (scent marks, lifetime of dams and dwellings). The data suggest that a high density of the biological signaling field is an additional sign of possible depletion of food resources. Beavers can rapidly occupy habitats with no elements of the signaling field, which contributed to the formation of their large range.

Keywords: beaver, ecosystem engineering, biological signaling field, marking behavior
DOI: 10.1134/S1062359016090107

INTRODUCTION

The concept of a biological signaling field was created by N.P. Naumov (Naumov, 1973, 1977). In recent years, there have been a number of studies on signal-mediated communication (Rozhnov, 2011), including long-term signals (stable elements) that can store information and serve as tools of ecological inheritance (Nikolsky, 2013, 2014). Stable elements of signaling field are burrows, trail, excrement accumulations, scent marks, and visual marks (Vanisova and Nikolsky, 2012).

Beavers are ecosystem engineers that physically modify their habitats (Rosell et al., 2005; Zavyalov, 2013) by building dams and dwellings; digging burrows, canals, and tunnels; and making trails. These long-lasting signs of beaver activity are the elements of their biological signaling field. Beavers also have communication signals, which have a shorter duration; the most important of such signals are scent marks.

Eurasian beavers (*Castor fiber* L. 1758) have two sources for scent marking: castoreum and anal gland secretions (Lavrov, 1981; Shchennikov, 1992). Beavers mark their territories by constructing scent mounts and marking sites (Zavyalov, 2013a, 2013b).

The signaling fields of beavers are easy to study in conservation areas. The anthropogenic impact on ecosystems here is small; the environmental conditions are regularly monitored; and the data of the first introduction of beavers and the parameters of their populations are recorded. One of the nature reserves inhabited by beavers for quite a long time, in which the beaver populations have been monitored, is the Prioksko-Terrasny Reserve. Two pairs of beavers were introduced here near the Tadenka and Ponikovka rivers in 1948 and 1955. Now the majority of population inhabits the basin of Tadenka River (*Rechnoi bobr*..., 2012).

The purpose of this study is to determine the stability of different elements of the signaling field, the consistency of scent mark distribution, the spatial dynamics of settlements, and the life-time of dams and dwellings of beavers.

MATERIALS AND METHODS

This study was performed in the basin of the Tadenka River (Prioksko-Terrasny Nature Reserve, Serpukhov region, Moscow oblast, Russia). The area of this nature reserve is 4945 ha. The average annual temperature is 3.9°C. The average annual precipitation 500–550 mm. Prioksko-Terrasny Nature Reserve lies on a terraced slope in the valley of Oka River. This area is located in a belt of mixed coniferous-broadleaved forest (Zablotskaya, 1989; *Atlas*..., 2005).

The Tadenka River crosses the reserve from north to south; the river is around 10 km long, and 3/4 of this length lies within the reserve. The width of nonimpounded channel is 4 m; the depth ~~is~~ up to 1 m. The

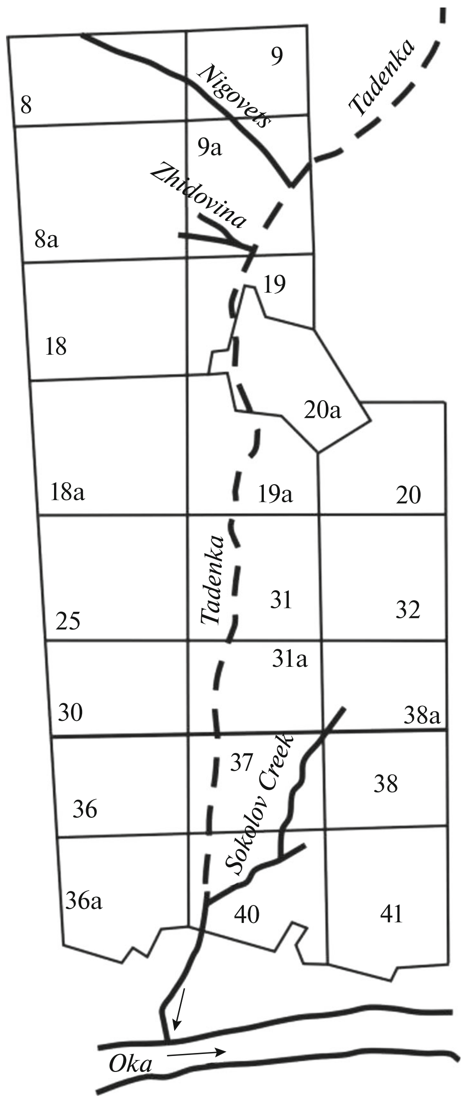

Fig. 1. The areas and water courses of the basin of the Tadenka River. The dashed line designates the part of the river channel with a length of 7.7 km where scent mounts and scent marks were counted.

channel slope is 8 m/km. The river is fed by both precipitation and springs; in the periods of drought it becomes shallow. The largest tributaries of the Tadenka are Nigovets Creek (right tributary to the northern part of the river; length of about 2 km), Zhidovina Creek (right tributary; to the south from Nigovets; around 1 km), and Sokolov Creek (left tributary to the southern part; around 2 km) (Fig. 1).

In this article, all data obtained in the basin of Tadenka River in the years 2007–2012 are included in the analysis. The size of the beaver population was estimated annually in October or November (according to Lavrov, 1952). The following scale was used for the estimation: small settlement: 1–2 beavers; medium settlement: 3–5 (on average, 4) beavers; large settlement: 6–8 (on average, 7) beavers. When counting the number of beavers, we also recorded the location of constructed objects in the settlements: dams (working and damaged), inhabited dwellings, trails, canals, and food caches. Since 2010 the lifetime of settlements after spring flooding and the number of scent mounts were determined soon after the seasonal flood (end of April–beginning of May). Other types of marks were not counted in this work (Zavyalov, 2013a, 2013b). The number of scent mounts was determined on a part of Tadenka River with a length of 7.7 km: from upstream to downstream (Fig. 1). The mounts were counted within each 100-meter-long section of channel.

The detection of dwellings was rather easy, since the Tadenka River is shallow and has high transparency. There is often a dam near a burrow. Even single beavers construct dams so that the entrance to their burrow is under water. Inhabited dwellings are easily noticeable due to tracks and muddy traces in the water near the entrance.

The coordinates of all objects were determined using GPS. For the comparison of mark distribution and settlement usage between different years, we used chi-squared test (Plokhinsky, 1980) and Spearman's correlation coefficient. Variance to the mean ratio was used as the index of aggregation (Shilov, 2001).

RESULTS

Parameters and Distribution of Settlements in the Basin of the Tadenka River

In the period from 2008 to 2012, there were 10–13 settlements of beavers in the basin of the Tadenka (Fig. 2, Table 1). The density varied from 7 to 9 settlements per 10 km of the river channel. The population size varied from 29 to 41 beavers (Table 1).

The analysis showed that there had been 7 settlements in the channel of the Tadenka (1–3, 5–8), 2 settlements in the Nigovets Creek (9, 11), and 1 settlement in the Sokolov Creek (11) during all the period of studies. In 2009 two new settlements were created: one on the Tadenka (4) and one on Zhidovina Creek (13). A single beaver inhabited the Nigovets Creek in winter 2009 (10). There was also a small settlement in the the Tadenka in 2011 (14) (Fig. 2).

Each family of beavers changed the wintering areas several times. For example, family no. 3 built a settlement near the mouth of Nigovets Creek and changed the wintering area every year (Fig. 2). In 2008 this family wintered on the Tadenka 450 m upstream from Nigovets Creek. In autumn 2009 they moved downstream and wintered on Nigovets Creek. There they built a new lodge 170 upstream from the mouth, while the dam was constructed at the mouth. In summer 2010 the beavers moved to the Tadenka, but now downstream from the mouth of Nigovets Creek. In 2010/2011 they built a lodge for wintering on the left bank 80 m downstream from Nigovets Creek. In

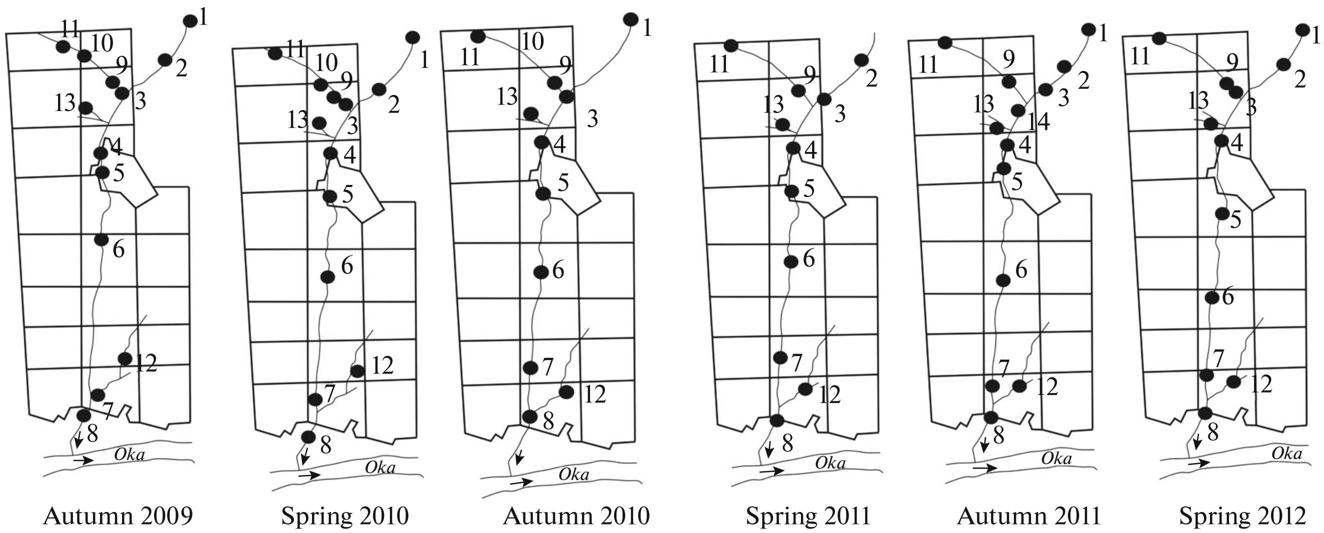

Fig. 2. Changes in the location of settlements in the basin of the Tadenka River in the years 2009–2012. The settlements are designated by black circles; their numbers correspond with the numbers in Table 1.

spring 2011 the family was divided into two parts; one part moved upstream to the dam that they repaired for wintering in 2008. However, in 2011/2012 all beavers wintered in the mouth of Nigovets Creek. In spring 2012 the family stayed there, and then moved 250 m downstream the Tadenka River for wintering.

The family no. 4 (northwestern part of quarter 20a) wintered in the same burrow for 3 years; then, after the spring flood, they moved 100 m downstream and wintered there for 2 years (Fig. 2).

The family no. 5 occupied an area from the southwestern part of quarter 20a to the northern part of quarter 31 (Fig. 2). In 2008/2009 this family wintered 300 m downstream from the area of wintering in 2007/2008. Then in summer the beavers built a big dam 250 m upstream and wintered there for 2 years.

Table 1. Changes in the size of settlements in the basin of the Tadenka River in the autumn

Dwelling no.	2008	2009	2010	2011	2012
1	?	+	Medium	?	?
2	+	Large	+	Medium	+
3	Medium	Large	Large	Medium	Small
4	–	Small	Small	Medium	Small
5	Medium	Large	Large	Large	Large
6	Small	Large	Medium	Medium	Large
7	Medium	Medium	Medium	Medium	Medium
8	Medium	Medium	Small	Medium	Small
9	Medium	Medium	Medium	Medium	Medium
10	–	Small	–	–	–
11	Small	Small	Small	Small	Medium
12	Large	Medium	Small	Medium	Medium
13	–	Small	Small	Medium	Medium
14	–	–	–	Small	–
Total number of beavers	29	41	32	40	40

"+" designates inhabited settlements the sizes of which were not determined; "–" designates uninhabited settlements; "?" designates settlements that were not investigated.

The river in this area is fed by springs and surrounded by willow thickets. This helped the beavers to survive during the drought in summer 2010. In spring 2011 a flood damaged the dam, but the beavers repaired it. In summer they repaired another dam 180 m downstream from the first one, but then moved back to the settlement where they had lived in 2007. The family repaired this settlement and the dam; in spring 2012 this dam was damaged again. In summer the family moved 1.2 km downstream of the Tadenka and built dams; some of them were new, and some contained elements of older ones. Two of these dams were only working in summer, and another two were working during the wintering period.

Family no. 6 occupied the middle part of the Tadenka (quarter 31, 31a, and 37) (Fig. 2). In 2009 the family moved three times: in summer they moved from the wintering area 340 m downstream, then moved back in autumn, and 180 m upstream for winter. Here the beavers wintered for 2 years, although all the dams were damaged in the spring. In 2011/2012 the family wintered 1.1 km downstream; in 2012/2013 they moved 500 m downstream.

Family no. 7 changed the wintering areas almost every year (Fig. 2). In winter 2009/2010 they lived in the southeastern part of the pond (quarter 40, Fig. 2). The summer in 2010 was hot, and this part of the pond was often visited by tourists; therefore, the beavers moved upstream and built a cascade of small dams. For the wintering period, they moved 850 km upstream (37), where the Tadenka River is fed by springs. In autumn 2011 the family moved back to the pond and wintered in a bank lodge on northwestern bank for two years.

Earlier (in autumn 2010) this bank lodge was occupied by family no. 8, which had moved there from downstream areas because of the lack of water. The beavers moved upstream along the dried river channel to water. They reached the pond, which was not inhabited by any families by then, and created a settlement.

Thus, the beaver families inhabiting the basin of the Tadenka River usually changed the wintering areas every year; in five cases, families wintered in the same area twice; in one case, for three years. One family moved back to an old wintering area four years later. In one case, the same area was used for wintering by two families in different years. The settlements were displaced by 200–1200 m; sometimes the families moved three times in a year.

Marking Activity

The analysis of mark distribution along the channel of the Tadenka showed that there is a complex and variable pattern of marking (Fig. 3). In spring 2010, 91 marks were found. The marks were distributed almost evenly (variance to mean ratio = 0.938). During and after the summer drought in 2010, the families moved several times. As a result, 215 marks were found in the same area in spring 2011; in spring 2012 we found 210 marks, which were more aggregated (variance to mean ratio = 3.590 and 3.260).

The mark distribution patterns were compared using the chi-squared test. It was found that the patterns in 2010 and 2011 were significantly different ($\chi^2 = 26.467$, $P < 0.05$), while no significant difference were observed between 2011 and 2012.

In spring 2010 the family from large settlement no. 2 moved upstream from the wintering area, which resulted in intense marking in sections 4, 5, 7, 9, and 11 (Fig. 3). Settlement 3, which was also large, was located in Nigovets Creek near its mouth. The family marked the banks of the Tadenka near the downstream dam, although the density of marks was low. Settlement 4 (single beaver) had a well-marked center (section 30) and upper boundaries (500–600 m from the dwelling; sections 25 and 26). In large settlement 5, the intensity of marking was moderate and approximately the same in the center (section 34) and near the boundaries 200 and 500 m upstream and downstream (sections 32 and 39). The another large settlement (№6) had moved upstream for wintering a year earlier. In spring 2010, a high concentration of marks was observed in section 45 (upper boundary) and in the center of the settlement (sections 47 and 50); however, single marks were found 600 m upstream and even 1000 m downstream. Marks were also found downstream from this settlement (sections 66, 68, 70, 71, 75–77); these marks were probably made by family 7. The dwelling of this family was located in the southeastern part of the pond (quarter 40), which lies outside the area in which we investigated the marking activity.

In spring of 2011 family no. 2 stayed at the same place. A high concentration of marks was observed in section 1, where this settlement had a boundary with settlement 1 (Fig. 3). The distance from the settlement downstream was relatively long; therefore, the number of marks in this part of the river channel was lower. The next area where the concentration of marks was high (sections 24 and 25) lay near the boundary of the settlement no. 13 (Zhidovina Creek), where this family could encounter beavers from settlement no. 4. The latter also marked the other boundary (section 31) and the center of their settlement (section 29). The aggregation of marks between settlements 4 and 5 (section 31) may have been made by beavers of both settlements. The marks downstream from this place were distributed evenly along the river channel; the concentration of marks was only increased on the boundaries of settlements 5 and 6 and in settlement 7, especially on its boundaries (sections 70 and 77). This may have resulted from the migration of these beavers upstream or from the migration of family no. 8, which moved to

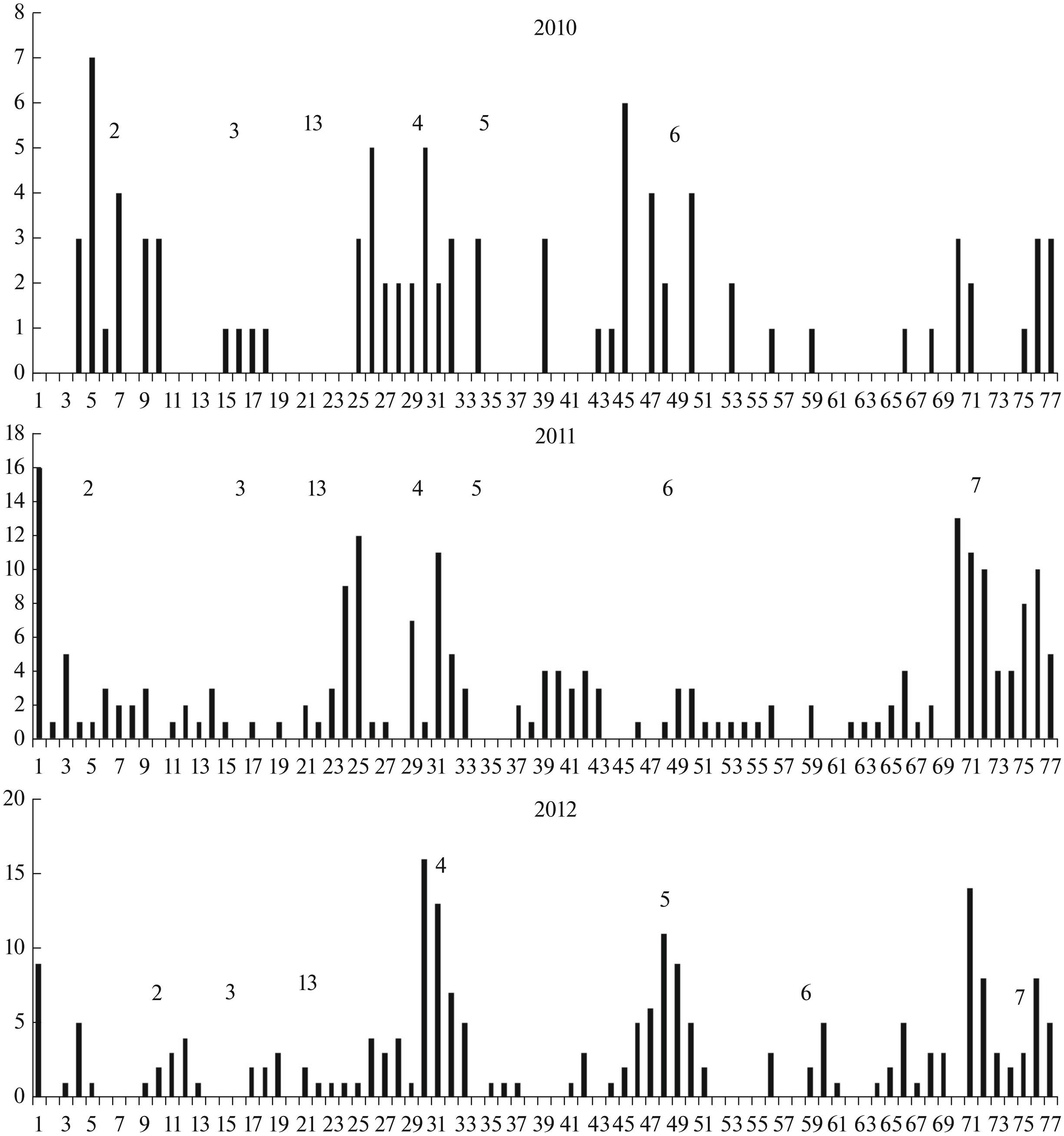

Fig. 3. The distribution of scent marks and inhabited dwellings in the basin of the Tadenka River in spring 2010–2012; *x*-axis: numbers of 100-meter-long parts of the river bed; *y*-axis: the number of marks. The upper digits designate the number and location centres of settlements (according to Table 1).

the northeastern part of the pond from downstream because of the drought and wintered there.

By winter 2011/2012 settlement no. 2 became smaller, and the family moved back downstream from the upper settlement. As a result, the number of marks in section 1 decreased in spring 2012, but the concentration of marks between settlements 2 and 3 remained the same (Fig. 3). After the seasonal flood, the beavers of settlement 4 moved to a burrow 100 m downstream from the previous one and started marking it intensely (sections 30 and 31). In summer 2011 the beavers of settlement no. 5 moved from the pond with two dwellings 250 m upstream, where they repaired a big dam. In spring 2012 this dam was damaged by a flood; the beavers repaired it, but then moved 1.2 km downstream. There they marked sections 48 and 49, which lay near their dwelling. The beavers of settlement no. 6 moved 500 m downstream, but left few marks. The

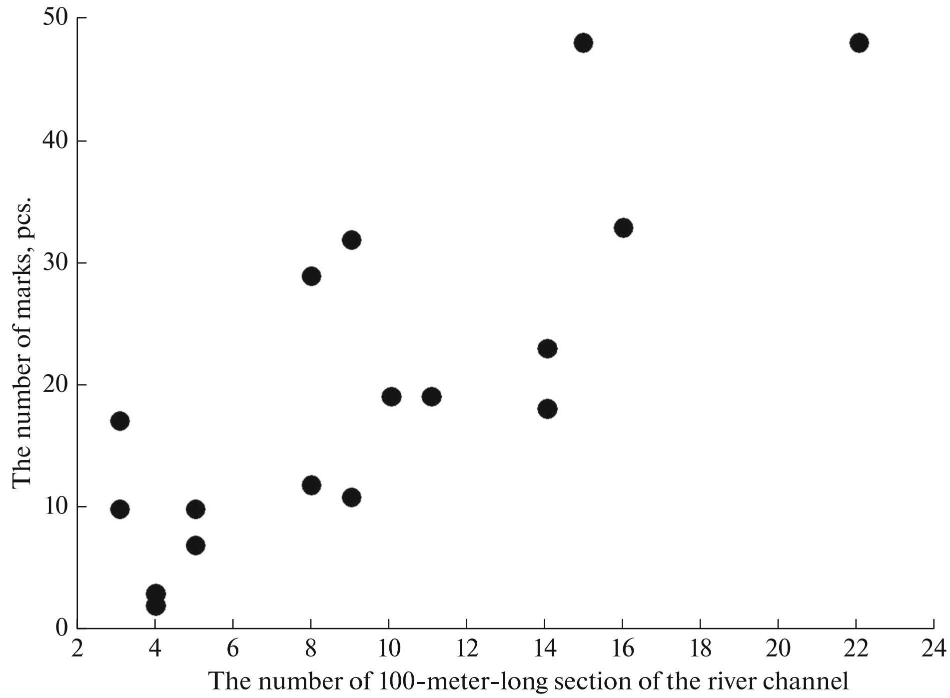

Fig. 4. The distance between adjacent inhabited settlements (x-axis) and the number of marks in these areas (y-axis). Data for all years were joined.

beavers of settlement 7 also moved downstream and actively marked the upper boundary (section 71).

We found a statistically significant positive correlation ($r_s = 0.805$, $N = 17$, $P < 0.001$) between the distance between settlements (counted as the number of 100-meter-long segments) and the intensity of marking (the total number of marks) (Fig. 4).

Thus, three years of observation of marking activity in the Tadenka River basin provided the following conclusions:

(1) In some cases beavers leave few marks on the boundaries of their settlements even if the settlements are moving.

(2) When the neighboring settlements are moving, the highest concentration of marks can be observed both in the center and on the boundaries of settlements.

(3) Scent mounts and scent marks can be found at a significant distance (up to 1 km) from the settlements, dams, and ponds.

The State of Dams and Dwellings

When moving to a new area, the beaver families leave their settlements and dams and build new ones. This leads to the destruction of some dams, while other dams are constructed and repaired. It is sometimes difficult to determine whether a dam is repaired or constructed, since beavers can use fragments of old dams to build new ones (*Rechnoi bobr*..., 2012).

The parameters and state of the elements of settlements were analyzed for two time periods: from 2007 to 2010 (in all the basin of the Tadenka River) and from 2007 to 2012 (in the channel of the Tadenka only).

The total number of dams found in the basin of the Tadenka River from 2007 to 2010 is 208 (Table 2). By autumn 2010 there were 174 dams (84%) and some of them were damaged. The state of dams in the channel of the Tadenka was generally worse than that in the creeks (80 and 85–100%, respectively). This can result from the greater size of the drainage basin, higher flow speed, and stronger flooding comparing with streams.

There were found 105 dams in the channel of the Tadenka River during the first four years of the study; by the end of 2010, 21 of them had been destroyed; 16 out of the remaining 84 dams were repaired. In summer 2010 the beavers built 12 new dams. Two of them were built in the areas with destroyed dams with the use of their fragments; ten dams were constructed in areas where there had not been other dams before. Six of the new dams only worked in summer and were damaged by autumn; the other six dams were repaired by beavers. Thus, four out of 16 dams repaired by winter were new; two of them were built with the use of materials from older dams; ten dams were used once again after repairing.

The second data set (six years) were collected in the channel of the Tadenka River only. In the period from 2007 till 2012, 125 dams were found in the channel of

Table 2. The lifetime of dams in the basin of the Tadenka River in the years 2007—2010

Water course	Total number of dams found, 2007—2010 (A)	Number of dams found in autumn 2010		
		absolute number (B) (% of A)	used and repaired — absolute number (% of B)	new dams/used and repaired new dams
Tadenka	105	84 (80)	16 (19)	12/6
Nigovets	62	53 (85)	3 (6)	No.
Zhidovina	12	12 (100)	2 (17)	2/2
Sokolov Creek	27	23 (85)	8 (35)	No.
Left tributary of Sokolov	2	2 (100)	No.	1/0
Total number of dams	208	174 (84)	29 (17)	15/8

the Tadenka; 81 of them were repaired at least once. However, 44 out of 125 dams (35%) were built before 2007 and never repaired.

Some families used the same dams again after one to four years. In 15 cases dams were used only in summer; in 60 cases, only in winter. In 79% of cases dams worked less than one year; in 20% of cases, for two years; in one case (1%) a dam was used for three consecutive years.

The state of dams left by beavers changed in different ways. One of the dams repaired during the study period was destroyed faster than the rest of them: it was repaired in summer and destroyed in autumn. Three dams worked for one year; another three dams, for two years; and one dam worked for three years. There were 48 dams that were not used for three years. During this period 12 of them (25%) were totally destroyed; the rest of them were damaged, and only separate fragments could be found. We also found 15 dams that were not repaired during all six years of the period studied. Seven of them were seriously damaged, and eight were totally destroyed. Fragments of one of the damaged dams were used for the construction of a new one. Three of these dams were impounded when the beavers moved back to those areas and built new dams.

Our findings show that dams that block only the river channel are destroyed faster. If a dam is also situated in the floodplain, this part is less damaged. Such dams are built in large settlements or in settlements that remain in the same area for several years.

Sometimes beavers move back to old dams, which is probably caused by their suitable location. We observed 11 cases when beavers built new dams instead of old ones. In one of these cases, the old dam was totally destroyed, and a new one was built in the area two years later. In other cases, the fragments of old dams were used for the construction. Only one dam was repaired and used three times. Every year we found several (from three to 11) dams in areas where there were no traces of older dams. The total number of such dams found during the study period is 37.

The types of dwellings used by beavers in the channel of the Tadenka River included burrows, lodges, and bank lodges. By now all sites suitable for burrows in the areas studied have been dug, and it is impossible to determine which of them are used and which are not. Therefore, we analyzed data on dwellings that were used at least once during the study period. The total number of dwellings used is 24: 10 burrows, 10 bank lodges, and 4 lodges. There was one settlement (no. 5) where we observed two types of dwellings (lodges and bank lodges) in 2010. When the families moved to new areas for wintering, they changed the type of dwellings. Out of these 24 dwellings, 13 (54%) were used for one year; nine (38%), for two years; and two (8%), for three years. There was no correlation between the type of dwellings and the duration of their use; however, burrows were the only type used for three consecutive years. One such burrow was used by family no. 4; the other one was located near the pond (quarter 40) and used by family no. 8 in 2010 and by family no. 7 in 2011 and 2013.

Different elements of the settlements were used for different periods of time (Table 3). The proportion of dwellings used for more than a year is higher than that of dams: $\chi^2 = 6.11$, $P = 0.013$. This difference results mainly from the fact that in many settlements the number of dams is higher than that of dwellings.

The dwellings left by families were rapidly destroyed. For example, a big lodge was built in the center of the pond in settlement no. 5 in 2010. In 2011 this lodge was found on the bank, where it was damaged; in 2013 only a pile of branches and a damaged entrance were remaining at that place. During the six years of this study, the beavers moved back to left dwellings only once. In 2011 family no. 5 moved to the bank lodge that they used in 2007.

Thus, the beavers inhabiting the channel of the Tadenka River often change wintering areas and, consequently, dams and dwellings.

Table 3. The duration of the use of dwellings and dams

Duration	Dwellings					Dams	
	burrow	bank lodge	lodge	total	%	total	%
Less than 1 year	6	4	3	13	54	75	79
2 years	2	6	1	9	38	19	20
3 years	2	0	0	2	8	1	1
Total	10	10	4	24	100	95	100

DISCUSSION

The habitat of beavers introduced in the studied area has unfavorable conditions. The river is rather shallow, and the beavers constantly need to build new dams; they also need to migrate often because of poor food resources. Moreover, dams are rapidly destroyed by flow when beavers leave them. Seasonal floods damage almost all the dams; some of them are totally destroyed. In ponds with a manmade dam (quarter 40), beavers can live without building new dams. In all other settlements beavers need to repair old dams and build new ones. In 1953 only two families and three dams were found in the basin of the Tadenka. In 1984 there were nine settlements and 146 dams; by the end of 2010, there were 12 settlements and 208 dams in various states. The average length of dams also increased from 10.57 ± 0.91 m in 1984 to 26.0 ± 2.8 in 2009 (*Rechnoi bobr*..., 2012). Although few dams are used for more than one year, and most of them are rapidly destroyed when abandoned by beavers, it is notable that new dams are constantly constructed, often in places where there are no traces of older dams. More than half of the dams remained in good state during the period of our study. Since the introduction of beavers in this area (more than 60 years ago), the number of dams has increased by several tens of times. Now dams and their fragments can always be found in different parts of this river and its tributaries.

The food resources of beavers in this area are also greatly affected. Shrubbery in the riparian zone of 30 m along the channel of the Tadenka is depleted by many years of intense use, and its rapid regeneration is unlikely. Therefore, the beavers need constantly to search for new food resources and often move to new areas (*Rechnoi bobr*..., 2012). This is evidenced by the high mobility of settlements and short life of dams and dwellings. Thus, the beavers of the Tadenka River are living in a habitat changed by previous generations, and the density of the biological signaling field here is very high.

The analysis of mark distribution in the basin of the Tadenka showed that the density of marks at the boundaries of settlements is not always high, although such a distribution could have been expected based on the literature data (Rosell and Nolet, 1997; Rosell et al., 1998; Emelyanov, 2004; Zavyalov et al., 2011). On the other hand, the concentration of marks in Voronezh Nature Reserve, which has been inhabited by beavers for more than 70 years, was also low at the boundaries and highest in the centers of the settlements; as a result, temporary settlements could be created in the boundary areas (Nikolaev, 1997). The distribution of marks in the basin of the Tadenka was more even in 2010 and more aggregated in 2011–2012. The aggregations of marks were found both at the boundaries and in the centers of settlements.

In general, the pattern of mark distribution in the basin of the Tadenka is similar to that in the basin of smaller rivers in Voronezh Reserve (Nikolaev, 1997). In the channel of the Tadenka, the beavers need to migrate often because of poor food resources both in summer and in winter and their uneven distribution. After moving to a new area, beavers need to occupy a territory that was used previously by another family; therefore, they actively mark the center of their new settlement. The same behavior was observed in Denmark (Bau, 2001) and in the delta of the Mackenzie River (Canada) after building a new lodge (Aleksiuk, 1968).

A high concentration of marks on the boundaries of settlements in the basin of the Tadenka was only observed in cases when the centers of adjacent settlements were close to each other (for example, between settlements nos. 1 and 2, 4 and 5 in spring 2010).

We found a statistically significant positive correlation between the distance between settlements and the intensity of marking (Fig. 4). This finding does not correspond to the literature data: according to some studies, the number of marks increases as the distance between settlements decreases (Butler, R.G. and Butler, L.A., 1979; Rosell and Nolet, 1997). However, this can be explained if we suggest that marking can be not only territorial function. Since marking behavior can also serve for communication and orientation, we can conclude that an increased number of marks at greater distances from the centers of settlements is made when the beavers move along their territories in the spring. As a result, families communicate with each other and find new areas for settlements.

In their everyday activity, beavers often perceive short- and long-lasting elements of the biological signaling field. Scent marks are usually considered as stable elements of this field (Vanisova and Nikolsky, 2012). But scent marks are not long-lasting, and animals need to renew them or make new ones. Then the scent marks form aggregations, which are relatively stable (Rozhnov, 2011).

According to the data obtained, these aggregations do not serve as signals for the next generations of the beavers. In a 9-year-long study in the basin of the Redya River (Novgorod oblast), it was found that the concentration of scent marks in each area was high only in the course of one year. When old marks disappeared after a flood, new aggregations were formed in new areas (Zavyalov, 2013a). The analysis of data obtained in the basin of the Tadenka over three years of observation showed that the aggregations of scent marks are unstable both in the center and on the boundaries of settlements. Since scent marks are not long-lasting enough to serve for communication between generations, there should be other stable elements with this function.

The changing of generations is determined by the average lifespan of beavers in natural conditions, which is around 12–15 years (Dezhkin et al., 1986). Since beavers live in the settlements of their parents and do not reproduce for the first two to three years of their lives (Dyakov, 1975; Dezhkin et al., 1986), we suggest that a complete change of generations takes, on average, 10 years. This was proved by an analysis based on counting marked beavers (Zharkov, 1968).

The examples of stable elements of the signaling field include burrows and trails of arctic foxes (*Alopes lagopus semenovi*), systems of trails and burrows of bobak marmots (*Marmota bobak*), settlements of European badger (*Meles meles*), primary trails of different animals, and rookeries of pinnipeds (Vanisova and Nikolsky, 2012). In other words, the topographic elements of the biological signaling field are the most stable (Rozhnov, 2013). They include all elements built and constructed by beavers: burrows, lodges, bank lodges, trails, tunnels, canals, and dams.

There are no published data on the stability of dams built by beavers. Their lifetime can vary widely: from one year in rivers with a high flow speed (Dyakov, 1975) to 50 years (Martell et al., 2006). According to our data, 25% of dams left by beavers were destroyed after three years, and 53% were destroyed after six years. Only marginal parts of large dams had a longer lifetime. Only 35% of the dams found in the channel of the Tadenka over the six years of observation were not destroyed after six or more years.

Published data on the stability of dwellings are also scanty. There have been extraordinary cases when beavers lived in the same lodge for decades (Zharkov, 1968; Dezhkin et al., 1986). In our study there was only one lodge used by beavers for three consecutive years, and it was totally destroyed three years after the family moved to other area. Thus, most of the dwellings disappear a couple of years after they are left, although some of them, as well as some dams, can remain in good state.

The majority (79%) of dams in the Tadenka River were used for less than a year; 20%, for two consecutive years; 1%, for three years. There are published data on the lifetime of settlements. Most of the settlements are inhabited for less than four years; some of them are used for more than five years; there have been cases when a settlement was inhabited for decades. Some areas are inhabited again after 3–30 years, although some are not used for 50 years. The vast majority of settlements are left and used again several times (Zavyalov, 2013).

Therefore, most of the elements of the signaling field have a short lifetime but are stable and can remain in several generations of a family, since beavers move back to old settlements, repair dwellings and dams, and build new ones.

Some authors consider the habitats as “vacant sites” that can be left by animals and then used again by every next generation (Vanisova and Nikolsky, 2012). From 1950 to 1990, all the areas inhabited by beavers in Voronezh Reserve were enumerated, which provided a map of their annual movements. The number of settlements inhabited by beavers at each moment of the study period did not exceed 100, while the total number of settlements was 384 (Nikolaev, 1997). Thus, there were 384 vacant sites, 237 (62%) of which were used during more than a half of the study period (permanent), while 147 (38%) sites were used for less than half of this period (temporary sites). The system of settlements in Voronezh Reserve was surprisingly stable: the permanent centers of activity remained in the same areas for decades, and temporary settlements were created in areas where there were found 5–10 years ago (Nikolaev, 1997). As a result, some parts of the territories, rather than dwellings, were used for long periods of time. However, some lodges and dams could also be used for decades. Based on our data, we suggest that the stability of the biological signaling field was provided not by the stability of separate elements (dams and dwellings) but the complex of these elements. At the same time, the location and properties of each of the elements can be changed. For example, there was one study in Newfoundland, during which beavers were returned into an area after experimental trapping in 14 settlements. Although there were lodges and dams left by previous inhabitants, and the amount of food resources was sufficient, the beavers changed the location of settlements (Bergerud and Miller, 1977). The study of Kudryashov (1975) in Oka Nature Reserve showed that the boundaries of settlements are constantly moved by beavers. In some cases, beavers try to extend their territory by occupying part of an adjacent settlement; in other cases they create new settlements in the area of existing ones. When food resources are rapidly depleted, each generation of beavers needs to move to new areas and find new ways of using territory that was previously used by other families, i.e., building new elements and repairing or reconstructing old dams and dwellings. As a result, the lifetime of settlements in the whole basin is generally long.

In the basin of the Tadenka River, the depletion of food resources was associated with aggregation of signaling field elements, both stable (dams, lodges, burrows) and unstable (scent marks). The concentration of elements was highest in the areas of large settlements, i.e., where the consumption of food resources was maximal. The biological signaling field regulates the spatial distribution of animals; therefore, the proportion of positive and negative reactions to signals is very important (Poyarkov, 2013). Apparently, a high density of the signaling field can cause negative reactions in beavers. This is evidenced by some of our findings: the settlements located in areas with a dense signaling field had a shorter lifetime. Some published data also prove this conclusion. For example, a 20-year-long study in the Adirondack Mountains (United States) showed that the frequency of new settlements in areas previously inhabited by other families is significantly lower than that in areas that have never been inhabited (Wright et al., 2004). Such a tendency (reconstruction of areas that were previously used and constant search for new areas) can result from a limited amount of food resources, since it helps to prevent their depletion. According to the published data on changes in the range of beavers in the twentieth century, these animals can easily inhabit areas with no traces of activity of previous generations. Their ability to inhabit areas without a biological signaling field can be a factor that contributes to the fast extension of their range, the boundaries of which are sometimes wider than the boundaries of their natural range.

CONCLUSIONS

(1) The beavers of the Tadenka River are living in a habitat changed by previous generations, and the density of the biological signaling field here is very high.

(2) The beavers need to migrate often because of poor food resources and their uneven distribution. After moving to a new area, the beavers built a settlement and mark its center more actively than the boundaries. The aggregations of scent marks have a short lifetime and cannot serve as signals for the next generation.

(3) The topographic elements of a signaling field, such as dwellings and dams, are stable and can serve for communication between generations. The majority of these elements are used for short periods of times, but then they are repaired or reconstructed when the settlement is inhabited by a new family. As a result, the number of dwellings and dams increases significantly and they become a permanent part of the habitat of beavers.

(4) The depletion of food resources is associated with the aggregation of signaling elements. We suggest that a high density of the biological signaling field can serve as a signal of possible depletion of food resources. Therefore, the signaling field can cause both positive and negative reactions. Beavers ability to inhabit areas without a biological signaling field can be a factor that contributes to the fast extension of their range.

ACKNOWLEDGMENTS

This work was supported by the Russian Foundation for Basic Research, project nos. 15-04-06423 and 15-29-02550.

REFERENCES

Aleksiuk, M., Scent-mound communication, territoriallity, and population regulation in beaver (*Castor canadensis*), *J. Mammol.*, 1968, vol. 49, no. 4, pp. 759–762.

Atlas kart Prioksko-Terrasnogo zapovednika (Atlas of Maps of the Prioksko-Terrasnyi Reserve), Bobrovskii, M.V. and Brynskikh, M.N., Eds., Pushchino: Biopress, 2005.

Bau, L., Behavioral ecology of reintroduced beavers (*Castor fiber*) in Klosterheden State Forest, Denmark, 2001 [electronic resource]. http://www.naturstyrelsen.dk/NR/rdonlyres/CCB2F98D-8543-4BD4-B776-2FB7E8E1FA08/0/Castorfiber.pdf.

Bergerud, A.T. and Miller, D.R., Population dynamics of Newfoundland beaver, *Can. J. Zool.*, 1977, vol. 55, pp. 1480–1492.

Butler, R.G. and Butler, L.A., Toward a functional interpretation of scent marking in beaver (*Castor canadensis*), *Behav. Neural Biol.*, 1979, vol. 26, pp. 442–454.

Dezhkin, V.V., D'yakov, Yu.V., and Safonov, V.G., *Bobr* (Beaver), Moscow: Agropromizdat, 1986.

D'yakov, Yu.V., *Bobry Evropeiskoi chasti Sovetskogo Soyuza* (Beavers of the European Part of the Soviet Union), Moscow: Moskovskii rabochii, 1975.

Emel'yanov, A.V., Population ecology of the beaver (*Castor fiber* L.) in the middle of the Vorona River basin, *Extended Abstract of Cand. Sci. (Biol.) Dissertation*, Saratov, 2004.

Kudryashov, V.S., Factors regulating the abundance dynamics of the beaver in the Oka Reserve, in *Mlekopitayushchie, chislennost', ee dinamika i faktory, ikh opredelyayushchie* (Mammals: Abundance, Its Dynamics, and the Factors That Determine Them), Trudy Okskogo Gos. Zapov., Ryazan, 1975, vol. 11, pp. 5–124.

Lavrov, L.S., *Bobry Palearktiki* (Beavers of the Palearctic), Voronezh: Izd. VGU, 1981.

Lavrov, L.S., Counts of beaver by identifying the population abundance, in *Metody ucheta chislennosti i geograficheskogo rasprostraneniya nazemnykh pozvonochnykh* (Methods of Counts and Determination of Geographical Distribution of Terrestrial Vertebrates), Moscow: Izd. Akad. Nauk SSSR, 1952, pp. 148–155.

Martell, K.A., Foot, A.L., and Cummimg, S.G., Riparian disturbance due to beaver (*Castor canadensis*) in Alberta's boreal mixedwood forests: implications for management, *Ecoscience*, 2006, vol. 13, no. 2, pp. 164–171.

Naumov, N.P., Signal (biological) fields and their significance for animals, *Zh. Obshch. Biol.* 1973, vol. XXXIV, no. 6, pp. 808–817.

Naumov, N.P., Biological (signal) fields and their significance for the life of animals, in *Uspekhi sovremmennoi teriologii* (Advances in Modern Theriology), Moscow, 1977, pp. 93–110.

Nikol'skii, A.A., The concept of a biological signaling field as a section of general ecology, in *Biologicheskoe signal'noe pole mlekopitayushchikh* (The Biological Signaling Field of Mammals), Nikol'skii, A.A. and Rozhnov, V.V., Eds., Moscow: Tovar. Nauch. Izd. KMK, 2013.

Nikol'skii, A.A., Ecological inheritance in the biological signaling field of mammals, *Russ. J. Ecol.*, 2014, vol. 46, no. 1, pp. 7–11.

Nikolaev, A.G., Long-term dynamics of the abundance of beavers at the Voronezh Biosphere Reserve, in *Razvitie prirodnykh kompleksov Usman'-Voronezhskikh lesov na zapovednoi i antropogennoi territoriyakh. Trudy Voronezhskogo biosfernogo gosudarstvennogo zapovednika* (The Development of Natural Complexes of Usman–Voronezh Forests in the Protected and Anthropogenic Areas. Transactions of the Voronezh Biosphere State Reserve), Voronezh: Biomik, 1997, pp. 81–98.

Plokhinskii, N.A., *Algoritmy biometrii* (Biometrics Algorithms), Moscow: Izd. Mosk. Univ., 1980.

Poyarkov, A.D., Biological signaling field: ethological, ecological, and evolutionary aspects of the problem, in *Biologicheskoe signal'noe pole mlekopitayushchikh* (The Biological Signaling Field of Mammals), Nikol'skii, A.A., and Rozhnov, V.V., Eds., Moscow: Tovar. Nauch. Izd. KMK, 2013.

Rechnoi bobr kak klyuchevoi vid ekosistemy maloi reki (na primere Prioksko-Terrasnogo gosudarstvennogo biosfernogo prirodnogo zapovednika) (Eurasian Beaver as the Key Component of a Small River Ecosystem (a Case Study of the Prioksko-Terrasnyi State Biosphere Nature Reserve)), Dgebuadze, Yu.Yu., Zavyalov, N.A., and Petrosyan, V.G., Eds., Moscow: Tovar. Nauch. Izd. KMK, 2012.

Rosell, F., Bergan, F., and Parker, H., Scent-marking in Eurasian beaver (*Castor fiber*) as a means of territory defense, *J. Chem. Ecol.*, 1998, vol. 24, no. 2, pp. 207–219.

Rosell, F., Borzer, O., Collen, P., and Parker, H., Ecological impact of beavers *Castor fiber* and *Castor canadensis* and their ability to modify ecosystems, *Mamm. Rev.*, 1998, vol. 35, no. 3, pp. 248–276.

Rosell, F. and Nolet, B.A., Factors affecting scent marking behavior in Eurasian beaver (*Castor fiber*), *J. Chem. Ecol.*, 1997, vol. 23, no. 3, pp. 673–689.

Rozhnov, V.V., Place of the concept of mediated chemocommunication in the biological signaling field theory by N.P. Naumov, in *Biologicheskoe signal'noe pole mlekopitayushchikh* (The Biological Signaling Field of Mammals), Nikol'skii, A.A. and Rozhnov, V.V., Eds., Moscow: Tovar. Nauch. Izd. KMK, 2013.

Rozhnov, V.V., *Oposredovannaya khemokommunikatsiya v sotsial'nom povedenii mlekopitayushchikh* (Mediated Chemocommunication in the Social Behavior of Mammals), Moscow: Tovar. Nauch. Izd. KMK, 2011.

Shchennikov, G.N., Morphology and functional significance of anal glands of the Eurasian beaver, *Extended Abstract of Cand. Sci. (Biol.) Dissertation*, Moscow, 1992.

Shilov, I.A., *Ekologiya* (Ecology), Moscow: Vysshaya shkola, 2001.

Vanisova, E.A. and Nikol'skii, A.A., *Biologicheskoe signal'noe pole mlekopitayushchikh (k 110-letiyu so dnya rozhdeniya professora N.P. Naumova)*, *Zh. Obshch. Biol.*, 2012, vol. 73, no. 6, pp. 403–417.

Wright, J.P., Gurney, W.S., and Jones, C.G., Patch dynamics in a landscape modified by ecosystem engineers, *Oikos*, 2004, vol. 105, pp. 336–348.

Zablotskaya, L.V., Prioksko-Terrasnyi Reserve, in *Zapovedniki SSSR* (Reserves of the USSR), vol. II: *Zapovedniki Evropeiskoi chasti RSFSR* (Reserves of the European Part of the RSFSR), Moscow: Mysl', 1989, pp. 30–51.

Zavyalov, N.A., Zheltukhin, A.S., and Korablev, N.P., Beavers of the Tyud'ma River basin (Tsentral'nyi Lesnoi Reserve): from the first reintroductions to an "ideal" population, *Byull. Mosk. Obshch. Ispyt. Prirody, Otd. Biol.*, 2011, vol. 116, no. 3, pp. 12–23.

Zavyalov, N.A., Beavers (*Castor fiber, C. canadensis*)—environment-forming species and phytophages, *Usp. Sovrem. Biol.*, 2013, vol. 133, no. 5, pp. 502–528.

Zavyalov, N.A., Long-term variability in the intensity of territory marking in beavers (*Castor fiber* L.) and the formation of biological signaling fields, *Byull. Mosk. Obshch. Ispytat. Prirody, Otd. Biol.*, 2013a, vol. 118, no. 5, pp. 3–11.

Zavyalov, N.A., The biological signaling field of the beaver (*Castor fiber*): its elements, structure, and functions, in *Biologicheskoe signal'noe pole mlekopitayushchikh* (Biological Signaling Field of Mammals), Nikol'skii, A.A. and Rozhnov, V.V., Eds., Moscow: Tovar. Nauch. Izd. KMK, 2013b.

Zharkov, I.V., The structure and dynamics of the population of mammals: a case study of the beaver in the USSR, *Extended Abstract of Doctoral (Biol.) Dissertation (by the aggregate of published works)*, 1968.

Translated by Ya. Lavrenchuk