FACTORS AFFECTING SCENT MARKING BEHAVIOR IN THE EUROPEAN BEAVER

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Abstract-We tested the hypothesis that a main function of territory marking in European beaver (*Castor fiber*) is defence of the territory. The results showed that:1) beaver colonies with close neighbors scent-mark more often than isolated ones; 2) the number of scent markings increased significantly with the number of neighboring territories and individuals, the mean distance to all other territories, duration of territory occupancy and length of wooded banks within the territory; 3) the number of scent markings by a colony was not related to the number of animals in the colony, the distance to nearest neighbors main resting-site or age of beaver; 4) the number of scent mounds or scent markings in territories with breeding and non-breeding beaver did not differ; 5) there was no significant difference in the number of scent markings during the season (16 April - 31 August); and 6) some of the scent mounds were concentrated at feeding-sites, resting-sites and near trails, but most had no apparent relationship to any of these sites. Therefore we concluded that scent marking apparently plays an important role in territory defence of the European beaver.

Key words-Beaver, *Castor fiber*, scent communication, scent mound, scent marking, radiotelemetry, territorial behavior, Netherlands.

INTRODUCTION

By marking their territories, animals might deter or intimidate potential intruders (Geist, 1964; Hediger, 1949; Mykytowycz, 1965). A scent mark may provide an intraspecific warning signal ("no trespassing") or even a "psychological fence", both decreasing the probability of an agonistic encounter with its risk of injury or even death (Welsh and Müller-Schwarze, 1989). The individuals resident in a territory have more to gain from retaining the territory than intruders do from taking it over, and will, therefore, be more likely to escalate an encounter than will an intruder. This is because residents will have invested a great deal of energy and time into getting to know their areas and resources, may have modified the habitat, and may have dependent young (Gorman, 1990). In essence, the scent marks in a territory act as a cue to potential fighting ability and willingness to fight in an asymmetric contest between resident and intruder (Maynard Smith and Parker, 1976). Gosling (1982) presented an alternative hypothesis, suggesting that the function of territory marking is to provide an olfactory association between the resident and the defended area which allows intruders to identify the resident when they meet and thus reduce the frequency of escalated agonistic encounters. Other possibilities are discussed by Gosling (1990) and Richardson (1991).

All age classes of beaver (*Castor spp.*) and both sexes participate in marking the territory boundaries at scent mounds close to the water's edge (Aleksiuk, 1968; Wilsson 1971; Butler and Butler, 1979; Svendsen, 1980a). Beaver mounds are marked with urine and castoreum from the castor sacs, and possibly with anal gland secretion (Bollinger, 1980; Schulte, et al. 1994; see also Müller-Schwarze and Houlihan, 1991). Scent communication is important in beaver; they lack long-distance acoustic communication, and as a primarily nocturnal species, they cannot rely on visual communication (Tang et al., 1993). While marking may serve multiple purposes, recent studies have supported a territorial function as primary (Houlihan, 1989; Welsh and Müller-Schwarze, 1989). Hay (1958) and Aleksiuk (1968) also suggested that scent marking is related to territoriality in *C. canadensis*. Wilsson (1971) suggested a similar function for scent marking in *C. fiber*. Müller-Schwarze and

Heckman (1980) demonstrated for the first time that experimentally used odor cues affect colonization by free-ranging beaver (*C. canadensis*). The experimentally scented sites were colonized less often than the unscented. However, aggressive encounters are not rare. For instance, in a dense population of *C. fiber* along the Elbe, bite wounds from conspecifics are the most important cause of death in adult beaver, occurring mostly in May at the time new territories are established (Piechocki, 1977).

Beaver should scent-mark before the main arrival period of intruders if the maximum preventive effect is to be obtained. Therefore a marking peak in April should be expected, because at that time young beaver usually disperse from their natal site in order to establish their own territory (Beer, 1955; Bergerud and Miller, 1977; Svendsen, 1980b). Most transients are dispersing subadults (2 years of age, in their third summer of life), but they may also include adult males temporarily leaving their family lodge or adult females without young (Townsend, 1953).

We hypothesize that the European beaver scent marks as a means of territory defence. The following predictions were deduced and subsequently tested: 1) the number of scent markings in resident beaver increases with increasing number of neighboring territories or individuals; 2) residents scent mark more frequently with increased duration of territory occupancy and territory quality; 3) the number of scent mounds present and the number of scent markings does not differ between breeding and non-breeding beaver territories; 4) scent marking is more frequent at the presumed period of dispersal; and 5) most of the scent mounds are not located at specific resources (feeding-sites, resting-sites, trails).

METHODS AND MATERIALS

Study Area. The study was conducted in the Biesbosch region (about 100 km^2) in the freshwater estuary of the rivers Rhine and Meuse in the Netherlands (51º45’N, 4º50’E). The central part is a nature reserve (about 50 km^2) with a tidal amplitude of 30 cm, but the water levels are influenced much more by wind and river discharge than by the tide. The nature reserve consists of willow coppices and reedbeds intersected by creeks and no longer exploited by man. It is surrounded by agricultural fields with creeks with stable water levels and more or less intact banks. The dominant vegetation on the banks of waterways > 5 m wide (615 km in total) was classified either as wooded (184 km), with herbs (126 km), with reeds (217 km) or barren (88 km). The banks were digitized from a 1:10,000 map into a Geographical Information System (ARC/INFO).

Study Animals. In October-November 1988 to 1991, a total of 42 European beaver originating from the river Elbe, Germany, were sequentially released as part of a reintroduction program (Nolet, 1995). The founder group contained 17 adults, 7 subadults, 10 yearlings and 8 kits. Prior to release, the animals were marked with colored plastic and aluminum eartags for visual identification. We attempted to catch beaver born in the study area. However, the tidal fluctuation in water levels negatively affected trapping success with Hancock live-traps and we caught only four unmarked beaver (total trapping success 5%).

Delineation of Territories. From 1 April to 31 August 1993 we mapped all 13 territories present either by locating scent mounds supplemented with sight observations of mostly marked individuals (8 territories) or by radiotelemetry (3 territories) (Figure 1). We used the locations (concentrations) of scent mounds, sight observations and radiotelemetry data to define the territorial boundaries (see also below). In three territories (A, C and F, Figure 1), this did not provide enough information, and the locations of fresh feeding-sites and sight observations by others were used in addition. The scent mounds, sight observations and radio fixes were digitized from a 1:10,000 scale map into a GIS-system (ARC/INFO) (Figure 1). We considered territories to be one- rather than two-dimensional, i.e. territory sizes were expressed as total length of banks [see Nolet and Rosell (1994) for further details].

Scent Mounds. This phase of the study was conducted between 16 April and 31 August 1993. The type, smell (strong or weak), and locations of scent mounds (see definition in Table 1) were recorded once a week in the whole study area, except in one territory (G, Figure 1, see also Table 2) located outside the nature reserve, which was visited only once a month. Scent mounds were assigned to a beaver colony according to the origin of an ear-tagged beaver sighted nearest to the scent mound. A scent mound which had recently been used was called a scent marking (see definition in Table 1). Freshly built scent mounds without odor were also designated as scent markings because they can contain chemical substances from the castor sacs (castoreum) and/or the anal glands that cannot be smelled by the human nose (see Bollinger, 1980; Schulte, 1993). The approximate distance to the nearest neighboring territory (see definition in Table 1) was measured as a straight line between the main resting-sites of neighboring territories (den used most during the study period). To classify peripheral and central territories we measured the straight line distance to all other territories (main resting-site) and classified mean distances of < 2.0 km as central and those distances to ≥ 2.0 km as peripheral. To test the validity of the use of scent mounds in delineation of the territories, we arbitrarily distinguished three zones of 0-299 m, 300-600 m and > 600 m from the drawn territorial borders (measured along the waterway) and counted the number of scent markings in each zone (Figure 2). All three zones were searched with equal intensity. Eleven (of 13) of the main resting-sites were found in the latter zone, and two were located in the middle zone. Although the zone > 600 m from the border contained more length of banks, the zone nearest to the border had the highest mean number of scent markings (Figure 3). These data indicated that the scent mounds were not randomly distributed over the territory but were lumped instead. This gave us confidence that the scent mound data could be used to delineate the territories. However, beaver in colonies located at the periphery of the study area marked much less frequently than those in the central part (see results), but fortunately we had radio-tracking data for two of the three territories outside the nature reserve (see Figure 1).

Breeding Status of Territories. Breeding territories were defined as those containing young of the year.

Statistical Methods. Statistical analyses were performed with SPSS (version 6.0) (Norusis, 1990). We used nonparametric statistics in accordance with Siegel and Castellan (1988). Nonparametric tests were corrected for ties. Probability values are two-tailed and 5 % was used as the level of significance. Mean values are shown with standard deviations.

RESULTS

Number of Scent Markings. The 286 scent mounds were located at 214 sites (see definition in Table 1) within the 13 occupied territories (Table 2). Scent mounds were checked a total of 3326 times of which 933 (28.1%) were determined to be freshly used (scent marked) (Table 2). Of the 933 freshly used mounds, 352 (37.7%) had a strong smell, 175 (18.8%) a weak smell and 406 (43.5%) no discernible smell. Of the 214 scent mound sites, 46 had more than one scent mound (range 2-8). Beaver did not maintain all mounds following initial use, and 36.4% of the scent mounds were marked only once, whereas others were marked repeatedly. Beaver in the three colonies located at the periphery (F, G and J, Figure 1) (Table 2) scent-marked 28.0 ± 45.1 times on average during the study period (N=3) which was significantly less often than in the central colonies ($\bar{x}$ = 84.9 ± 38.4, N=10) (Mann-Whitney U-test, z=-2.02, p=0.043). The number of scent markings increased significantly with the number of neighboring territories (Figure 4). The same pattern was also shown for the number of neighboring individuals (Figure 5). The number of scent markings decreased with the mean distance to all other territories (Figure 6). A significant correlation was also found between number of scent markings and duration of territory occupancy (of the pair member that established first) (Figure 7) and length of wooded banks within the territory (Figure 8). No significant correlation was found between number of scent markings by a colony and distance to the nearest neighbors main resting-site (Table 2, r_S=-0.197, N=13, *P*=0.520), number of beaver per territory (r_S=-0.100, N=13, *P*=0.744) or age of beaver (of the pair member that was oldest) (r_S=-0.088, N=13, *P*=0.775). Colonies of breeding beaver (N=5) (Table 2) made an average of 19.4 ± 12.0 scent mounds and scent-marked on the average 64.8 ± 41.4 times, which was not significantly different from non-breeding beaver colonies (N=8) ($\bar{x}$ = 26.6 ± 12.4 and 76.1 ± 50.1 respectively, Mann-Whitney U-test, z=-0.73, *P*=0.464 for number of scent mounds and z=-0.59, *P*=0.558 for number of scent markings).

Variation with Season. Table 3 show how the significant trends in Figure 4-8 hold up over the course of the season. The results in Table 3 indicate a significant relationship between both the number of neighboring territories and the number of neighboring individuals, and number of scent markings, for most bi-monthly periods. Also, there were significant correlations between the number of scent markings and all 5 parameters for the period 01-15 August. There was no significant difference in the number of scent markings from 16 of April to 31 August (Figure 9). The scent mound construction was highest during the last week in April and the first week in May (Table 4).

Location of Scent Mounds. Of the total number of scent mounds (N=286) observed during the entire period 16 April - 31 August, 34.6% were located at feeding-sites, 6.6% near (< 5 m) a resting-site (den, hole, lair), 5.3% near a trail though 53.5% had no apparent relationship to any of these sites. Of the 286 scent mounds 97.2% were self-constructed, while the rest (2.8%) were located on rocks, tussocks or directly on the ground. The week to week variation in scent mound numbers and locations during the peak period of marking/dispersal by beaver is showed in Table 4.

DISCUSSION

Beaver sites with more neighbors, and therefore a greater number of potential intruders, were expected to scent mark more often. In this study beaver colonies in the central part scent-marked significantly more than did colonies at the periphery. The number of scent markings increased significantly with the number of neighboring territories and individuals. This pattern held for most of the bi-monthly periods from 16 April - 31 August, further indicating the importance of scent marking as a defence against neighbors. We also found that the number of scent markings decreased with increasing mean distance to all other territories. This may be regarded as a measure of how central a territory was situated. Thus, these findings are in accordance with our first prediction. We found, however, no significant correlation between the number of scent markings and distance to the nearest neighbors main resting-site, as found by other authors (Butler and Butler, 1979; Müller-Schwarze and Heckman, 1980; Svendsen, 1980a; Houlihan, 1989).

That the number of scent markings is density dependent has previously been shown for both *C. canadensis* (Butler and Butler, 1979; Müller-Schwarze and Heckman, 1980; Houlihan, 1989) and *C. fiber* (Andersson and Westerling, 1984). Thus when beaver have many close neighbors they apparently need to scent mark more often to be unambiguously recognized. Gosling (1982) predicted that the owner should remove or replace marks in the territory that do not match its own odor. We recorded two observations that support this prediction: in both cases a nonresident adult male beaver scent-marked and the resident adult male beaver scent-marked the same mound minutes later.

Nolet et al. (1995) found that, in contrast to other food studies on beaver, in the Biesbosch they nearly exclusively ate woody plants all year round. Wooded banks within the territory were therefore clearly an important resource. Beaver released in unoccupied habitat spent considerable time exploring their surroundings, especially during the first two years of the reintroduction (Nolet and Rosell, 1994). Thus, once established, these (large) territories were presumably well worth defending. Theoretically, the greater potential value of the territory for residents, in contrast to intruders, makes it worth fighting harder for. Thus intruders should retreat (Maynard Smith, 1976). Nolet and Rosell (1994) found that the earliest arrivals claimed larger territories, and also territories of better quality, than later arrivals. We found a significant positive correlation between both the number of scent markings and the duration of territory occupancy and length of wooded banks as did Hodgdon (1978), which is in accordance with our second prediction. It appears that residents invest more in scent marking in good quality territories, and when a territory has been occupied for a long time, as a means of defending it better.

The number of scent mounds and scent markings in breeding and non-breeding beaver territories did not differ, which is in accordance with our third prediction. This indicates that scent marking is not associated with having young. It also suggests that constructing scent mounds is relatively uncostly and that breeding beaver are not forced to save energy by scent marking less.

There was no significant difference in the number of scent markings during the season. However, we observed a small peak in the number of scent markings in May. We also observed a peak in scent mound construction in the last week in April and the first week in May, which is in accordance with our fourth prediction. These peaks could be explained by the greater need for scent marking early in the season (spring) to inform transient beaver that the area is occupied (intercolony communication; Butler and Butler, 1979). Intrusion by neighboring beaver, especially during spring dispersal of two-years olds, has been hypothesized to be the cause of the increase in the construction of scent mounds observed by some authors (Aleksiuk, 1968; Houlihan, 1989). Molini et al. (1980) predicted that scent marking would be greatest when interactions between dispersing and resident beaver peaked. As individuals begin to find available sites, the number of "floaters" also decreases, as should scent marking. Their model predicted a peak in spring, which nearly coincided with an observed peak in scent marking for *C. canadensis.* Nitsche (1985) found a peak in April and May for *C. fiber* (see also Klenner-Fringes, 1992), whereas for *C. canadensis* a peak from March through July has been found (Fabel, 1977; Hodgdon, 1978; Butler and Butler, 1979; Bollinger, 1980; Svendsen, 1980a; Walro, 1980). Svendsen (1980a) suggested that both residents and transients respond to each others scent mounds, and that the high numbers of scent markings in spring reflect the combined behaviors of both residents and transients. The model advanced is one where the presence of one fresh scent mound induces another. The significant increase in number of scent markings in the beginning of August may coincide with the period for the emergence of kits from the dens. Buech (1995) also recorded a peak in scent mound construction (for males) during the beginning of August in North American beaver. However, this peak in scent markings could also be associated with dispersal of yearlings. Hartman's (1994) results, from a low density population, showed that six of nine beavers dispersed as yearlings, and three of these in the early fall.

Müller-Schwarze and Heckman (1980) found that scent mounds were located at trails, lodges and dams. Hay (1958) reported that scent mounds occurred in concentrated patterns around inhabited lodges. Butler and Butler’s (1979) examination of scent mound placement indicated that 84% of the scent mounds constructed by beaver colonies occurred in areas of high colony activity (e.g., feeding areas, trails leading away from the pond, grooming areas). The scent mounds in this study were located near feeding-sites, resting-sites and near trails (near areas with high activity), but more than half of the scent mounds had no apparent relationship to any of these sites, which is in accordance with our fifth prediction. These scent mounds at "other sites" also seem to play a role in territory defence, as indicated by the high frequency of scent mound construction here at the end of April and first week in May.

The number of scent markings by a colony of beaver in this study was not related to the number of animals in the colony or age of beaver. Other authors also found no correlation between the number of scent markings and the number of animals in the colony (Butler and Butler, 1979; Svendsen, 1980a; Houlihan, 1989). It seems that the beaver in the Biesbosch manage to maintain, independent of group size and age, the scent mounds intact so that they can serve their function in territory maintenance. Apparently, a pair can defend the territory equally well as a large family.

The scent marking communication system therefore appears to play a major role in maintaining territorial borders. An important aspect of the system is that transient beaver and members of neighboring colonies appear to voluntarily avoid areas harboring scent mounds (Müller-Schwarze and Heckman, 1980; Welsh and Müller-Schwarze, 1989).

The scent marking communication system of maintaining territories suggested here is not necessarily the only functional mechanism, as one function need not necessarily exclude others.

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Table 1. Explanation of the terminology used in the text.

Term	Definition
Scent mound	A location (for instance, a pile of mud, vegetation, twigs, leaves or grass) where scent marking was recorded at least once. The minimum distance between separate scent mounds was 10 cm.
Scent marking	Freshly used scent mound, i.e. the characteristic odor was smelled or new vegetation had been deposited on the mound since last check.
Scent mound site	A site with one or more scent mounds. Sites are considered separate if more than 5 m apart.
Neighboring territories	Territories that share a common "water-border", i.e. land borders were not included in the definition (see also Figure 1).

Table 2. The number of neighboring territories, scent mounds, scent mound sites, scent markings, nearest neighbor distance (number of kilometers between main resting-sites), colony size and age (of the pair member that was oldest) at 13 occupied beaver territories in the Biesbosch in 1993.

Territory	Number of neighboring territories	Number of scent mounds	Number of scent mound sites	Number of scent markings	Nearest neighbor distance (km)	Colony size	Age in 1993[c]
A	4	38	25	136	1.2	2	7
B	2	25	21	103	0.8	6 [b]	4
C	3	26	19	91	1.0	4 [b]	12.5
D	3	30	24	81	0.8	8 [b]	12.5
E	2	27	22	88	0.7	2	12.5
F[a]	1	23	16	80	0.7	2	12.5
G[a]	0	4	4	4	2.3	2	12.5
H	1	7	7	7	1.4	2	12.5
I	3	23	18	58	1.1	2	5
J[a]	1	0	0	0	1.5	3 [b]	3

K	3	33	19	119	1.1	2	12.5
L	2	34	23	117	1.0	2	4
M	1	16	16	49	1.0	6[b]	12.5
Total:		286	214	933			

[a] peripheral territories (see Methods and Materials)
[b] breeding beaver territories
[c] beavers released as adults were assumed to be 7.5 years old at the time of release, which was the average age of adults in the Elbe population (Heidecke, 1991)

Table 3. Spearman rank correlation coefficients for the correlation between the number of scent markings (i.e. the y-axis in Figure 4-8; 13 territories) per territory and the 5 parameters listed below (i.e. the x-axis in Figure 4-8) for bi-monthly periods from 16 April to 31 August.

Date	**Number of neighboring territories**	**Number of neighboring individuals**	**Mean distance to all other territories**	**Duration of territory occupancy**	**Length of wooded banks**
16-30 April	0.53	0.57*	-0.40	0.19	0.19
01-15 May	0.57*	0.57*	-0.53	0.35	0.19
16-31 May	0.62*	0.75**	-0.64*	0.62*	0.39
01-15 June	0.75**	0.65*	-0.69**	0.56*	0.54
16-30 June	0.67*	0.55	-0.43	0.57*	0.76**
01-15 July	0.55	0.59*	-0.28	0.27	0.37
16-31 July	0.53	0.74**	-0.55	0.47	0.35
01-15 August	0.86***	0.83***	-0.74**	0.78**	0.70**
16-31 August	0.59*	0.50	-0.37	0.42	0.60*

*0.01<P < 0.05; **0.001<P<0.01 and ***P<0.001

Table 4. Week to week variation in 13 territories in scent mound numbers and locations during the peak period of marking and dispersal by beaver.

Date	Total number of scent mounds	Number of scent mounds at:			
		Feeding-sites	Resting-site	Trail	Other sites[a]
16-22 April	21	5	2	0	14
23-30 April	46	7	6	4	29
01-08 May	44	12	2	3	27
09-16 May	21	7	4	1	9
17-24 May	12	7	0	0	5
25-31 May	19	10	0	0	9

[a] Scent mounds located at various other sites

Figure legends

Fig. 1. Map of the Biesbosch with the locations of radio fixes, sight observations and scent mounds in the summer of 1993 and the delineation of beaver territories based on these data.

Fig. 2. A graphical illustration of the location of zones 1, 2 and 3 with respect to territorial borders. Zone one was located 0-299 m from the border, zone two 300-600 m and zone three > 600 m.

Fig. 3. Pooled data from 13 beaver territories in the Biesbosch showing the mean number of scent markings in three zones at arbitrarily chosen distances from the territorial border. Vertical bars show 95% confidence intervals; N= total number of scent marking in each zone (Kruskal-Wallis one-way ANOVA, X^2=7.23, df=2, P=0.027).

Fig. 4. The relationship between the number of neighboring territories and the number of scent markings for the period 16 April - 31 August 1993 for all 13 beaver territories (r_S=0.753, N=13, P=0.003).

Fig. 5. The relationship between the number of neighboring individuals and the number of scent markings for the period 16 April - 31 August 1993 for all 13 beaver territories (r_S=0.807, N=13, P=0.001).

Fig. 6. The relationship between the mean distance to all other territories and the number of scent markings for the period 16 April - 31 August 1993 for all 13 beaver territories (r_S=-0.710, N=13, P=0.007).

Fig. 7. The relationship between the duration of territory occupancy in years, for the pair member that established first, and the number of scent markings for the period 16 April - 31 August 1993 for all 13 territories (r_S=0.601, N=13, P=0.030).

Fig. 8. The relationship between the length of wooded banks within the territory and the number of scent markings for the period 16 April - 31 August 1993 for all 13 territories (r_S=0.575, N=13, P=0.040).

Fig. 9. Bi-monthly changes in the mean number of scent markings for all 13 territories combined for the period 16 April - 31 August 1993 (Kruskal-Wallis one-way ANOVA, X^2=7.38, *df*=8, P=0.497). Vertical bars show 95 % confidence limits; N= total number of scent markings. The date notation 16-30.4 indicates 16 April to 30 April.

Fig. 2, Rosell and Nolet

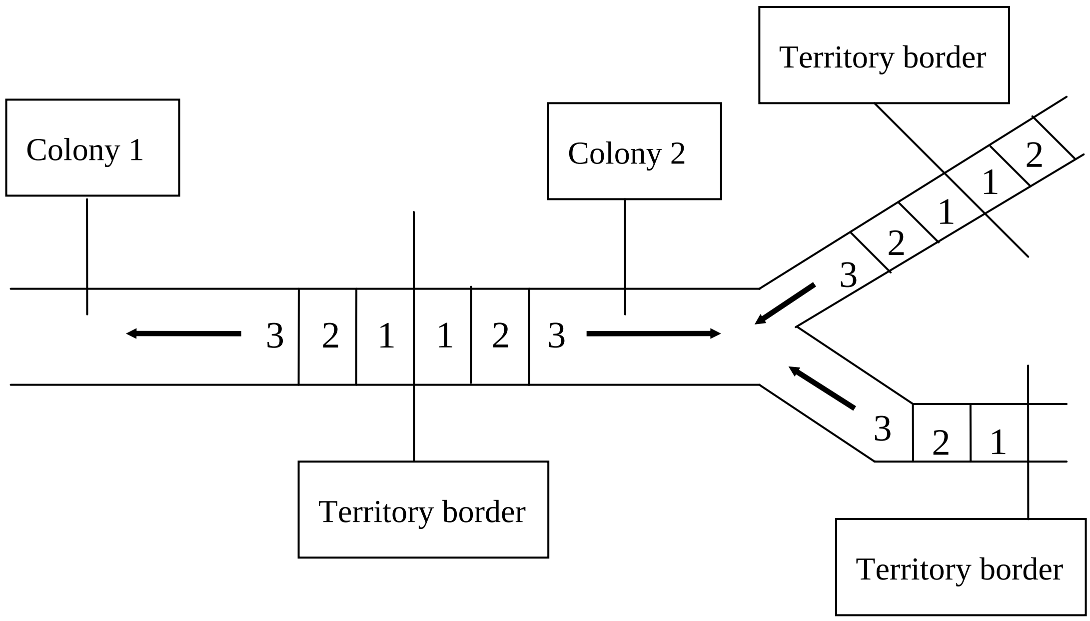

Fig. 3, Rosell and Nolet

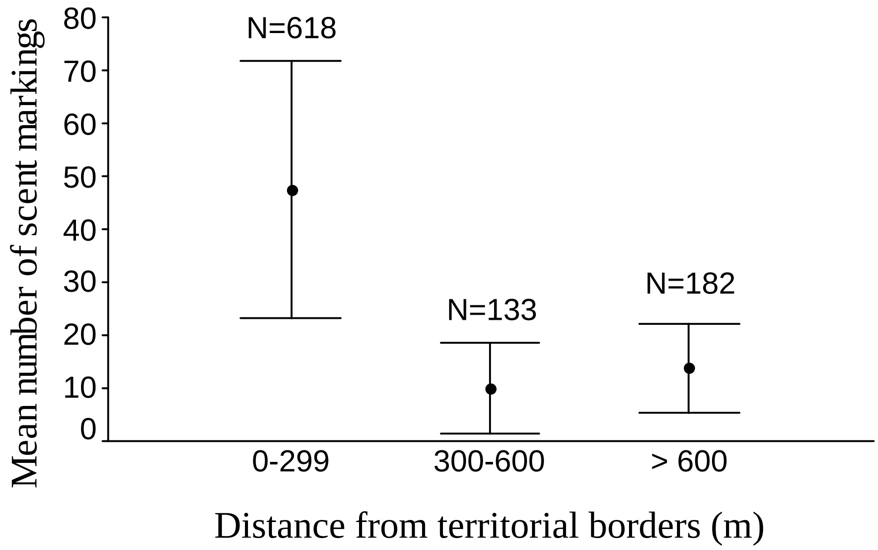

Fig. 4, Rosell and Nolet

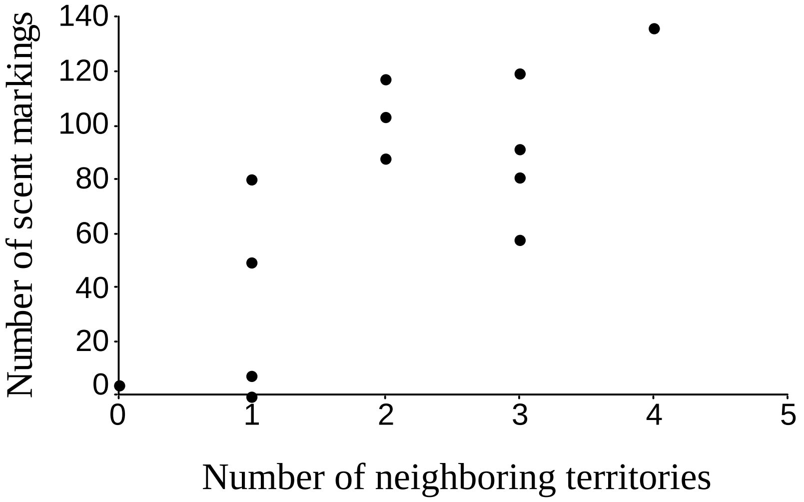

Fig. 5, Rosell and Nolet

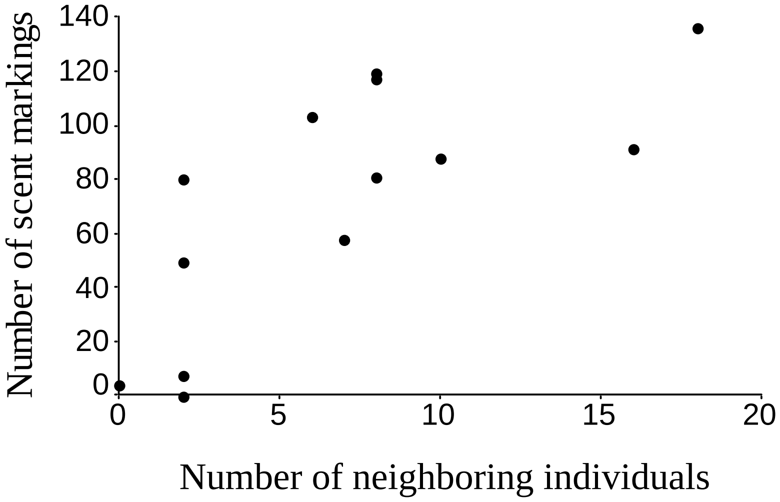

Fig. 6, Rosell and Nolet

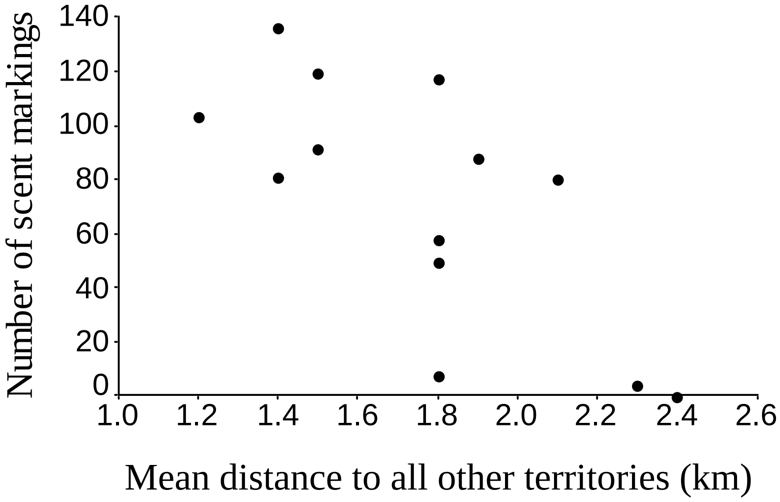

Fig. 7, Rosell and Nolet

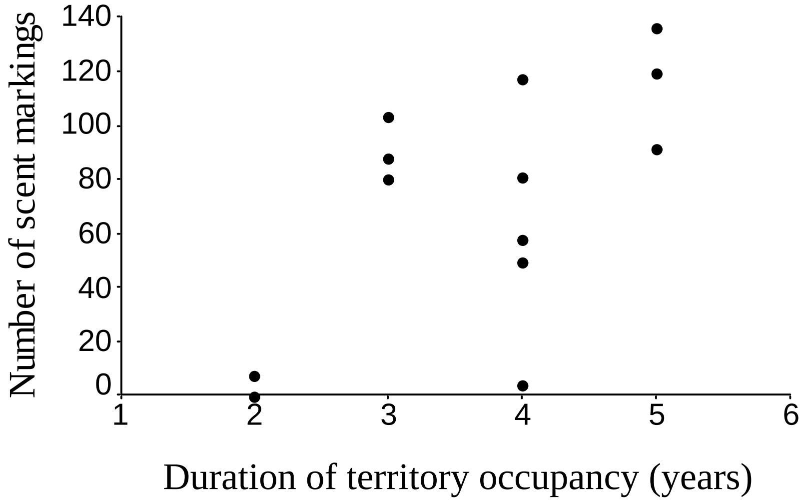

Fig. 8, Rosell and Nolet

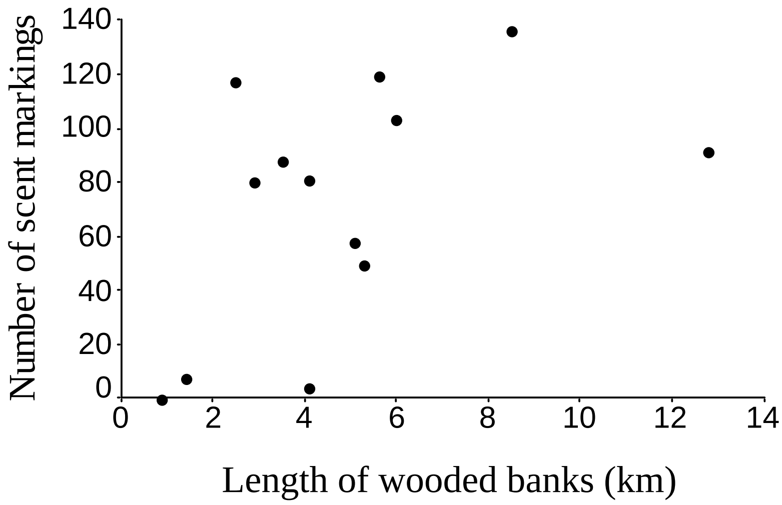

Fig. 9, Rosell and Nolet