



Research article

Determinants of reproductive success in voles: space use in relation to food and litter size manipulation

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Received 1 November 2001; accepted 11 June 2002

Co-ordinating editor: P. Lundberg

Abstract. Spacing behaviour of female mammals is suggested to depend on the distribution and abundance of food. In addition, food limitation has been found to constrain the reproductive success of females. However, whether females maximize their reproductive success by adjusting space use in relation to current food availability and reproductive effort (e.g. litter size) has not been experimentally studied. We examined these questions by manipulating simultaneously food resources (control vs. food supplementation) and litter sizes (control vs. plus two pups) of territorial female bank voles (*Clethrionomys glareolus*) in large outdoor enclosures. Females with supplementary food had smaller home ranges (foraging area) and home range overlaps than control females, whereas litter size manipulation had no effect on space use. In contrast, the size of territory (exclusive area) was not affected by food supplementation or litter size manipulation. As we have previously shown elsewhere, extra food increases the reproductive success of bank vole females in terms of size and proportion of weaned offspring. According to the present data, greater overlap of female home ranges had a negative effect on reproductive success of females, particularly on survival of offspring. We conclude that higher food availability increases the reproductive success of bank vole females, and this effect may be mediated through lower vulnerability of offspring to direct killing and/or detrimental effects from other females in the population. Moreover, it seems that when density of conspecifics is controlled for, home range sizes of females, but not territoriality, is related to food resources in *Clethrionomys* voles.

Key words: *Clethrionomys*, food limitation, litter size manipulation, *Microtus*, reproductive success, spacing behaviour, territoriality, voles

Introduction

According to large number of studies conducted in avian and mammalian species, food abundance and distribution play a significant role in shaping the reproductive strategies of individuals (reviewed in Martin, 1987 and Boutin, 1990). As reproduction is in general limited by food resources, experiments

often report higher reproductive success (offspring growth and/or survival) for females with supplemental food (e.g. Doonan and Slade, 1995; Duquette and Millar, 1995; Koskela *et al.*, 1998). In some studies females have also been found to increase their reproductive effort with an increase in food (nutrient) availability (e.g. Dobson and Kjelgaard, 1985; Batzli, 1986; Doonan and Slade, 1995).

Additionally, food is considered as one of the most important factors affecting spacing behaviour in breeding female mammals (Ostfeld, 1985, 1990; Ims, 1987; Maher and Lott, 2000). The general trend from experiments where food resources have been manipulated show that female home range size is largely a function of resource availability (reviewed in Boutin, 1990, see also Maher and Lott, 2000). However, while the food resources and thus possibly the reproductive effort of females increase with home range (territory) size, so does the costs of space defence. Consequently, to maximize reproductive success, space use of territorially breeding females should be adjusted in relation to food availability as well as their reproductive effort.

The data relating measures of space use and aspects of reproductive success are almost totally lacking in small mammals. This is surprising considering the vast number of capture–recapture studies conducted particularly in voles during the past decades (for references see e.g. Bondrup-Nielsen, 1985; Norrdahl, 1995). Breeding success of females has previously most often been estimated on the basis of the number of pregnancies or by determining the number of weanlings in the population (e.g. Gliwicz, 1990; Mappes *et al.*, 1995b; de la Maza *et al.*, 1999; Prévot-Julliard *et al.*, 1999), and only some studies have utilized radionuclide labelling techniques (e.g. Sheridan and Tamarin, 1988; Ostfeld *et al.*, 1988; Pusenius *et al.*, 1998) or marked individually new-born pups (e.g. Lambin and Krebs, 1993; Mappes *et al.*, 1995a; Oksanen *et al.*, 2001). Ideally, adequate investigation of the relationship between spacing behaviour and reproductive success would require monitoring of individually marked females and their pups in a free-living population. This has been methodologically difficult, and only few studies have experimentally tried to focus on these mechanisms e.g. by manipulating spacing behaviour through density manipulation and studying the subsequent reproductive success of individuals (Koskela, *et al.*, 1999).

In this paper we studied two main questions. First, we examined whether female bank voles adjust their space use according to food availability and reproductive effort. This was studied in a fully factorial experiment where the food resources (control vs. supplemental) and the litter sizes (control vs. + two pups) of nursing females were manipulated in large outdoor enclosures. Secondly, we relate the results on space use to the reproductive success of females. As we have previously shown (Koskela *et al.*, 1998), extra food

increases the reproductive success of bank vole females in terms of size and proportion of weaned offspring. Here we study whether the differences in reproductive success of females under different food conditions are due to different patterns of space use. In this paper we define home range as a foraging area, usually overlapping, whereas territory is part of home range and mutually exclusive apart from other females. Territory could also be considered as a breeding area. These definitions are in accordance with the general definition of female territoriality in small mammals (Kaufmann, 1983) and that earlier used in the bank vole (Koskela *et al.*, 1997; Bujalska and Saitoh, 2000).

Methods

Study site and animals

The study was conducted during June–September 1997 at Konnevesi, central Finland (62°37'N, 26°20'E). Two separate runs of the experiment were performed in eight 0.25 ha enclosures, all located in a homogenous field (for details of the enclosures see Koskela *et al.*, 1997). The enclosures were surrounded by a galvanized metal sheet approximately 1 m high and buried 0.5 m deep, to prevent escape and entering of other animals (such as mustelid predators). The enclosures are large enough to enable normal space use (i.e. reproducing females have exclusive territories, Koskela *et al.*, 1997) and reproduction of bank vole females compared to natural populations (Bondrup-Nielsen and Karlsson, 1985; Mappes *et al.*, 1995b). To monitor the animals (individually marked by ear tags), 25 Ugglan multiple-capture traps were placed in a 5 × 5 array with a trap interval of 10 m in each enclosure. Traps were baited with sunflower seeds and potatoes, and covered with a metal trap chimney. The study animals were trapped from the forest nearby during the spring. To get pregnant females for the study, females were paired at the same time both in the enclosures and in the laboratory. Before parturition, all females were brought into the laboratory to give birth. The proportion of pregnant females from the enclosures ($n = 43$) and the laboratory ($n = 21$) were equally assigned to the different treatment groups. There was no difference in initial body mass, size (width of the head) or initial litter size between females mated in enclosures or laboratory (t -test, $p > 0.2$ for all variables).

Study design

At the start of the study, pregnant females were inspected twice a day for the actual time of parturition. Pups were individually marked, weighed and

cross-fostered to randomise the prenatal maternal effects on their further performance. In the bank vole the survival or growth of pups does not differ between a female's own pups and foreign pups (Mappes *et al.*, 1995a). The litter size of females was manipulated by either giving the female an original or an enlarged litter size (with two extra pups). In each enclosure we had two control females and two females with enlarged litter size. To manipulate food resources we had two treatments: supplemental food and control, where no extra food was available. Thus, as a result of manipulations (in both study runs) we had four food-supplemented enclosures and four control enclosures, with four females in each, two females with unchanged litters and two with enlarged litters (16 females per treatment, total $n = 64$).

Extra food was supplied in wire-mesh feeders placed at each trap station (inside the rain-proof trap chimney) in four out of eight enclosures. Each feeder contained laboratory rodent chow (Labfor R36) *ad libitum*, and was constructed so that the voles could not hoard the food. The feeders were removed after 20 days, when the weanlings still were too young to utilize them. There was no difference in initial litter size of females (before manipulation) between the runs and the treatment groups (three-way ANOVA, run: $F_{(1,59)} = 0.83$, $p = 0.367$, food: $F_{(1,59)} = 0.05$, $p = 0.821$, litter: $F_{(1,59)} = 0.47$, $p = 0.498$, food by litter: $F_{(1,59)} = 0.47$, $p = 0.498$). Neither was there significant difference in the size of the females (weight and width of head) between treatments (two-way ANOVA, p for all > 0.23).

Females with their litters (about 1–3 days old) were released at the same time into the enclosures. Each female with her litter was transferred in a breeding cage and placed in one corner of the enclosures under a rainproof cover. On the following day, cages were opened so the female could carry the pups to a safe place. Four days after the release of the voles, the spacing behaviour of the females (home range size, home range overlap and territory size) was monitored during 10 trappings. To minimize the disturbance to the females during early lactation we trapped three times per day (late evening, midnight and early morning) and in between the morning and evening trapping the traps were left opened. During trapping we recorded identity, reproductive condition, body weight and trap station for each individual and directly after that we released the vole at the trap site. Home range size was estimated using the minimum convex polygon method (Kenward, 1987) while the home range overlap was measured as the home range area shared by neighbouring females. The amount of exclusive space (territory size) was estimated as the difference between the female home range size (foraging area) and the home range overlap. The trappability of females was calculated as number of captures per total number of trappings. We observed no difference in the number of females caught (trappability) between the treatment groups (mean \pm SD for all females: $79 \pm 2\%$, three-way ANOVA, run: $F_{(1,56)} = 0.51$, $p = 0.477$, food: $F_{(1,56)} =$

0.46, $p = 0.503$, litter: $F_{(1,56)} = 0.19$, $p = 0.661$, food by litter: $F_{(1,56)} = 1.58$, $p = 0.214$). Moreover, trappability did not correlate with any of the spacing behaviour variables (Spearman: p for all variables > 0.3).

At the end of the first run of the experiment, we trapped out all weanlings (about 30 days of age) and adult females from the enclosures. The second run started once the enclosures were empty, using the same experimental design, but with new females. The assignment of enclosures into food and control treatments was switched between study runs.

Data analysis

As a result of manipulations (in both study runs), we had four food-supplemented enclosures and four control enclosures with four females in each, two females with unchanged litters and two with enlarged litters. The space use of nursing females (home range size, home range overlap, territory size) in relation to the treatments were studied using ANOVA models, where study run and food and litter size manipulations were entered as fixed factors and enclosure as a random factor. The relationship between space use and breeding success of females (proportion and number of weaned offspring, offspring body mass at weaning) was studied using ANOVA models, where breeding success variables were dependent variables (one at a time) and study run, food and litter size manipulations and enclosure (random factor) were explaining factors and spacing behaviour variables covariates. This leads to obtaining nine probability levels addressing basically the same null hypothesis, and rejection of the null hypothesis is possible when only some of the tests are found to be individually significant (Rice, 1989). To control for this, we used meta-analytic techniques which are considered as powerful tool to combine the results of multiple experiments when publication bias does not exist (e.g. Kotiaho and Tomkins, 2002). The three probability levels obtained for each space use variable were combined to give an overall test of significance for the set of three analyses using the technique described in Rosenthal (1991). The corresponding Z 's values of (one-tailed) p -values were first summed and then divided by the square root of number of tests (notice that the Z 's will have the same sign only when all studies show effects in the same direction). This new Z corresponds to the p -value that the results of the three analyses combined could have occurred if the null hypothesis of no relationship between space use and breeding success were true.

To meet the assumptions for parametric tests, the spacing behaviour variables were $\sqrt{x + 0.5}$ and the proportion of weaned offspring variable arcsine square root transformed before analyses. Only the individuals that were alive throughout the study were used in the analyses ($n = 54$). All the tests were two-tailed.

Results

Females in food-supplemented enclosures had smaller home ranges than control females, whereas there was no difference between the litter size manipulation groups (Fig. 1, Table 1). Moreover, the home range overlap be-

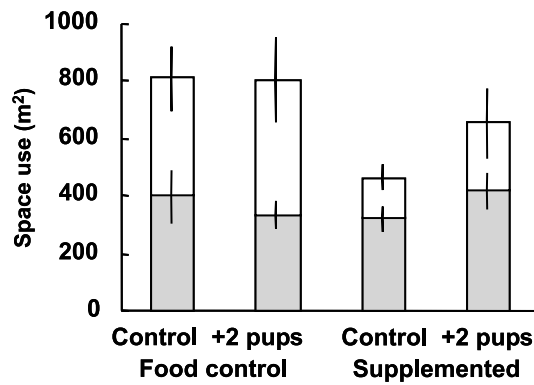


Figure 1. The space use of female bank voles in different treatments. Bars show the home range size (mean \pm SE) divided into overlapping area (white) and territory size (grey). For statistics see Table 1.

Table 1. Spacing behaviour of females in relation to the manipulation groups. Run = study period, food = control/supplemented, litter = control/enlarged litter

	d.f.	MS	F	p
Home range size				
Run	1, 42	71.40	1.69	0.200
Food	1, 42	205.14	4.87	0.033
Litter	1, 42	61.25	1.45	0.235
Food \times litter	1, 42	31.90	0.76	0.389
Enclosure	7, 42	41.859	0.99	0.449
Overlap				
Run	1, 42	581.63	10.80	0.002
Food	1, 42	394.05	7.32	0.010
Litter	1, 42	42.58	0.79	0.379
Food \times litter	1, 42	0.01	0.00	0.991
Enclosure	7, 42	183.05	3.40	0.006
Territory size				
Run	1, 42	2.06	0.04	0.838
Food	1, 42	0.464	0.01	0.923
Litter	1, 42	23.45	0.48	0.491
Food \times litter	1, 42	36.17	0.74	0.393
Enclosure	7, 42	76.16	1.58	0.172

Enclosure added in the models as a random factor.

Table 2. The relationship between space use and reproductive success in female bank voles

	Weaning success		Offspring number		Offspring body mass		Overall test of significance	
	<i>F</i>	<i>p</i>	<i>F</i>	<i>p</i>	<i>F</i>	<i>p</i>	<i>Z</i>	<i>p</i>
HR size	1.10	0.301	0.63	0.432	1.05	0.314	1.63	0.103
HR overlap	4.28	0.045	3.46	0.070	3.66	0.067	3.26	0.001
Territory size	0.00	0.955	0.04	0.845	0.06	0.804	0.00	1.000

Values give the statistics for covariates in ANOVA models where breeding success variables were dependent variables (one at a time) and study run, food and litter size manipulations and enclosure (random factor) were explaining factors. For overall test of significance see Methods.

tween neighbouring females was smaller with supplemental food, whereas again no difference between litter size manipulation groups was found (Fig. 1, Table 1). Territory size of the females did not differ between the treatment groups (Fig. 1, Table 1).

As reported in Koskela *et al.* (1998), females with food supplementation significantly increased their weaning success (proportion of weaned young per litter). Enlarging the litter size decreased the size of weaned offspring, but if food was simultaneously supplemented, offspring body mass was unaffected by litter enlargement (see details in Koskela *et al.*, 1998). Consequently, food abundance affected both the space use and reproductive success of females. According to the nine separate analyses of the relationship between the reproductive success (proportion, number or body mass of weaned offspring) and space use of the females, the mothers with less overlapping home ranges had significantly higher weaning success (Table 2), although the effect seems quite weak (Fig. 2). Moreover, there was a tendency that lower home range overlap had positive effects on offspring number and body mass. An overall test of significance (see methods) revealed a significant negative relationship between the home range area shared by neighbouring females and the reproductive success of mothers (Table 2).

Home range size correlated significantly with home range overlap and territory size (Overlap: $r_s = 0.595$, $n = 54$, $p < 0.001$; Territory: $r_s = 0.535$, $n = 54$, $p < 0.001$), and there was also a tendency that females with larger shared area had smaller territories ($r_s = -0.243$, $n = 54$, $p < 0.077$). Female spacing behaviour (home range size, overlap, territory size) at lactation did not correlate with their (post-partum) weight (Spearman, p for all >0.3).

Discussion

In this experiment, we manipulated the reproductive effort and food resources of nursing bank vole females in outdoor enclosures. According to the results

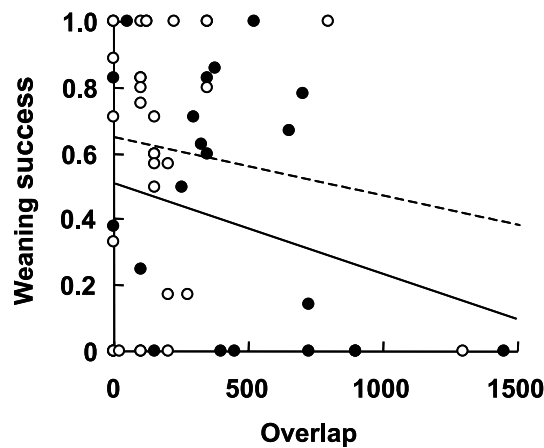


Figure 2. Weaning success of females (proportion of weaned offspring) plotted against home range overlap. Dashed line = food supplemented females, solid line = control females. For statistics see Table 2.

females had smaller home ranges when supplemental food was available. This agrees with earlier studies conducted on open grids where the extra food was evenly distributed (Andrzejewski and Mazurkiewicz, 1976; Taitt, 1981; Taitt and Krebs, 1981; Henttonen, 2000). However, in these studies food supplementation led also to an increase in population density which confounds the conclusions. For instance, out of 11 food addition studies in mammals listed in Boutin (1990) all but one report decrease in home range size. However, as Boutin points out, the general conclusion of food addition leading to a decrease in home range size is hampered by uncontrolled effect of changing density on spacing behaviour of individuals. In their experiment with *Microtus pennsylvanicus* Fortier and Tamarin (1998) aimed to separate the effects of food and density on space use patterns by using a two-by-two factorial design, where both the density and food resources were manipulated. Unfortunately, due to methodological problems they did not obtain data on treatment group 'high density – non-supplemented'. Consequently, their conclusion that breeding female voles do not adjust their spacing behaviour to food resources can only be generalized to low population densities, where food resources are not necessarily limiting reproduction (Fortier and Tamarin, 1998). Moreover, because of large differences in the diets of *Microtus* and *Clethrionomys* species (see below), the importance of food abundance on spacing patterns may also differ between these two genera (Ostfeld, 1985).

The present study did not show any significant relationship between litter size enlargement and space use of nursing females. This supports the earlier findings in Mappes *et al.* (1995a), where the sizes of home ranges did not change from pregnancy to lactation as a function of artificial reduction or

enlargement of litter size. These results are slightly unexpected having in mind that, as in many other vole species, the breeding success of bank vole females is constrained by food abundance (Koskela *et al.*, 1998) and larger home ranges should in general provide more food. One explanation for lack of relationship between litter size and home range size may be density-dependent factors: in saturated breeding density females cannot increase the size of their home ranges (Mappes *et al.*, 1995a). Koskela *et al.* (1999) studied this hypothesis by manipulating simultaneously the litter size and breeding density of bank vole females. In general, lactating females responded to the reduced density by increasing the sizes of their home ranges. However, enlargement of litter size had no significant effects on spacing behaviour of females even in low density enclosures, where they were not constrained by high breeding density. Together these earlier and present results indicate, that bank vole females do not adjust their home range or territory size according to their reproductive effort during nursing period. A simple explanation for this might be that costs of patrolling over a larger home range exceed the benefits because energy spent gathering resources would be greater than energy gained. This conclusion is not necessarily universal, as net benefits of enlarged home range size are dependent on habitat quality as well as the patchiness of resources.

Successful adjustment of space use to the current ecological settings could be reflected in higher reproductive success. In the present data, the reproductive success of females increased with supplemental food in terms of offspring size and proportion of weaned offspring (Koskela *et al.*, 1998). The causal effects affecting reproductive success were further studied by relating the results on space use to the reproductive success of individual females. Our study gives relatively weak, although significant, evidence that low home range overlap is beneficial for female reproductive success, particularly in terms of proportion of survived offspring until weaning. This result is not necessarily easy to relate to other territorial mammals, mostly because of lack of earlier data.

Ostfeld *et al.* (1988) used radiotelemetry and radionuclide-electrophoresis to investigate sex differences in space use and reproductive success in a population of meadow voles *Microtus pennsylvanicus*. The main finding of their study was that females who successfully weaned offspring had smaller home ranges than unsuccessful females. The similar result in the same species was found by Sheridan and Tamarin (1988) using radionuclide-electrophoresis and live-trapping data. In the study by Pusenius *et al.* (1998) field voles *Microtus agrestis* living further away from neighbouring (founder) females had better reproductive success. This result is supported by Mappes *et al.* (1995b), where number of recruits per birth was positively correlated with the distances between the nearest breeding (non-kin) bank vole females. Although these earlier studies demonstrate that females with different reproductive (weaning) success

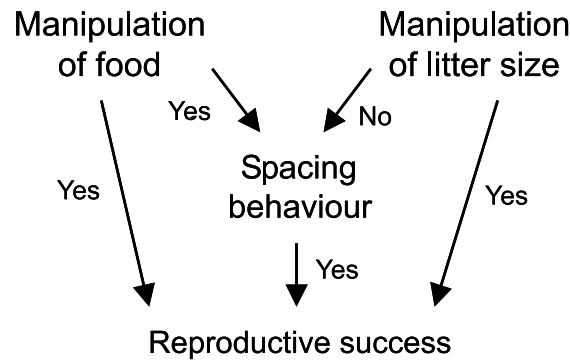


Figure 3. The design and conclusions of the present study. We manipulated the food resources and the litter sizes of territorial bank vole females. Food affects both the reproductive success and spacing behaviour of females, and different patterns of space use may serve as one mechanism explaining higher breeding success when high quality food is abundant.

differ in their space use, there has been no experiments studying the causality of this relationship. Our results indicate, as suggested already in Koskela *et al.* (1998), that spacing behaviour may in fact serve as a potential mechanism leading to higher reproductive success in conditions of high food availability (Fig. 3). Abundant evidence indicates that adult microtines, particularly females, are the major cause of poor juvenile survival in the field (e.g. Boonstra, 1978; Galindo and Krebs, 1987; Rodd and Boonstra, 1988; Lambin and Yoccoz, 1998). Consequently, we suggest that in conditions of high food abundance, smaller home range overlap between adult females may decrease disturbance towards juveniles and/or result in smaller risk of infanticide, which then leads to higher reproductive success.

Although *Clethrionomys* voles have a great variability in their food preferences from grasses and forbs to seeds, lichens and fungi, their diet is generally considered as semi-granivorous. The *Microtus* species, on the other hand, are often considered as true folivores, whose staple food consists mainly of grasses and forbs (Larsson and Hansson, 1977; Hansson, 1985a). In both genera large geographical changes in food supply take place when moving from temperate deciduous forests to boreal conifer forests (Hansson, 1985b; Hansson *et al.*, 2000). It could be expected that the further to the granivore end a vole species lies along the folivore–granivore axis, the higher the degree of resource limitation and the stronger the behavioural and reproductive responses to food manipulation (Oksanen *et al.*, 2000). More restrictive food quality requirements of *Clethrionomys* compared to *Microtus* voles in boreal habitats could even cause that bank voles would have a greater potential for reducing home range size (foraging area) as a response to appearance of high quality food. Unfortunately, although the significance of food generating regional differences in bank vole dynamics in Europe is well documented (reviewed in

Hansson *et al.*, 2000), the data describing concurrent changes in spacing patterns is either scarce or totally lacking and at present does not allow accurate testing of this idea.

The present results could also be interpreted taking into account the ongoing debate on the proximate and ultimate causes of territoriality in female mammals (Ostfeld, 1985; Ims, 1987; Ostfeld, 1990; Bujalska, 1991; Wolff, 1993; Koskela *et al.*, 1997; Tuomi *et al.*, 1997; Agrell *et al.*, 1998; Wolff and Peterson, 1998; Fortier and Tamarin, 1998). The food-defence hypothesis states that the distribution and abundance of food determine the spacing behaviour of the female voles (Ims, 1987; Ostfeld, 1990). An alternative hypothesis explaining territoriality is the pup-defence hypothesis, where females defend space to deter infanticide (Wolff and Cicirello, 1989; Wolff, 1993). Our result that home range sizes were dependent on the availability of food is in accordance with the food-defence hypothesis. On the other hand, in contrary to earlier expectations (Ostfeld, 1985), territory sizes were independent of food abundance indicating that the exclusive space serves some other function for breeding females (e.g. protection against infanticide). Our data also supports suggestion (Yoccoz *et al.*, 2001) that social system of bank voles is not affected by food supplementation. Nevertheless, as our experiment was not specifically designed to study the evolution of territoriality, the present results cannot refute or accept either the food or infanticide hypotheses. Testing of these hypotheses in voles requires experiments (preferably both in *Microtus* and *Clethrionomys* species) where territorial or infanticidal behaviour is directly manipulated.

To conclude, we studied the relationships between food resources, spacing behaviour and reproductive success in bank vole females. Our experiment suggests that breeding females adjust their spacing behaviour in relation to food abundance but not according to their litter size. Food resources influence the spacing behaviour of breeding females and limit their nursing effort, and different patterns of space use may serve as one mechanism explaining higher breeding success when high quality food is abundant. Moreover, in the conditions where density of conspecifics is controlled for, home range size, but not territoriality, is related to food resources in female bank voles.

Acknowledgements

We thank G. Bujalska, T. Horne, L. Lindström, J. Mappes, L. Oksanen and one anonymous referee for valuable comments on the manuscript. Konnevesi Research Station provided facilities for this study. The study was supported financially by the Academy of Finland (grant no. 63789), H-Axelson foundation, Royal Academy of Sweden, the Swedish Institute and Collianders foundation.

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