Population ecology of the raccoon dog in Finland - a synthesis

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REVIEW Because of its applied character, wildlife science needs opportunities to summarise existing knowledge by reviewing, either by presenting leading ideas and results of study teams, or summarising advanced knowledge of selected scientific or management problems. Reviews should be concise.

Population ecology of the raccoon dog in Finland - a synthesis

Kaarina Kauhala & Eero Helle

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The population ecology of the raccoon dog *Nyctereutes procyonoides* was investigated in Finland from 1973 to 1992. Annual mean temperature explained most of the regional variation in the growth rate and present density of the population. Climate explained most of the regional variation in the productivity of the raccoon dog population; the length of the annual snow-free period accounted for most of the regional variation in the weight and fat reserves of young females in late autumn which, in turn, affected the proportion of reproducing females in the population the following spring. Of the independent variables examined, the abundance of wild berries is the dominating factor in explaining the annual variation in density; mortality is highest during the first year of life and the availability of berries probably affects the mortality of juveniles during autumn and winter. The abundance of voles and the population density of raccoon dogs in spring affects the fat reserves of adult females which, in turn, affect their litter size. The productivity of adult females is density dependent, and, thus, regulates population density to some extent. Changes in population size seem to be density dependent after the population peaked around the mid-1980s.

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The raccoon dog *Nyctereutes procyonoides* Gray, 1834 originally comes from eastern Asia, but in 1935-53 it was introduced to the northwestern parts of the former Soviet Union (Lavrov 1971). Many of the introductions were successful and the populations increased rapidly in the new areas. It did not take long before the raccoon dog started spreading to neighbouring countries, Finland among them, and the southern and central parts of Finland were colonised by the mid-1970s (Helle & Kauhala 1991).

We studied the factors affecting variation in both the growth rate and density of the raccoon dog population in Finland after the first phase of rapid increase. This paper is a synthesis partly based on previously published papers (for distribution history, see Helle & Kauhala 1991, for weight and fat indices, see Kauhala 1993, for life tables, see Helle & Kauhala 1993, and for data on productivity, see Helle & Kauhala 1995). Some new data (e.g. annual density from Häme and more years from the other provinces) and new analyses have also been added; prior to the present study, the factors determining the population size of the raccoon dog have not been analysed in detail.

Material and methods

Population abundance and carcass material

The abundance of the raccoon dog population in Finland was examined using game inquiries conducted in 1955-92. The game inquiries are organised by the Finnish

Game and Fisheries Research Institute in order to monitor the abundance of different game species from year to year. In these, ca 500 observers were asked to estimate the abundance classes of raccoon dogs in their observation area each year in March using one of the following designations: »absent« = 0, »rare« = 1, »moderate« = 2, »abundant« = 3. The maximum value of the abundance index calculated from game inquiries is 3, and the minimum value is 0 (more details of game inquiries are explained e.g. in Helle & Kauhala 1991).

The abundance indices derived from game inquiries present some problems, because opinions regarding abundance levels are subjective and may change with time (e.g. Siivonen 1951, Wirén 1974, Caughley 1977, Lindén 1988). However, these indices were used for relatively short periods only, and the same observers were used. Furthermore, we compared the abundance indices to trap-indices (raccoon dogs captured per 100 trap-nights, Helle & Kauhala 1991) both by province and annually in the province of Häme in 1987-91. The abundance and trap-indices were normally distributed (Kolmogorov-Smirnov test) and correlated with each other both regionally ($r = 0.84$, $P = 0.002$, $n = 10$) and annually ($r = 0.93$, $P = 0.023$, $n = 5$), indicating that the results of game inquiries are reliable for the present purpose.

We studied the productivity of females (litter size x proportion of reproducing females), age, weight and fat reserves of raccoon dogs by examining carcasses ($n = 3655$) collected by hunters in the provinces of Turku-Pori, Uusimaa, Häme, Kymi, North Karelia and Oulu (see the map in Fig. 2 for location) in 1986-92. For age determination, see Kauhala & Helle (1990), for determining the weight and fat reserves, see Kauhala (1993), and for determining litter size and proportion of reproducing females, see Helle & Kauhala (1995).

We also calculated a life table starting from the number of ova ovulated in order to establish the mortality rate at different stages of the life cycle. For details concerning the life table, see Helle & Kauhala (1993).

Environmental variables

Factors affecting abundance (regionally and annually) and population growth rate (regionally) were examined using stepwise regression analyses. The numerical values of the growth rate were the slopes of regression lines calculated for the phase when the most rapid increase took place (see also Helle & Kauhala 1991: Fig. 3).

The effects of different variables on the annual variation in density were examined in five provinces during the whole study period and in three intervals according to the trends in the populations (Fig. 1): (I) the period after the first peak in the 1970s (1973 in Kymi and Oulu, and 1976 in Mikkeli and North Karelia) when the population was either decreasing (Kymi and Mikkeli) or rather stable (North Karelia and Oulu), (II) the phase of increase in the 1980s (1981-1986 in Kymi, 1983-1986 in North Karelia, and 1982-1987 in Mikkeli and Oulu) and (III) the period after the second peak in the mid-1980s (altogether 170 regressions). In the province of Häme the population did not peak until the mid-1980s, and the analysis was based on data from the period after the population peak only. We also studied the effect of density on the change in density during periods I (also in Häme) and III, the latter representing a period of higher population density. The number of observers each year were 37-54 in Häme, 42-60 in Kymi, 23-46 in Mikkeli, 42-80 in North Karelia and 45-106 in Oulu.

The independent variables were selected for the analyses using a correlation matrix (altogether 2057 correlations). The climatic variables were: annual mean temperature, snow depth at the end of March, duration of the snow cover, and number of days with a maximum temperature below zero. When examining regional variation, we used the means of the climatic variables and abundance indices for 1985-90. When the annual variation in numbers was tested, data concerning all the climatic var-

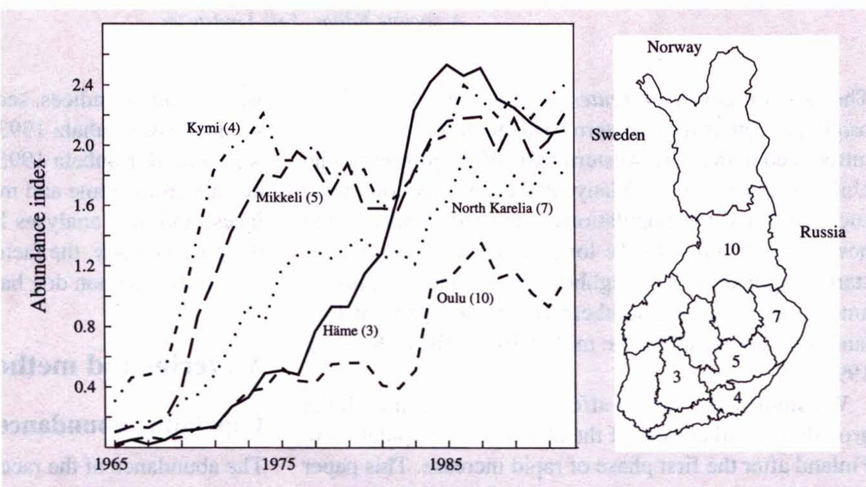

Figure 1. Changes in raccoon dog abundance in five Finnish provinces from 1965 to 1992 according to game inquiries (See Helle & Kauhala 1991 for game inquiries, and the legend of Fig. 2 for names of provinces).

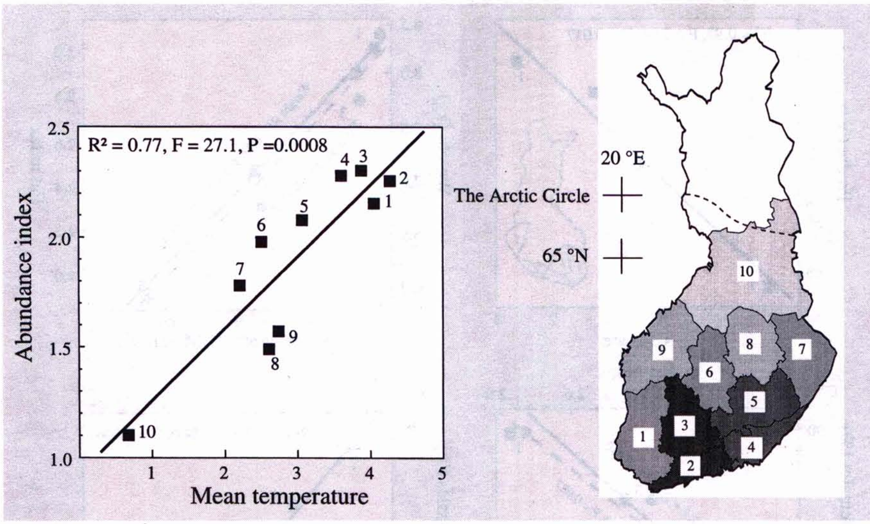

Figure 2. Relationship between the abundance index and the annual mean temperature in 10 Finnish provinces (Y = 0.33x + 0.93) and the present relative density of the raccoon dog in Finland 1987-91 (map), based on both the abundance index and the trap index; for calculation of indices, see Helle & Kauhala (1991). The relative density gives the order from the highest to the lowest density, calculated by province. The dotted line roughly indicates the true northern distribution limit. Provinces: 1 = Turku-Pori, 2 = Uusimaa, 3 = Häme, 4 = Kymi, 5 = Mikkeli, 6 = Central Finland, 7 = North Karelia, 8 = Kuopio, 9 = Vaasa, 10 = Oulu.

iables were from the previous calendar year. The climatic variables were based on Meteorological Yearbooks of Finland (the Finnish Meteorological Institute 1973-1992).

The other independent variables were: abundance of voles (mainly *Microtus* and *Clethrionomys* sp.) in March, abundance of wild berries (bilberries, *Vaccinium myrtillus*, and lingonberries, *V. vitis-idaea*) the previous autumn (voles and berries are among the main food items of the raccoon dog (Kauhala et al. 1993), the abundance of red fox *Vulpes vulpes*, badger *Meles meles* and lynx *Lynx lynx* in March (potential competitors or predators), and size of the annual catch of raccoon dogs during the previous hunting season. The abundances of voles, red fox, badger and lynx were tested both without a time-lag and with a time-lag of one year. All information except that on the annual catch, which was based on data from the Finnish Game and Fisheries Research Institute, was taken from game inquiries, a nationwide monitoring method organised by the Finnish Game and Fisheries Research Institute, described by e.g. Helle & Kauhala (1991). The numerical values (abundance indices) calculated on the basis of game inquiries are in the archives of the Finnish Game and Fisheries Research Institute. The data are too extensive to be presented here in full, but the original data can be obtained from the authors on request. To explain in what way the variables selected in the models affect the growth rate or density of the population, we tested their effect on the weight, condition (fat index) and productivity of raccoon dog females with regression analyses.

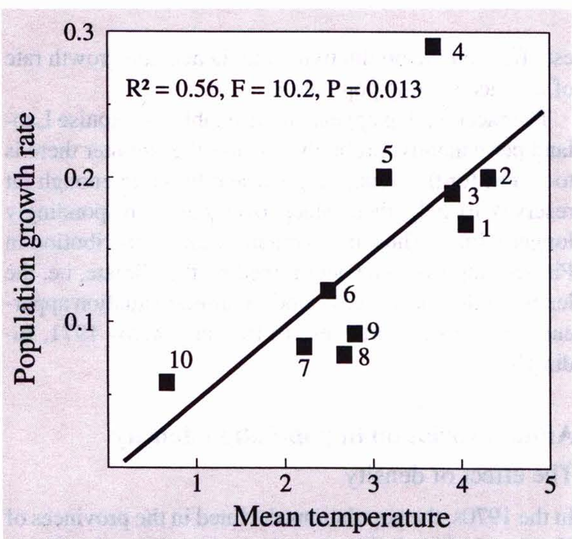

Figure 3. Relationship between the growth rate of the population and the annual mean temperature in 10 Finnish provinces (Y = 0.05x - 0.005). The numerical values for the growth rate are the slopes of regression lines calculated for the period with the most rapid increase. (See the legend of Fig. 2 for the names of the provinces.)

Results and discussion

Regional variation in population growth and present density

The population growth rate was highest in southern and southeastern Finland, and lowest in the province of Oulu (Lapland excluded) (Helle & Kauhala 1991). The slopes of the regression lines calculated for the phase of rapid increase in various provinces were: Kymi 0.29, Mikkeli and Uusimaa 0.20, Häme 0.19, Turku-Pori 0.17, Central Finland 0.12, Vaasa 0.09, Kuopio and North Karelia 0.08, and Oulu 0.06 (see also Fig. 1). The present density of the raccoon dog is highest in southern Finland, especially in the provinces of Häme and Uusimaa (Fig. 2). The northern limit of permanent distribution lies between 65°N and the Arctic Circle; the raccoon dog is rare in Lapland, the northernmost part of Finland.

The annual mean temperature offered a good explanation of the regional variation in the growth rate of the population (R^2 = 0.56, F = 10.2, P = 0.013, Fig. 3), but all climatic variables correlated with each other. The annual mean temperature offered an even better explanation of the regional variation in raccoon dog density in Finland (R^2 = 0.77, F = 27.1, P = 0.0008; Fig. 2).

Climate effectively explained the regional variation in the productivity of raccoon dog females (R^2 = 0.97, F = 74.4, P = 0.017, Fig. 4A). The depth of the snow cover at the end of March explained most of the variation in the weight and fat reserves of juveniles in late autumn (Fig. 4B, Kauhala 1993), and these, in turn, explained most of the variation in the proportion of reproducing females in the population (Fig. 4C). Thus, the snow depth at the end of March offers a fairly complete explanation (99%) for the regional variation in the proportion of reproducing females (R^2 = 0.99, F = 164, P = 0.006, Fig. 4D).

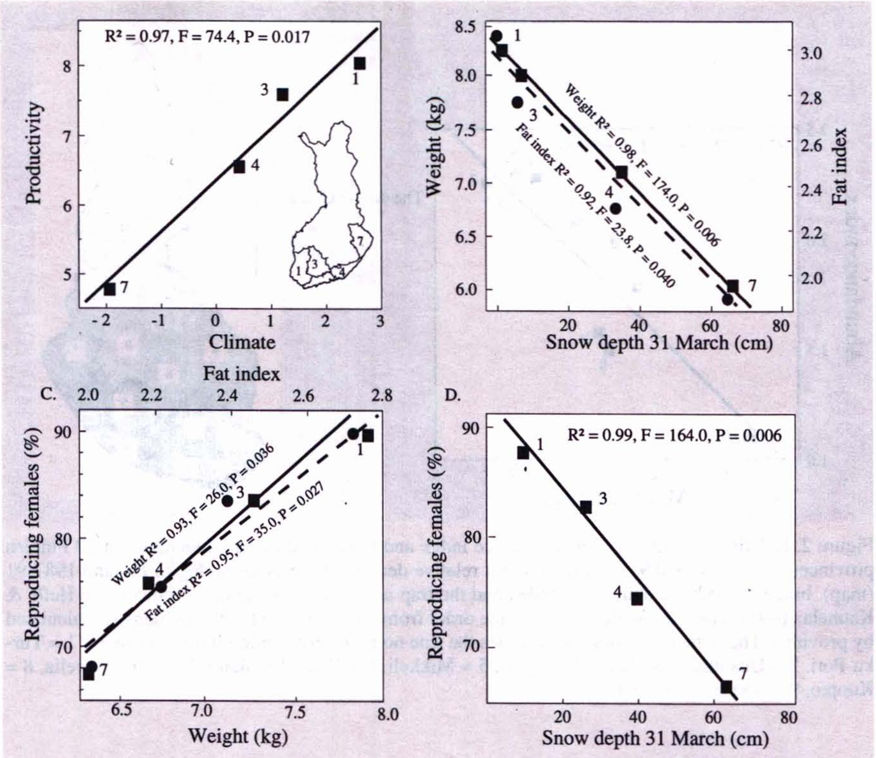

Figure 4. Relationship between climate and mean regional productivity of the raccoon dog population in four Finnish provinces (Y = 0.75x + 6.36). A: Principal component analysis was used to form one climatic variable based on the four climatic variables mentioned above (Kauhala 1992). This relationship is explained by three other regressions; B: the weight and fat reserves of juveniles in late autumn against snow depth on 31 March (Kauhala 1993); C: the proportion of reproducing females against weight and fat reserves of juveniles in late autumn; D: the proportion of reproducing females against snow depth on 31 March.

The snow depth at the end of March indicates the advancement of spring, which affects the time of estrus and parturition. Thus, in southern Finland, cubs are born earlier and have more time to grow and accumulate fat reserves before winter than cubs born farther north. As females of the youngest age class in southern Finland are bigger and have larger fat reserves than elsewhere in the country, a higher proportion of them reproduce. The youngest age class produces almost 40% of the cubs (Helle & Kauhala 1995), implying that the length of the annual snow-free period is the factor which has the largest effect on the productivity and, hence, the growth rate of the raccoon dog population.

The raccoon dog appears to be unable to colonise Lapland permanently, probably because the summer there is too short for the young to grow and build up enough fat reserves to help them sleep over the correspondingly longer winter. Thus, the northern limit of distribution in Finland appears to be determined by the climate, i.e. the length of the snow-free period. A similar situation apparently prevails in northwestern Russia (Lavrov 1971, Judin 1977).

Annual variation in population density

The effect of density

In the 1970s, the populations declined in the provinces of Kymi and Mikkeli (Fig. 1) independent of density (Table 1). In the province of Häme, no density dependence could be detected during the population increase before the mid-1980s. In the provinces of North Karelia and Oulu, the populations were rather steady in the 1970s, and some density dependence could be detected.

In all the provinces studied, the populations increased in the early 1980s and peaked around the mid-1980s. Since then, population change has been clearly density dependent (Table 1), indicating that the populations have reached the carrying capacity of their environment.

The effect of environmental factors

During the whole study period, the availability of wild berries explained some of the annual variation in the population density in the provinces of Kymi ($R^2 = 0.29$, $F = 7.9$, $P = 0.01$), Mikkeli ($R^2 = 0.22$, $F = 4.4$, $P = 0.05$) and North Karelia ($R^2 = 0.30$, $F = 6.8$, $P = 0.02$).

The results covering the three separate periods of population development are presented in Table 2. We have only listed the independent variables that explained significantly variation in at least one province.

The abundance of wild berries most often explained the variation in raccoon dog density. In 6 out of 13 cases (see Table 2 for provinces and periods) berries explained the annual variation in raccoon dog density, and the relationship was positive in all cases. During the first half of the 1980s, berries explained a significant amount of the increase in density in all the provinces analysed, and after

Table 1. Relationship between density and the annual change in density of raccoon dog populations in five Finnish provinces (sign of correlation coefficient/coefficient of determination, R^2/P). Period I is the phase in the 1970s when the population was either stable or decreasing (except in Häme where the population was increasing); period III is the period after the peak in the mid-1980s (see Fig. 1). The raccoon dog density is the abundance index obtained from game inquiries (see Helle & Kauhala 1991).

Province	Period	Model sign/R^2/P
Häme	I	+/0.02/0.674
	III	-/0.83/0.012
Kymi	I	-/0.13/0.371
	III	-/0.63/0.034
Mikkeli	I	-/0.39/0.183
	III	-/0.61/0.039
North Karelia	I	-/0.56/0.054
	III	-/0.66/0.026
Oulu	I	-/0.38/0.079
	III	-/0.69/0.041

Table 2. Relationship between environmental factors and the annual density of raccoon dog populations in five Finnish provinces (Stepwise regression analysis, sign of correlation coefficient/coefficient of determination, R^2/P). Dependent variable: abundance index of the raccoon dog; independent variables: mean abundance indices of bilberries and lingonberries, abundance index of voles, abundance index of red fox, and duration of the snow cover. The abundance indices are based on game inquiries (Helle & Kauhala 1991). Period I is the phase in the 1970s when the population was either stable or decreasing, II is the phase in the early 1980s, when the population was increasing, and III is the more or less stable period after the peak in the mid-1980s (see Fig. 1).

Province	Period	Independent variable				Model R^2/P
		Berries	Voles	Red fox	Snow cover	
Häme	III	ns	ns	-/0.76/0.005	ns	0.76/0.005
Kymi	I	ns	ns	-/0.52/0.029	ns	0.52/0.029
	II	+/0.90/0.004	ns	ns	ns	0.90/0.004
	III	+/0.61/0.039	ns	ns	ns	0.61/0.039
Mikkeli	I	ns	+/0.67/0.024	ns	-/0.74/0.014	0.90/0.009
	II	+/0.80/0.016	ns	ns	ns	0.80/0.016
	III	+/0.69/0.041	ns	ns	ns	0.69/0.041
North Karelia	I	ns	ns	ns	ns	-
	II	+/0.95/0.27	ns	ns	ns	0.95/0.027
	III	ns	ns	ns	ns	-
Oulu	I	ns	+/0.53/0.016	ns	ns	0.53/0.016
	II	+/0.81/0.015	ns	ns	ns	-
	III	ns	ns	ns	ns	-

Table 3. Life table for the raccoon dog in southern Finland starting from the number of egg cells ovulated (i.e. number of corpora lutea); the table is constructed using the life table starting from birth (Helle & Kauhala 1993) and data on reproduction (Helle & Kauhala 1995) of the raccoon dog in southern Finland.

Life cycle stage	l_x	d_x	q_x
Ova	1.0000	0.165	0.165
Embryos	0.8351	0.061	0.073
Cubs at birth	0.7740	0.684	0.884
1-year-old animals	0.0898	0.057	0.629
2-year-old animals	0.0333	0.014	0.419
3-year-old animals	0.0193	0.009	0.440
4-year-old animals	0.0108	0.004	0.357
5-year old animals	0.0070	0.005	0.667
6-year-old animals	0.0023	0.002	0.667
7-year-old animals	0.0008	0.001	1.000

the peak in the mid-1980s, when the population had reached its carrying capacity, it also explained a significant amount of the annual variation in density in the provinces of Kymi and Mikkeli.

The life table indicated that the mortality of juveniles during their first year of life is the major mortality factor (Table 3). The availability of wild berries the previous autumn most often explained the annual variation in density, and as the time-lag was only half a year, the only possible way berries could affect density would be through mortality. Thus, we conclude that the availability of berries, to a particularly high degree, affects the mortality of the young during autumn and winter, and thus the density of the population the following spring. The abundance of wild berries probably affects the fat reserves accumulated before the winter sleep, and thus the mortality during autumn and winter. Lindström (1983) found that the occurrence of fruit and berries in foxes' stomachs correlated with the amount of fat deposited during autumn.

The effect of vole density could be detected both without a time-lag (the province of Mikkeli) and with a time-lag of one year (the province of Oulu). The abundance of voles in the current spring explained most of the yearly variation in the weight and fat indices of adult females in March (Fig. 5A, see also Kauhala 1993), and fat index, in turn, largely explained the annual variation in litter size ($R^2 = 0.93$, $F = 57.3$, $P = 0.002$, Fig. 5B). There was a negative relationship between the density of raccoon dogs in relation to the density of voles and the fat reserves of adult females (in their second year or older) in March ($R^2 = 0.89$, $F = 32.8$, $P = 0.005$) and between the density of raccoon dogs in relation to the density of voles and litter size of adult females ($R^2 = 0.98$, $F = 174.1$, $P = 0.0002$). These relationships could not be detected among females born the previous spring.

When the density of the population is high and/or voles are scarce, there appears to be intraspecific competition because of a shortage of resources, and females are in poorer condition than when the density of the population

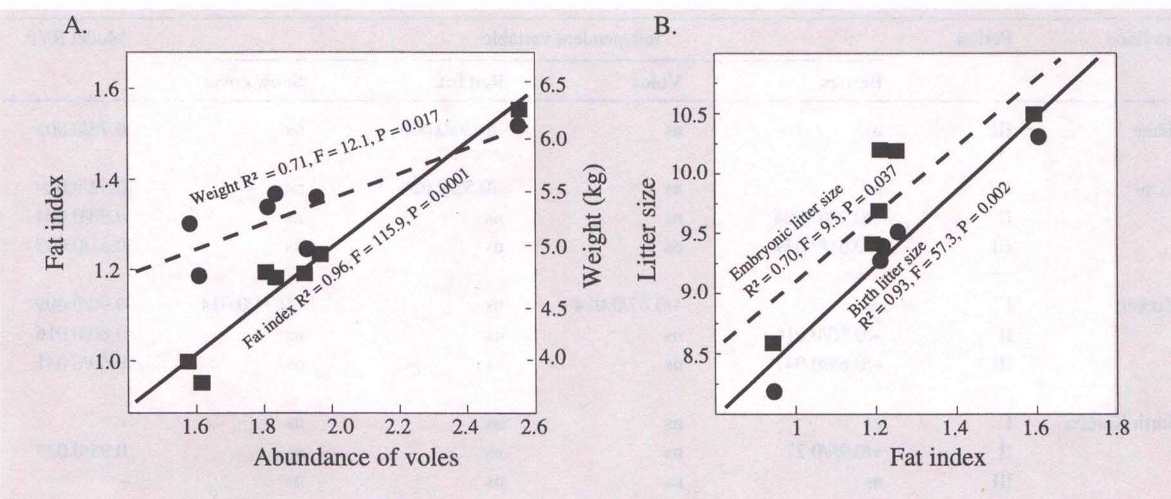

Figure 5. A: Regression of fat index (Y = 0.64x - 0.006) and weight (Y = 1.2x + 3.1) against the abundance of voles in March; B: regression of mean yearly litter size (birth litter size: Y = 0.30x - 1.56; embryonic litter size: Y = 0.25x - 1.22) against fat index in March in adult raccoon dog females (in their second year or older) in the province of Häme in Finland in 1987-92. For the abundance index of voles, see Helle & Kauhala (1991), for fat indices and weight, see Kauhala (1993), and for litter size, see Helle & Kauhala (1995).

is lower and/or voles are more abundant. Thus, the abundance of voles and population density affect the condition of adult females, which, in turn, affects the litter size of these females. Angerbjörn et al. (1991) came to a similar conclusion in their studies of the arctic fox *Alopex lagopus*; they suggested that there is a relationship between the litter size of the arctic fox and the availability of winter food. The condition of young raccoon dog females did not correlate with their litter size, probably because the youngest females in very poor condition do not reproduce at all.

The abundance of the red fox also explained some of the annual variation in density. Any effect of the red fox on the raccoon dog population would be through competition or predation, and that would be very difficult to prove. It is also possible that the two species do not affect each other but in fact react to a common factor.

Conclusions

After the 1950s, the raccoon dog population increased very rapidly in Finland and reached its peak and probably its carrying capacity in the mid-1980s. Subsequent population changes have been density dependent. The major factors behind the success of the raccoon dog in Finland are its extraordinarily high reproductive potential, the fact that it is omnivorous and able to use man-made food resources and that it is able to sleep throughout winter (Kauhala 1992).

Climate is certainly the most important factor affecting regional variation in the growth rate, density and distribution of the raccoon dog population in Finland. The length of the snow-free period (in relation to the length of the winter) has an effect on reproduction and mortality, especially where the youngest age class is concerned.

The availability of wild berries most often explained annual variation in density. As the mortality rate of juveniles seemed to have the most profound effect on the population, the availability of berries most probably affects the mortality rate of the youngest age class during autumn and winter. So, this is the most important factor determining the annual population size. Unfortunately, we could not test, whether juvenile mortality in raccoon dogs was density dependent or not.

The condition and litter size of adult females showed density dependency, and thus, the productivity of adult females to some extent regulates population density. However, productivity of adults is not the major factor determining the population size of raccoon dogs.

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