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# A model of population dynamics in territorial animals

## En modell för populationsdynamik hos territoriella djur

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En modell för populationsreglering hos territoriella djur presenteras. Det visas att med givna värden för revirtäthet, fortplantningsframgång och överlevnad hos ungdjur, icke territoriella djur och territoriella djur samt om migrationen kan negligeras finns det ett jämnviktsvärde för populationstätheten. Detta täthetsvärde ökar obegränsat och linjärt med ökande revirtäthet och ökande fortplantningsframgång samt linjärt och uppåt begränsat med ökande överlevnad hos ungdjur och territoriella djur. Då överlevnaden hos icke-territoriella djur närmar sig 1,0 ökar jämnviktstätheten obegränsat. För populationer vars dynamik med tillräckligt god precision avbildas kan modellen användas för att förutsäga effekten av olika ingrepp.

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### Introduction

This paper presents a model that demonstrates numerical consequences of a territorial system for the population dynamics of animals. It is pointed out that this system not only limits the breeding population but also the total population in an area. Severe restrictions are assumed, and for most populations modifications are necessary if a higher degree of realism and precision is required. In its present form it is inspired from my work on the hooded crow *Corvus cornix*, a species for which I believe the model is fairly realistic. The principle of the model has previously been suggested by Haartman (1971) but in the present paper, formulas for the calculation of the size of populations obeying the assumptions are also given.

### Assumptions

1. The basic reproductive unit is a pair, male and female. 2. Reproduction takes place during a limited season, once a year. 3. In a given area, the number of pairs starting reproductive attemts is limited. Though not necessary for the model, each such pair is usually associated with a more or less exclusive area, a territory. They will be called territorial pairs in the following. 4. Mortality in all age-classes is equal between the sexes. 5. All animals are potentially able to reproduce from one year of age. 6. The reproductive success, calculated as the number of independent youngs per territorial pair and year is fixed for each population. In particular, it is not dependent on the total population density during different years. 7. The yearly mortality for different categories of animals is fixed for each population and thus also independent of population density. The categories distinguished in the model are juveniles (from independence to one year of age), older non-territorials and territorials. 8. The exchange of individuals between the population under study and other populations is negligible.

### The model in words

The mechanism and the consequences of the model can be formulated as follows. Under the given assumptions a population can not exceed the density at which the mortality is balanced by the yearly production of independent young. As the production of independent young in one area is limited by the number of breeding

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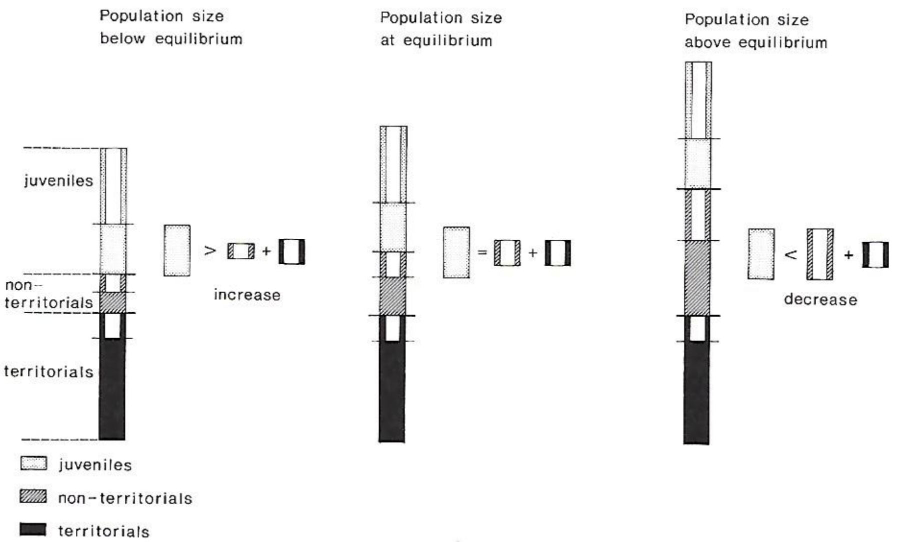


Fig. 1. The population composition at three different size levels at the end of the breeding season. The filled parts of the bars represent those animals that will survive at least until just before the next breeding season, whereas the other parts represent those that have died by then.

Populationssammansättningen vid beståndstätheter, mätt vid slutet av fortplantningssäsongen. De fyllda delarna av staplarna representerar de djur som överlever åtminstone till just före nästa fortplantningssäsong medan de andra delarna representerar de djur som dött till dess.

pairs this will also apply to the whole population. This is not very surprising but it gives a possibility to calculate the population density if other data are known. A picture model is given in Fig. 1.

If the reproductive output (here counted as surviving juveniles, one year of age) is insufficient to replace at least those territorials which died from one year to the next, the population will decrease until it is eliminated. If it is just sufficient, there will be an unstable equilibrium at any density the population may have. If the output exceeds the mortality of territorials, the population will increase until there are more animals than will fill the territories. At some level above this, mortality will balance the production of juveniles. This level is unique, because, at any level above equilibrium, mortality will exceed the production that is fixed by the number of territories. At any level below equilibrium, production will exceed the mortality and the population increase.

It is thus clear that, if through some external cause, violating the assumptions, the population increases above the equilibrium level (if this cause is only temporary) it will again decrease until equilibrium is reached. Such causes could be artificial introductions of individuals or immigration.

Likewise, if again against the assumptions the population has decreased for some reason, it will increase until the equilibrium level is reached. Such causes could be exceptionally high mortality following human persecution or weather catastrophes. Such incidents could also cause breeding failure in singel years.

The model makes no predictions as to what animals take up empty territories. Usually, dead territorials are likely to be replaced by older nonterritorials and these, as well as dead non-territorials, by surviving juveniles.

## The numerical model

The following notations are used:

T: Number of territories per unit area.
R: Reproductive success, expressed as the number of independent young per pair.
N: Number of non-territorials per unit area.
P: Number of animals per unit area.
j: Proportion of juveniles surviving from independence to one year of age.
n: proportion of non-territorials surviving one year.
t: Proportion of territorials surviving one year.

If the population under study is in equilibrium, the number of one-year old animals immediately before one breeding season (jRT) will be equal to the number of territorial and non-territorial animals that have died during the previous year ($((1 - n)N + (1 - t)2T)$). Note that N and T refer to the number of animals alive at the beginning of the preceding breeding season and that they include the number of animals one-year old at that time. From this equality it is possible to calculate the number of non-territorials.

(1) $$jRT = (1 - n)N + (1 - t)2T$$

$$N = \frac{jRT - (1 - t)2T}{1 - n}$$

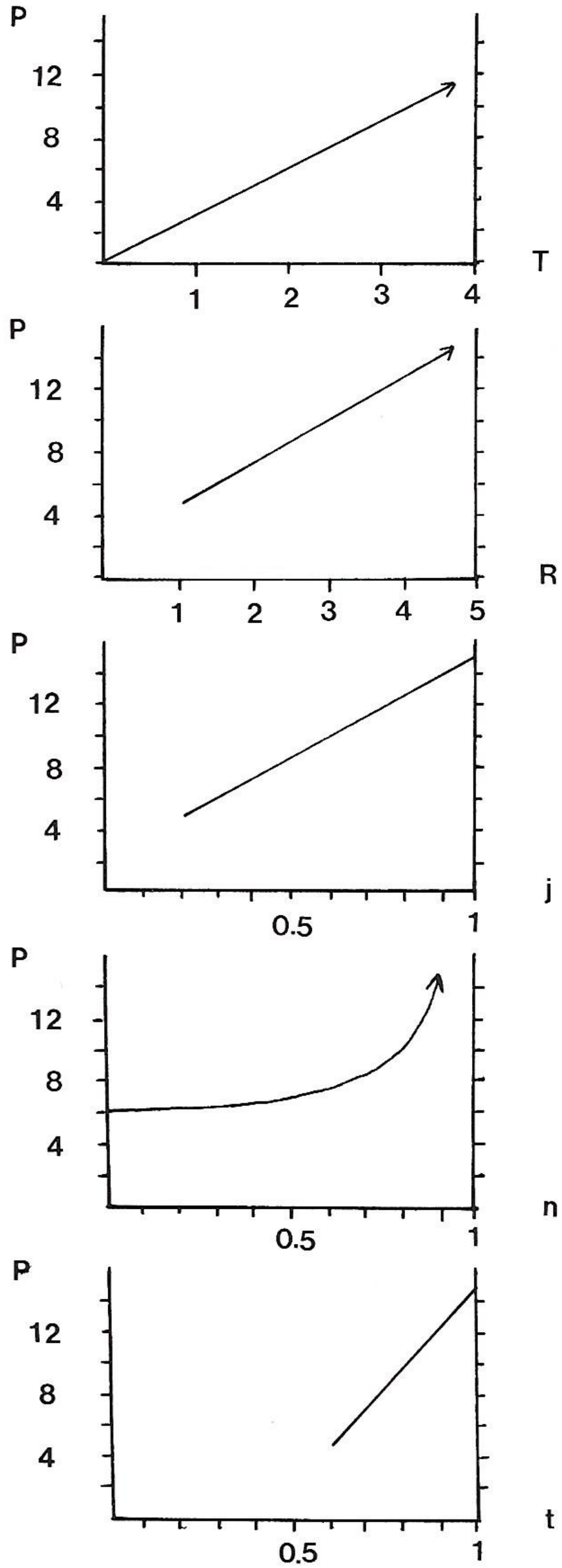


Fig. 2. The relation between the parameters and the population size at equilibrium. For notations, see text. Except when represented on a graph, the parameters have been fixed at the following levels: T = 2.5, R = 2.0, j = 0.4, n = 0.6 and t = 0.8. For values below R = 1, j = 0.2 and t = 0.6 respectively, the condition for a positive equilibrium (eq. 4) is not ful-filled, and the population will go extinct.

Relationer mellan de olika parametrarna och beståndstätheten vid jämvikt. P = antal djur per ytenhet, T = antal territorier per ytenhet, R = antal självständiga ungar per territorium och år, j = andel ungar som överlever från självständighet till ett års ålder, n = andel icke-territoriella djur som överlever per år, t = andel territorella djur som överlever per år. På varje graf varierar en parameter medan de övriga är fixerade vid följande värden: T = 2,5, R = 2,0, j = 0,4, n = 0,6 och t = 0,8. För värden under R = 1, j = 0,2 respektive t = 0,6 finns inget positivt jämviktsvärde utan populationen elimineras.

The number of animals at the beginning of the breeding season is given by:

(2) $$P = N + 2T$$

$$P = \frac{jRT - (1 - t)2T}{1 - n} + 2T$$

As the breeding season is of limited duration, the mortality during this time is neglected, and the population size by the end of the breeding season given by:

(3) $$P = N + 2T + RT$$

From the word model also follows that the population will only have a stable equilibrium, apart from zero if the recruitment of the population exceeds the mortality of territorial animals during one year as expressed in the equation below:

(4) $$jRT > (1 - t)2T$$

$$R > \frac{2(1 - t)}{j}$$

If assumption 5 is changed to:

5. All animals are potentially able to reproduce from two years of age, the formulas (1) – (3) will not be affected but the condition expressed in (4) will. It will now be required that the »production« of two-year old animals is sufficient to replace the dead territorials:

(5) $$njRT > (1 - t)2T$$

$$R > \frac{2(1 - t)}{nj}$$

**The influence of parameter values on population size**

If formula (1) is examined, the following facts are found. The population size will increase linearly as the values of reproductive success, density of territories, and survival of juveniles and territorials increase. Furthermore, the population size is directly proportional to the density of territories. It has, the other parameters fixed, an upper limit for juvenile and territorial survival of 1. The dependence of population size on the survival of non-territorials is different. If their survival is high, the population can hold a large »pool« of these birds regardless of the limits set by the territorial system. As the survival of non-territorials approaches 1, the population size will increase indefinitely. These relations are illustrated in Fig. 2.

## Discussion

To test the applicability of the model to a set of populations, representing the whole of a species or all populations living under similar conditions, two different lines can be followed. One can, from knowledge of the species' biology or, preferrably by experimental tests of assumptions 3, 6 and 7, make sure that the assumptions are fulfilled. If some of the assumptions 1, 2 4 or 5 are not fullfilled it may be possible to change only details of the model but keep the basic princible. One can also measure all parameters of eq. (1) and check that it holds. This should be made for several sets of values, representing different populations in the set under study. The model can then be applied to the whole set. This approach has the advantage that one does not have to bother about how important possible deviations from the assumptions that may be found are for the numerical results when one applies the model.

If the model is applicable, it can be used e.g. to predict the result of different management policies or to estimate the importance of reduced fertility due to environmental pollution.

## Reference

Haartman, L. von 1971. Population dynamics. – In: Avian biology I. Ed. D. Farner & J. King. Academic press.