

Territory economics and population stability - can populations be socially regulated?

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Abstract

Although Wynne-Edwards' group selectionist theory of population regulation was soon rejected, the concept of social regulation still remains in the literature. Here I examine the importance of social behaviour (e.g. territoriality) in population regulation from an individual selectionist point of view. One of Watson and Moss' criteria for population regulation through social behaviour is that the individuals should defend resources that exceed their need for survival and reproduction. This is an analogy to Verner's super territory model which is not compatible with optimality theory. Moreover, the observations that per capita reproductive rate decreases with increased group size has often been taken as a sign of social regulation at the group level. However, it can be demonstrated, both theoretically and empirically, that population rate of increase as well as the population's efficiency of converting

resources into reproduction can increase with increased population density in spite of a decrease in per capita reproductive rate. These correlations reduce population stability in variable environments. To be effectively regulative social behaviour must induce a negative correlation between efficiency of converting resources into reproduction and population density. With this background I conclude that the importance of social regulation is highly exaggerated. It is only in a special case that social behaviour can induce population stability in variable environments, viz. in permanently territorial species whose life expectancy exceeds the average time period of the environmental fluctuations.

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Selection favours those phenotypes which leave the greatest number of reproductive descendants. Why, then, does not evolution lead to populations of individuals being so effective and fertile that they overexploit their resources and become extinct? Although this may be a seemingly naive problem for population geneticists (e.g. Haldane 1957, but see Maynard Smith 1968), it remains a major task for population ecologists to identify the constraints of population growth (e.g. Thompson 1929, Nicholson 1933, Andrewartha & Birch 1954, Lack 1954, Chitty 1960, Hairston et al. 1960, Wynne-Edwards 1962, Smith 1963). In his famous book, Wynne-Edwards (1962) suggested that most types of social behaviour have evolved to prevent animal populations from overexploiting their resources. Wynne-Edwards considered territorial behaviour to be one of the most powerful factors in preventing "overpopulation". The idea was that populations with this type of social regulation were less likely to go extinct and they would therefore outcompete populations without any self-regulation. However, Wynne-Edwards was severely criticized and the idea of group selection was soon

abandoned in favour of individual, or rather, kin selection (Maynard Smith 1964, 1976, Williams 1966). Still, many ecologists insist that populations can be regulated by social behaviour (e.g. Watson & Moss 1970, Klomp 1972, 1980, Patterson 1980, Begon & Mortimer 1981, Hassel & May 1985, Moss & Watson 1985). Others are less precise, only suggesting that social behaviour affects population dynamics (e.g. Fretwell & Lucas 1969, Maynard Smith 1974, Emlen 1984, Clutton-Brock & Albon 1985, Krebs 1985), whereas still others deny that social behaviour can regulate populations (e.g. Lack 1954, 1968, Brown 1969a, b, 1975). Here I will examine whether populations really can be socially regulated by spacing behaviour and if social behaviour increases population stability in variable environments.

Terminology

Population regulation

Much confusion in population ecology is caused by different authors using expressions such as "population control", "limitation" and "regulation" without

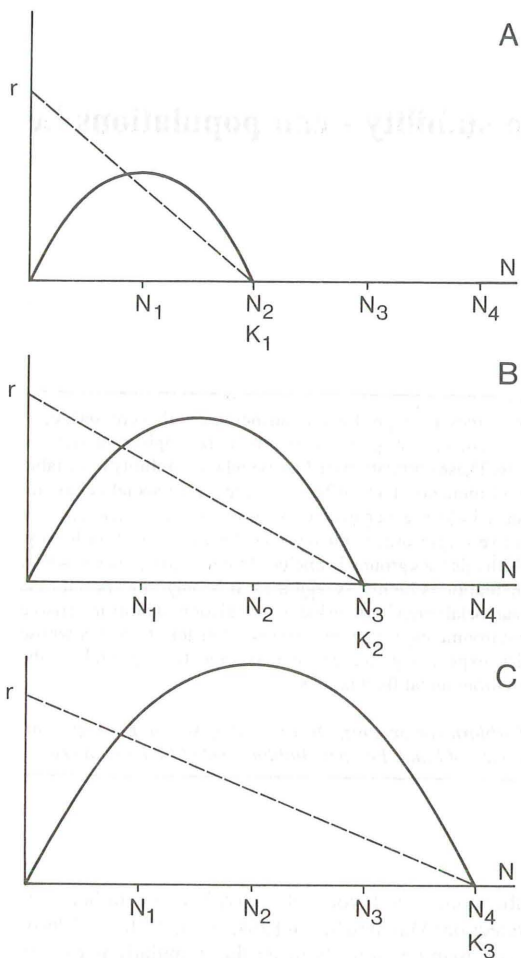


Fig. 1. Relationship between per capita reproductive rate (broken line), population rate of increase (solid line) and population density (N) at different carrying capacities (K₁, K₂ and K₃).

Sambandet mellan föryngringshastigheten per individ (bruten linje), populationens ökningshastighet (hel linje) och populationstätheten (N) vid olika bärligheter (K₁, K₂ och K₃) hos biotopen.

defining them. Here I define population regulation according to the logistic model in which the per capita rate of increase decreases with increased density of conspecifics, i.e.:

$$(1/N) (dN/dt) = r (1 - (N/K))$$

where r = innate rate of increase, N = population density, and K = carrying capacity.

Another reason for confusion is a lack of generality concerning the level at which the regulatory factors are acting; is it the geographical distribution of the popu-

lation, or the density of adults, or the number of breeding units, or, e.g. the number of adults plus the recruits of the year that is regulated? Again the logistic is useful in identifying the population rate of increase as the level at which the population is regulated, i.e.:

$$dN/dt = rN(1 - (N/K))$$

Theoretically, by identifying the factors that set the carrying capacity of a population (K) one has also, by my definition, identified the factors that regulate the population. Examples of this are given in Fig. 1. In case A some factor sets K at a population density of N_2 . In B K is set at N_3 and in C at N_4 . Assume that A, B, and C in Fig. 1 describe the same population and that the factors that set K in each case are predation (A), resources for winter survival (B), and breeding resources (C). Then, according to my definition, it is correct to state that this population is regulated by predation. If, however, the predators are removed, the population will be regulated by winter mortality. Similarly, if also the winter mortality does not occur, by e.g. supplying the population with an excess of resources essential for surviving the winter, then the population will be regulated by breeding resources.

Population stability

In the real world it is likely that the importance of different potential regulatory factors changes between seasons and years. How does this affect population stability?

In an analysis of population stability of r - and K -strategists at different density-dependent actions, Southwood et al. (1974) pointed out that the logistic equation was not useful since it does not allow for overshooting. Instead they used the difference equation by May et al. (1974) to predict changes in population size following perturbation. The highly sophisticated, but abstract, way of defining population stability mathematically (May 1974, May & Oster 1976) is of limited practical use since estimates from field populations of the parameters are seldom obtainable (but see e.g. Hassel et al. 1976).

To make the concept more concrete I use stability here as a relative term. To illustrate this, let K_1 , K_2 and K_3 in Fig. 1 be the carrying capacities set by the different resource (e.g. food) levels in a varying environment. Now let some other factor keep the population at some given density (N_1 , N_2 , or N_3 in Fig. 1). The effects of changes in the resource level (ΔR in Fig. 2) affects the rate of increase of population n_1 least and that of n_3 most; hence, I define population n_1 to be most

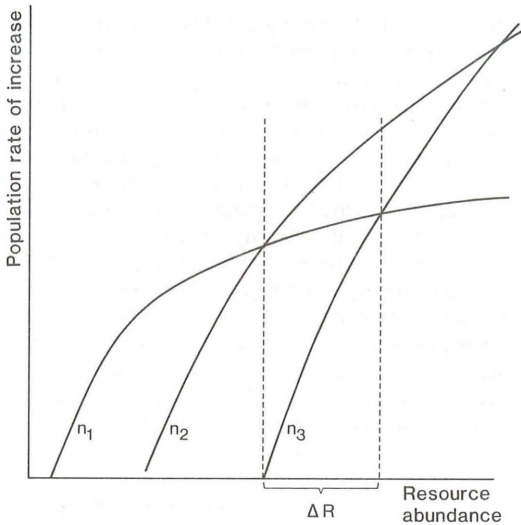


Fig. 2. Relationship between population rate of increase and resource abundance at different fixed population densities (n_1 , n_2 and n_3 correspond to N_1 , N_2 and N_3 , respectively in Fig. 1). *Sambandet mellan populationens ökningshastighet och mängden resurser vid olika givna populationstätheter (n_1 , n_2 och n_3 motsvarar N_1 , N_2 resp. N_3 i Fig. 1).*

stable. A most important conclusion from this is that rate of increase of a low density (for whatever the reason) population is hardly affected at all by a change in resource availability whereas the same change in resources has a most profound effect on rate of increase of a high density population. But can spacing behaviour keep the population density lower than that set by the carrying capacity of the environment, thereby inducing increased population stability? Normally population density should correlate positively with resource density, thereby reducing stability according to Fig. 2.

Social regulation

Watson & Moss (1970) listed different conditions for determining whether breeding density is regulated by social behaviour.

1. A substantial proportion of the population does not breed.
2. Such non-breeders are physiologically capable of breeding.
3. The breeding animals are not using up the resources themselves but are preventing competitors from doing so.
4. The regulatory effects shall be density dependent.

In their reviews, both Watson & Moss (1970) and Klomp (1972) pointed out that very few, if any, studies have given data from a single population that fulfill all of Watson & Moss' (1970) four conditions.

Much of the problems of identifying the existence of social regulation lies, I believe, in the fact that point three above is theoretically controversial.

Super territories and population regulation

Undoubtedly, for social behaviour to be regulative, it is necessary to show that the breeding animals are not completely using up some resource, such as food. If they are the resource itself is a regulating agent. Hence, as Watson & Moss (1970) pointed out, the breeding animals shall not only prevent other animals from using the resource, but the breeders must also leave a resource surplus that is not fully utilized by themselves.

This statement is analogous to Verner's (1977) idea of super territories. Verner (1977) suggested that natural selection favours individuals that defend territories larger than necessary to include resources sufficient to optimize survival and reproduction. Verner meant that such a defence of a disproportionate share of space and resources by the super territory strategists increase their fitness in relation to less aggressive individuals which get a reduced possibility of survival and reproduction.

However, as several authors pointed out, Verner's (1977) model is not compatible with optimality theory. The main argument was that those individuals that maintain a territory of "just sufficient" size receive the same gain by the exclusion of competitors as the super territory holder does, but the latter bears all the costs (Colgan 1979, Getty 1979, Pleasants & Pleasants 1979, Rothstein 1979, Tullock 1979). Hence, unless the super territory strategists derive some benefit beyond those accruing to the just sufficient strategists, the former strategy cannot spread in the population. In the light of these findings it seems unlikely that spacing behaviour can regulate populations except in the case of the obstinate strategy described below.

Territory economics and population stability

Can social behaviour increase population stability in variable environments? Again, optimality theory is useful in such an analysis. A simple cost-benefit analysis of territorial behaviour is given in Fig. 3. The costs of defending the territory increase with territory size. The benefits increase rapidly with territory size initially but will reach an asymptote when the amount of resources in the territory exceeds the animal's need for survival and reproduction. The optimal territory size for the benefit curve B_1 in Fig. 3A is T_1 . With an increase of resources, the benefit curve will increase steeper (B_2 in Fig. 3A) and reach the asymptote at a

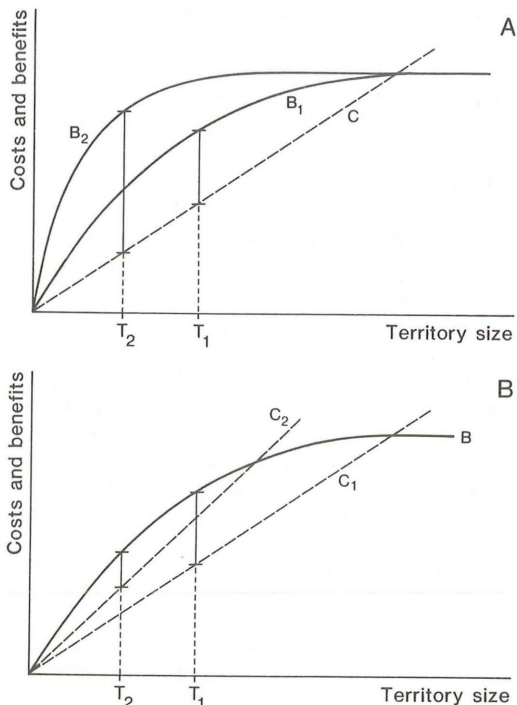


Fig. 3. Relationship between costs (broken lines) and benefits (solid lines) of territorial behaviour for different territory sizes. A: Optimal territory sizes at different resource levels. B: Optimal territory sizes at different intruder pressures.

Förhållandet mellan kostnad (bruten linje) och vinst (hel linje) för revirbeteende vid olika revirstorlekar. A: Optimala revirstorlekar vid olika resursnivåer. B: Optimala revirstorlekar vid olika tryck från inkräktare.

smaller territory size. In that case optimal territory size will decrease from T_1 to T_2 . Decreased territory size implies an increased density of breeding animals and thereby, according to Fig. 2, a decreased population stability. The same effect will occur when the costs of territorial defence increase (C_1 shifts to C_2 in Fig. 3B), due to e.g. an increased intruder pressure; i.e. optimal territory size will decrease from T_1 to T_2 .

Thus it appears that spacing behaviour cannot keep the population at a density below that set by the carrying capacity of the environment, nor does spacing behaviour seem to be an effective stabilizer in fluctuating environments.

Yet there exists at least one case where social behaviour effectively can damp population fluctuations in variable environments and, at least temporarily, keep the density of breeding animals far below the en-

vironmental K . I have suggested (von Schantz 1984a, b) that permanently territorial altricial vertebrates that feed on a fluctuating food resource keep a constant territory size if the animals' lifespan is longer than the average time period of the food fluctuations. The animals' territory sizes will be so adjusted that they contain enough food for reproduction, or at least survival, during the bottle-necks of food scarcity. By allowing their adult offspring, or other close relatives, to remain at home as non-breeders to exploit the resource surplus when resources are increasing the territory owners remedy the dilemma that confronts Verner's super territory holder. Later when resources are decreasing the territory owners expel their non-breeding relatives from the territory; this is the so called obstinate strategy (von Schantz 1984a). In effect, such a population will be socially regulated. When resources are abundant the breeding animals are not completely using up the resources themselves but they are preventing other animals from utilizing the resources for reproduction. Hence, the density of breeding animals will be lower than would have been the case if territory size instead had decreased in response of an increase in resources. Instead it is the number of non-breeding animals that fluctuates in parallel with the resources. This means that the environmental fluctuations mainly affect the density of non-breeders whereas the population rate of increase hardly is affected at all (cf. Fig. 2). This yields the following testable prediction: *to be effective in population regulation, social behaviour must induce a negative correlation between the population's efficiency of converting the resources into reproduction (rate of increase) and population density*. To illustrate this, let us go back to the model in Fig. 1.

Per capita reproductive rate, population rate of increase, and population efficiency of converting resources into reproduction

From Fig. 1 we see that when the per capita reproductive rate decreases linearly with population density, then the maximum population rate of increase is attained at a population density of $K/2$. Data from Lack (1968) and Perrins (1979) on Great Tits *Parus major* in Marley Wood show that the number of fledglings produced per pair does, in fact, decrease linearly with density of breeding adults (Fig. 4A). The equation of the regression line gives an estimated K of 260 breeding birds; hence $K/2=130$ individuals. Since the highest number of breeding birds ever recorded during the study was 172, the probable carrying capacity of breeding resources was obviously never reached. Instead Lack (1968, p. 280) suggested that starvation outside the

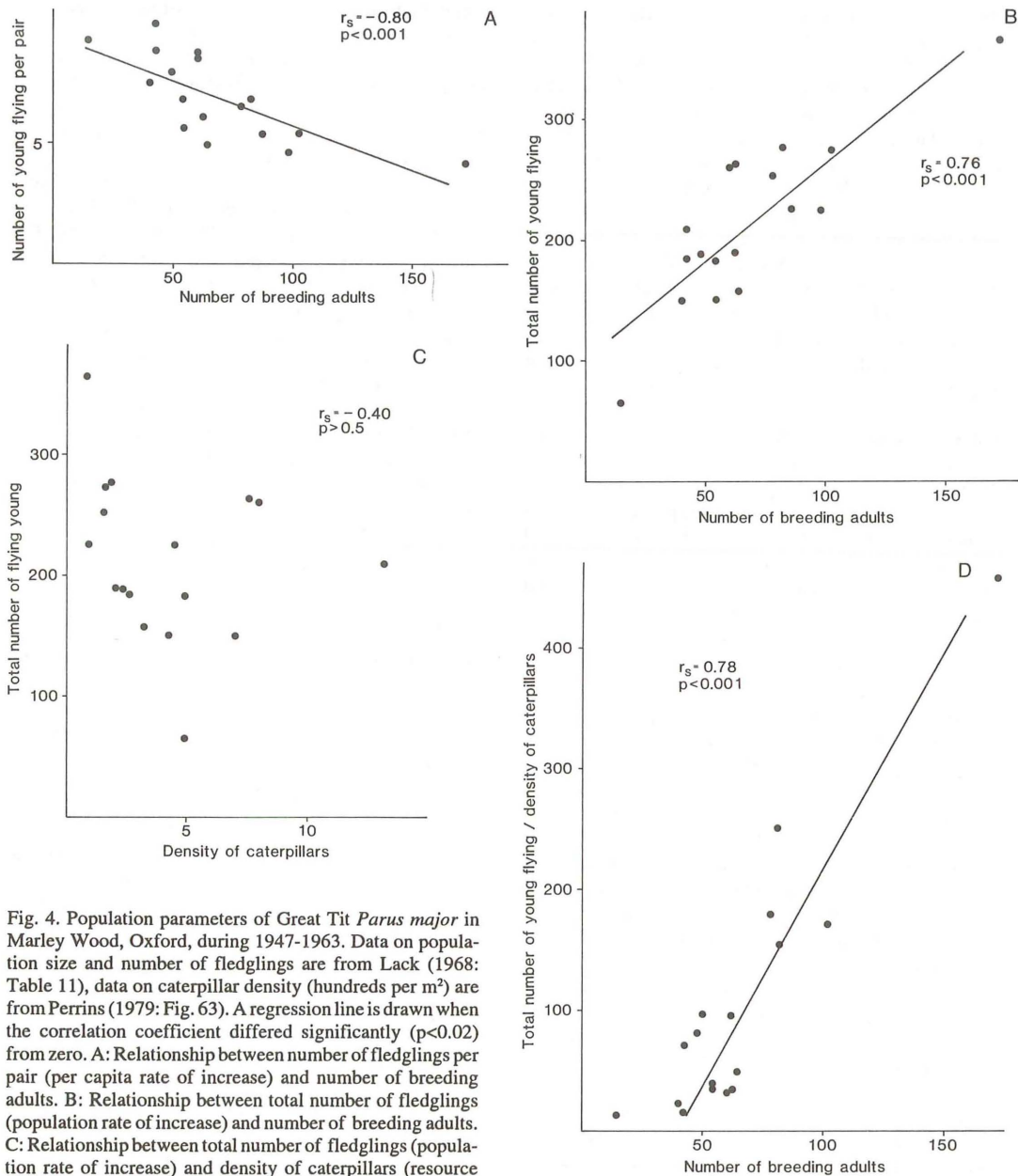


Fig. 4. Population parameters of Great Tit *Parus major* in Marley Wood, Oxford, during 1947-1963. Data on population size and number of fledglings are from Lack (1968: Table 11), data on caterpillar density (hundreds per m^2) are from Perrins (1979: Fig. 63). A regression line is drawn when the correlation coefficient differed significantly ($p < 0.02$) from zero. A: Relationship between number of fledglings per pair (per capita rate of increase) and number of breeding adults. B: Relationship between total number of fledglings (population rate of increase) and number of breeding adults. C: Relationship between total number of fledglings (population rate of increase) and density of caterpillars (resource abundance). D: Relationship between the ratio of total number of fledglings divided by density of caterpillars (population efficiency of converting resources into rate of increase) and number of breeding adults.

Populationens egenskaper hos talgoxe *Parus major* i Marley Wood, Oxford åren 1947-1963. Data om populationsstorlek och antal flygga ungar från Lack (1968, Tabell 11), data om larvtäthet (hundratal per m^2) från Perrins (1979, Fig. 63). En regressionslinje har ritats om korrelationskoefficienten skilt

sig signifikant från noll ($p < 0.02$). A: Sambandet mellan antalet flygga ungar per par och antalet häckande adulta. B: Förhållandet mellan totala antalet flygga ungar (populationens ökningshastighet) och antalet häckande adulta. C: Förhållandet mellan totala antalet flygga ungar och tätheten av larver (resurstillgången). D: Förhållandet mellan kvoten totala antalet flygga ungar dividerat med larvtätheten (dvs populationens effektivitet att omvandla resurser till ökningshastighet) och antalet häckande adulta fåglar.

breeding season was the most important density-dependent factor that regulated the population (see also McCleery & Perrins 1985). Accordingly, and in support of the model in Fig. 3 B, Krebs (1971) pointed out that breeding density, and hence territory size, of Great Tits in Marley Wood was a function of the number of individuals that survived the winter; i.e. the more Great Tits that competed for territories in spring the smaller the territories. Hence, the population did not show any signs of regulation through territorial behaviour (cf. Lack 1968, p. 278, McCleery & Perrins 1985). Since all data points except one are below $K/2$ the total number of young fledged by the population should be a positive function of the density of breeders (cf. the curves describing population rate of increase in Fig. 1). Fig. 4B shows that this indeed was the case; however, there is no correlation between density of caterpillars (main prey for the tits during the nestling period) and total number of young flying (Fig. 4C). At first sight this may seem paradoxical, but considering the fact that the overwhelming majority of the data points from the Great Tits fall in the density interval between 0 and $K/2$ the data make sense in the light of the model in Fig. 2 where the main conclusion is that the population rate of increase will be insensitive to changes in resource supply at low population densities.

In all the cases in Fig. 1 a constant resource level is assumed. Therefore the population's efficiency of converting available resources into population rate of increase will be a positive function of N as long as $N < K/2$. Again, this prediction is supported by the Great Tit data (Fig. 4D) showing that the total number of young flying divided by caterpillar density correlates positively with the density of breeding adults. Per capita rate of increase is a monotonously decreasing function of N but it is not until N reaches the interval between $K/2$ and K that the populations's efficiency of converting resources into rate of increase (PER), and the population rate of increase (PRI) itself, will be a decreasing function of N . These correlations have two important implications as concerns the interactions between per capita reproductive rate, PRI and PER:

(1) Based on observations that per capita reproductive success declines with group size in social animals, Clutton-Brock & Albon (1985) concluded that population regulation may commonly occur at the level of the group, rather than at the level of the population, and that this may "affect" population stability. Clutton-Brock & Albon (1985) implicitly took this as an example of social regulation. But since PRI is likely to be a positive function of N as long as $N < K/2$ (Fig. 1) in spite of a negative function of per capita rate of increase, there is no reason to believe that this density dependence is regulatory. Nor does it necessarily imply that the population will become more stable in the sense illustrated in Fig. 2. On the contrary it is more

likely that PRI becomes more sensitive to changes in resource supply with increased N .

(2) As described above both PRI and PER are expected to show the same function of N as illustrated by e.g. the curve K in Fig. 5A. Any environmental fluctuation that will reduce K to K_1 will reduce both PRI and PER whereas an increase of K to K_2 will create an increase in both PRI and PER (Fig. 5A). These changes will occur at any given value of N although the effect becomes negligible as N approaches zero (cf. Fig. 2). In contrast, changes in the carrying capacity will have quite a different effect in the case of the obstinate strategy described above. Here PRI will remain constant irrespective of N (Fig. 5B) since the territory owners (breeders) have adopted a fixed territory size adjusted to some minimum resource level (von Schantz 1984a). Changes in K will hence only affect the number of non-breeding animals whose presence devaluates PER. In this case PER will be a monotonously decreasing function of both N and K (Fig. 5B).

Conclusion

In general, when defence costs are related to territory size or intruder pressure, social behaviour cannot effectively regulate or stabilize population rate of increase in fluctuating environments. This statement is valid for species that are only seasonally territorial or have a short life span in relation to the time scale of the environmental fluctuations. It is only in species that are permanently territorial and whose life expectancy exceeds the time scale of the environmental fluctuations, that social behaviour can be regulatory. Two groups of contrasting predictions emerge from the analysis.

(1) In the absence of social regulation both PRI and PER will show the same dependence of N (cf. curve K in Fig. 5A), and both will be a positive function of N as long as $N < K/2$. In this case any change in carrying capacity (K) will change both PRI and PER in the same direction as K (Fig. 5A).

(2) In the presence of social regulation PRI remains constant and will not be affected by N and K (Fig. 5B). In contrast, PER will be a monotonously decreasing function of N and K (Fig. 5B), implying that an increase in K will decrease PER whereas a decrease in K will increase PER.

Empirical data support the first group of predictions (Fig. 4). Unfortunately, I have found no data to either verify or reject the second group of predictions. Perhaps this may indicate that social regulation does not exist in the real world, but if it does I hope that this paper provokes a search for such data.

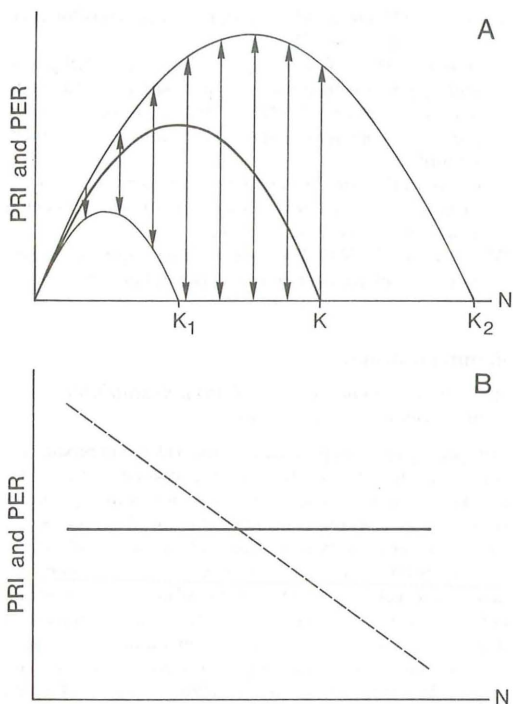


Fig. 5. Relationships between population rate of increase (PRI), population efficiency of converting resources into reproduction (PER) and population density. A: Without social regulation. Both PRI and PER are expected to show the same function of N . The effects on PRI and PER by changes in carrying capacity (resource abundance) from K to either K_1 or K_2 are indicated by the arrows at some given population densities. B: With social regulation. PRI (solid line) remains constant since the density of breeding units does not change with N . In this case, a change in carrying capacity will be compensated by a change in the density of non-breeding individuals so that PER (broken line) will be a monotonously decreasing function of N with its greatest value when no non-breeding animals are present.

Sambandet mellan populationens ökningshastighet (PRI), populationens effektivitet att omvandla resurser till reproduktion (PER) och populationstätheten. A: Utan social reglering. Både PRI och PER förväntas bero av N på samma sätt. Effekten på PRI och PER vid förändringar i biotopens bärighet (resurstillgång) från K till K_1 eller K_2 indikeras med pilarna vid vissa givna populationstätheter. B: Med social reglering. PRI (hel linje) håller sig konstant eftersom tätheten av häckande par inte ändras med N . I detta fall kompenseras en ändring av bärigheten med en ändring i tätheten av icke häckande individer så att PER (bruten linje) blir en ständigt minskande funktion av N med sitt största värde när det inte finns några icke häckande individer närvarande.

Acknowledgement

Thomas Alerstam, Sam Erlinge, Bo Ebenman, Torbjörn Fagerström, Mats Grahn, Görgen Göransson, Boel Jeppson, Charles Krebs, Olof Liberg, Jon Loman, Adam Lomnicki, Sigfrid Lundberg, Ingvar Nilsson, Jan-Åke Nilsson, Mikael Sandell, Henrik Smith and Håkan Wittzell kindly read the manuscript. Although I respect these persons' advices they will see that I have not responded to all (in some cases, to none) of their comments. Therefore they shall not be blamed for any inconsistencies, how unlikely it may seem, that still remain in the paper - these are all due to my own conceptual limitations. The study was supported by grants from the Swedish Natural Science Research Council.

References

- Andrewartha, H.G. & Birch, L.C. 1954. *The distribution and abundance of animals*. University of Chicago Press, Chicago.
- Begon, M. & Mortimer, M. 1981. *Population ecology: a unified study of animals and plants*. Blackwell, Oxford.
- Brown, J.L. 1969a. Territorial behaviour and population regulation in birds. *Wilson Bull.* 81:293-329.
- Brown, J.L. 1969b. The buffer effect and productivity in tit populations. *Am. Nat.* 103:347-354.
- Brown, J.L. 1975. *The evolution of behaviour*. W.W. Norton and Co. Inc., N.Y.
- Chitty, D. 1960. Population processes in the vole and their relevance to general theory. *Can. J. Zool.* 38:99-113.
- Clutton-Brock, T.H. & Albon, S.D. 1985. Competition and population regulation in social mammals. Pages 557-575 in Sibly, R.M. & Smith, R.H. (eds.). *Behavioural ecology: ecological consequences of adaptive behaviour*. Blackwell, Oxford.
- Colgan, P. 1979. Is a super-territory strategy stable? *Am. Nat.* 114: 604-605.
- Emlen, J.M. 1984. *Population biology: the evolution of population dynamics and behavior*. Macmillan Publishing Co., N.Y.
- Fretwell, S.D. & Lucas, H.I. 1969. On territorial behavior and other factors influencing distribution in birds. I. Theoretical development. *Acta Biotheor.* 19:16-36.
- Getty, T. 1979. On the benefits of aggression: the adaptiveness of inhibition and super territories. *Am. Nat.* 114:605-609.
- Hairston, N.G., Smith, F.E. & Slobodkin, L.B. 1960. Community structure, population control and competition. *Am. Nat.* 94:421-425.
- Haldane, J.B.S. 1957. The cost of natural selection. *J. Genet.* 55:511-524.
- Hassel, M.P., Lawton, J.H. & May, R.M. 1976. Patterns of dynamical behaviour in single populations. *J. Anim. Ecol.* 45:471-486.
- Hassel, M.P. & May, R.M. 1985. From individual behaviour to population dynamics. Pages 3-32 in Sibly R.M. & Smith, R.H. (eds.). *Behavioural ecology: ecological consequences of adaptive behaviour*. Blackwell, Oxford.
- Klomp, H. 1972. Regulation of the size of bird populations by means of territorial behaviour. *Neth. J. Zool.* 22:456-488.
- Klomp, H. 1980. Fluctuations and stability in great tit populations. *Ardea* 68:205-224.

- Krebs, C.J. 1985. Do changes in spacing behaviour drive population cycles in small mammals? Pages 295-312 in Sibly, R.M. & Smith, R.H. (eds.). *Behavioural ecology: ecological consequences of adaptive behaviour*. Blackwell, Oxford.
- Krebs, J.R. 1971. Territory and breeding density in the great tit, *Parus major* L. *Ecology* 52:2-22.
- Lack, D. 1954. *The natural regulation of animal numbers*. Oxford University Press, Oxford.
- Lack, D. 1968. *Population studies of birds*. Clarendon Press, Oxford.
- May, R.M. 1974. *Stability and complexity in model ecosystem*. Princeton University Press, Princeton, N.J.
- May, R.M., Conway, G.R., Hassel, M.P. & Southwood, T.R.E. 1974. Time delays, density dependence and single-species oscillations. *J. Anim. Ecol.* 43:747-770.
- May, R.M. & Oster, G.F. 1976. Bifurcations and dynamic complexity in simple ecological models. *Am. Nat.* 110:537-599.
- Maynard Smith, J. 1964. Group selection and kin selection. *Nature* (Lond.) 201:1145-1147.
- Maynard Smith, J. 1968. "Haldane's dilemma" and the rate of evolution. *Nature* (Lond.) 219:1114-1116.
- Maynard Smith, J. 1974. *Models in ecology*. Cambridge University Press, Cambridge.
- Maynard Smith, J. 1976. Group selection. *Q. Rev. Biol.* 51:277-283.
- McClerey, R.H. & Perrins, C.M. 1985. Territory size, reproductive success and population dynamics in the great tit, *Parus major*. Pages 353-373 in Sibly, R.M. & Smith, R.H. (eds.) *Behavioural ecology: ecological consequences of adaptive behaviour*. Blackwell, Oxford.
- Moss, R. & Watson, A. 1985. Adaptive value of spacing behaviour in population cycles of red grouse and other animals. Pages 275-294 in Sibly, R.M. & Smith, R.H. (eds.) *Behavioural ecology: ecological consequences of adaptive behaviour*. Blackwell, Oxford.
- Nicholson, A.J. 1933. The balance of animal populations. *J. Anim. Ecol.* 2:132-178.
- Patterson, I.J. 1980. Territorial behaviour and the limitation of population density. *Ardea* 68:53-62.
- Perrins, C.M. 1979. *British tits*. Collins, London.
- Pleasants, J.M. & Pleasants, B.Y. 1979. The super-territory hypothesis: a critique, or why there are so few bullies. *Am. Nat.* 114: 609-614.
- Rothstein, S.I. 1979. Gene frequencies and selection for inhibitory traits, with special emphasis on the adaptiveness of territoriality. *Am. Nat.* 113:317-333.
- Schantz, T. von. 1984a. Spacing strategies, kin selection and population regulation in altricial vertebrates. *Oikos* 42:48-58.
- Schantz, T. von. 1984b. Carnivore social behaviour - does it need patches? *Nature* (Lond.) 307:389-390.
- Smith, F.E. 1963. Population dynamics in *Daphnia magna* and a new model for population growth. *Ecology* 44:651-663.
- Southwood, T.R.E., May, R.M., Hassel, M.P. & Conway, G.R. 1974. Ecological strategies and population parameters. *Am. Nat.* 108: 791-804.
- Thompson, W.R. 1929. On natural control. *Parasitology* 21:269-281
- Tullock, G. 1979. On the adaptive significance of territoriality: comment. *Am. Nat.* 113:772-775.
- Verner, J. 1977. On the adaptive significance of territoriality. *Am. Nat.* 111:769-775.
- Watson, A. & Moss, R. 1970. Dominance, spacing behaviour and aggression in relation to population limitation in vertebrates. Pages 167-220 in Watson, A. (ed.) *Animal populations in relation to their food resources*. Blackwell, Oxford.
- Williams, G.C. 1966. *Adaptation and natural selection: a critique of some current evolutionary thought*. Princeton University Press, Princeton, N.J.
- Wynne-Edwards, V.C. 1962. *Animal dispersion in relation to social behaviour*. Oliver and Boyd, London.

Sammanfattning

Revirets lönsamhet och populationens stabilitet—kan populationer regleras socialt?

Det naturliga urvalet premierar de individer som producerar största mängden fortplantningsduglig avkomma. Varför leder då utvecklingen inte till populationer som exploaterar resurserna så effektivt och fortplanter sig så mycket att de överexploaterar resurserna och dör ut? I sin berömda bok från 1962 föreslog Wynne-Edwards att de flesta sociala beteenden hade utvecklats för att förhindra sådan överexploatering, och han ansåg att en av de kraftfullaste mekanismerna för att uppnå detta var att hålla revir. Tanken var att populationer som hade sådan social reglering skulle löpa mindre risk att dö ut än sådana som saknade dylik självreglering. Selektionen skulle alltså till stor del ske på populations- eller gruppnivå. Denna Wynne-Edwards's k gruppselektion utsattes emellertid för hård kritik och övergavs till förmån för selektion på individnivå. Ändå hävdar många ekologer att populationer kan regleras genom sociala beteenden.

I denna studie definieras populationsregleringen med hjälp av den logistiska ekvationen enligt vilken en individs genomsnittliga förokningsstakt minskar med ökande täthet: $(1/N) (dN/dt) = r(1 - (N/K))$, där r är den inneboende fortplantningsförmågan, N populationsstorleken och K biotopens bärighet för arten i fråga. Regleringen av populationen som helhet definieras också med den logistiska ekvationen: $dN/dt = rN(1 - (N/K))$. Med denna definition kan man nu teoretiskt bestämma vad som reglerar populationen genom att identifiera de faktorer som bestämmer bärigheten (K). Detta exemplifieras i Fig. 1. Här bestämmer tre resursnivåer K_1 , K_2 och K_3 populationsnivåerna N_1 , N_2 resp. N_3 . Anta att det i delfigur A är predationen som bestämmer K , i delfigur B resurserna för vinteröverlevnad och i delfigur C resurserna för häckning. Enligt definitionen är det då predationen som bestämmer N . Elimineras man predationen blir det i stället vinterresurserna som bestämmer N och eliminerar man också vinterödligheten blir det sommarresurserna som bestämmer N .

För att konkretisera begreppen används här stabilitet som en relativ term. Anta att en viss resurs, t ex föda, varierar i tiden motsvarande resursnivåer K_1 - K_3 i Fig. 1 och att det finns tre olika populationer med individtätheterna N_1 , N_2 och N_3 . Då får man det resultat som illustreras i Fig. 2. En förändring i resursnivå, t ex ΔR , påverkar populationen med den givna individtätheten n_i (motsvarande individtätheten N_i i Fig. 1) minst och n_3 (täthet N_3 i Fig. 1) mest. Därför definieras populationen n_1 som mest och n_3 som minst stabil. Den viktiga slutsatsen blir då att en förändring av resursmängden

föga påverkar en gles population men mycket kraftigt en tät population. Nu är frågan om sociala mekanismer, t ex revir, kan hålla populationen på en nivå som är lägre än den som bärigheten tillåter och därmed öka stabiliteten.

Watson och Moss satte 1970 upp fyra kriterier för att man skall kunna anse att en population regleras socialt, nämligen 1) en betydande del av populationen fortplantar sig ej trots att 2) dessa individer är fysiologiskt kapabla att göra det, 3) de häckande individerna uttömmar inte alla resurser men hindrar ändå konkurrenter från att göra det, samt 4) regleringen skall vara täthetsberoende. Man har hittat få om ens någon population som uppfyller alla kriterierna. Det verkar som om detta beror på att kriterium nr 3 är teoretiskt kontroversiellt.

Det är uppenbart att social reglering kan förekomma bara om de häckande individerna inte uttömmar resurserna ty eljest är det ju resurserna som sådana som sköter regleringen. Denna tanke är analog med den om s k super-revir som Verner förde fram 1977. Han menade att individer försvaret större revir än de behöver för optimal överlevnad och reproduktion genom att de på detta sätt höjer sin relativa anpassning, dvs inte ökar den egna absoluta anpassningen men i stället reducerar konkurrenternas överlevnad och reproduktion. Flera författare har emellertid funnit att detta inte fungerar enligt optimalitetsteorin därför att individerna med super-revir inte får någon extra vinst men måste bära de ökande kostnaderna för revirförsvaret. Om det är så förefaller det osannolikt att sociala beteenden kan reglera populationer utom i det fall en population använder den s k obstinata strategin enligt nedan.

Kan socialt beteende öka populationens stabilitet i en variabel miljö? Fig. 3 visar en enkel analys av kostnad och vinst för revirbeteende. Kostnaden för revirförsvaret ökar hela tiden med ökad revirstorlek. Vinsten ökar först snabbt men avtar så småningom och ökar inte alls när tillräckliga resurser finns inom reviret. I Fig. 3A representeras två populationer med kurvorna B_1 och B_2 , där den senare har tillgång till större resurser. Denna får därmed en mindre optimal revirstorlek (T_2) än den andra (T_1), vilket innebär att den når en högre populationstäthet. Detta i sin tur medför, enligt Fig. 2, minskad stabilitet. Samma effekt uppstår om i stället kostnaderna ändras, t ex från C_1 till C_2 enligt Fig. 3 B. Slutsatsen blir att sociala beteenden inte kan hålla en population på en nivå under bärigheten och inte heller kan stabilisera en population i en variabel miljö.

Ändå finns det åtminstone ett sätt på vilket sociala beteenden faktiskt kan hålla en population långt under bärighetsnivån, åtminstone temporärt. Jag har själv tidigare föreslagit att vertebrater som har permanenta revir, vars ungar kräver kotsam föräldravård och som lever på en varierande födokälla, håller revir av konstant storlek om deras livslängd är längre än den genomsnittliga perioden för födans variation. Revirets storlek bestäms av vad som behövs för att reproducera sig eller åtminstone överleva de tidpunkter då födotillgången är lägst. Det går till så att de häckande individerna tillåter släktingar att uppehålla sig i reviret men inte att häcka när födotillgången är riklig men kastar ut dem när det blir kärvt. Detta är den s k obstinata strategin. Här sker alltså en social reglering definitionsmässigt därför att resurserna inte helt konsumeras men andra djur förhindras att fortplanta sig. Antalet individer som fortplantar sig hålls konstant medan antalet individer som inte fortplantar sig växlar i takt med med resurstillgången. Det är just detta som illustreras i

Fig. 2, nämligen att populationens föryngringstakt knappast alls påverkas av resursvariationerna. Detta ger oss en testbar hypotes: för att effektivt kunna reglera en population måste socialt beteende medföra en negativ korrelation mellan populationens förmåga att omvandla miljöns resurser till avkomma (föroökningstakten) och populationstätheten. Vi återvänder därför till modellen i Fig. 1 och granskar data från en talgoxepopulation som studerats många år i Oxford.

Fig. 1 visar att om individernas genomsnittliga föroökningstakt minskar linjärt med ökande populationstäthet kommer högsta föroökningstakten på populationsnivå att inträffa när tätheten motsvarar $K/2$. Fig. 4A visar att detta var fallet för talgoxarna. Regressionskvantiteten ger en uppskattad bärighet för K på 260 par. Den högsta uppnådda tätheten var 172 par, sålunda långt under bärigheten. Lack menade att svält utanför häckningstiden var den viktigaste täthetsberoende regleringsfaktorn och Krebs stödde modellen i Fig. 3 B och menade att antalet häckare och därmed revirstorleken var en funktion av antalet som överlevde vintern. Följaktligen visade populationen inte någon täthetsberoende revirreglering. Eftersom alla datapunkter utom en ligger under $K/2$ skall antalet flygga ungar vara en positiv funktion av antalet häckande par. Så är också fallet enligt Fig. 4B, men det finns ingen korrelation mellan larvtillgången och antalet flygga ungar (Fig. 4C). Detta kan tyckas paradoxalt men eftersom antalet par nästan alla år ligger under $K/2$ stämmer bristen på korrelation med modellen i Fig. 2, enligt vilken populationens ökningstakt skall vara okänslig för resursförändringar vid låga populationstätheter.

Eftersom det förutsatts en konstant resursnivå i varje exempel i Fig. 1 skall en populations förmåga att omvandla biotopens resurser till ungar vara en positiv funktion av N så länge N är mindre än $K/2$. Detta visar sig återigen vara fallet för talgoxarna (Fig. 4D). Vi finner därför att det är först när N blir större än $K/2$ som den genomsnittliga individens förmåga att omvandla resurser till ökningstakt (PRI) liksom populationens ökningstakt som sådan (PER) blir en minskande funktion av N (Fig. 5). Dessa korrelationer får två viktiga konsekvenser när det gäller samspelet mellan PRI och PER. För det första innebär observationer av minskande genomsnittlig reproduktionstakt för individerna med ökande storlek av en grupp inte social reglering på populationsnivå. Det innebär inte heller att populationen blir mera stabil, tvärtom är det troligt att PRI blir känsligare för resursförändringar med ökande N . För det andra måste man vänta sig att både PRI och PER skall reagera på ändringar i N på samma sätt (t ex kurvan K i Fig. 5A) och vid alla värden av N även om effekterna är små för låga N . Den obstinata strategin ger ett helt annat resultat. PRI förblir konstant för alla N eftersom revirägarna håller ett revir av konstant storlek anpassat efter behovet de sämsta åren. PER kommer däremot att bli en ständigt minskande funktion av både N och K (Fig. 5B).

Slutsatsen av denna analys blir att när kostnaderna för revirförsvaret beror på revirstorlek eller trycket från konkurrenter kan social reglering inte stabilisera eller reglera populationer som bara hävdar revir vissa säsonger eller som har en livslängd som understiger miljöns variationsperioder. Social reglering kan bara förekomma hos arter som har permanenta revir och vars livslängd överstiger periodlängden i resursernas variationsmönster.