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Population regulation of cyclic mammals: the social fence hypothesis

Jay B. Hestbeck

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An alternative population regulation mechanism is hypothesized which integrates population regulation and social behavior. When neighboring densities are low, spacing behavior regulates a central population through emigration. As neighboring densities increase, the effectiveness of spacing behavior to regulate central population densities is impaired. When the neighboring areas reach a sufficiently high density, the neighboring groups socially "fence" the central population by inhibiting further emigration. Once emigration is blocked, population regulation is achieved through resource exhaustion. The social fence hypothesis proposes that the effectiveness of spacing behavior to regulate population densities decreases as the social impermeability of neighboring groups increases. The evolution, operation, and predictions of this hypothesis are discussed.

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Создана гипотеза относительно альтернативного популяционного механизма регуляции, интегрирующего регуляцию популяции и социальное поведение. При низких плотностях соседних популяций пространственное поведение регулирует плотность центральной популяции путем эмиграции. При возрастании плотности соседних популяций эффективность пространственного поведения с целью регуляции плотности центральной популяции ослабляется. Если на соседних участках достигается относительно высокая плотность, соседние группы социально "ограждают" центральную популяцию, тормозя дальнейшую эмиграцию. Когда эмиграция оказывается заблокированной, регуляция популяции осуществляется через истощение ресурсов. Гипотеза социального барьера предполагает, что эффективность пространственного поведения для регуляции плотности популяции снижается при увеличении "непроницаемости" соседних группировок. Обсуждаются развитие, разработка и прогнозы этой гипотезы.

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Introduction

Populations of several mammalian species go through cyclic fluctuations in density. Many alternate causal mechanisms have been hypothesized to account for the observed population fluctuations. The more prominent of these hypotheses concern resource depletion (Pitelka 1957, Batzli and Pitelka 1970, Keith and Windberg 1978), nutrient cycling (Schultz 1964), emigration (Anderson 1970), endocrine exhaustion (Christian 1980), change in individual quality (Chitty 1967, Krebs 1978), and multifactorial explanation (Lidicker 1973, 1975). In general these hypotheses concentrated on population processes operating within a group. It is my thesis that population regulation mechanisms must also incorporate interactions between groups.

I would like to propose the "social fence" as an alternate hypothesis which integrates population regulation and social behavior. The central mechanism of the social fence hypothesis is a positive feedback relationship between population growth rate and social group impermeability. The mechanism operates between social groups within a population. A social group is composed of several family units with adjacent home ranges. To simplify the discussion, only two social groups will be used. A central social group, the refuge group, occupies a position of good habitat. The social groups surrounding the refuge group will be collectively referred to as the neighbor group. The neighbor group occupies habitat of lesser quality.

After a population crash, individuals survive in areas of good habitat. The density is low within the refuge and near zero elsewhere. As the breeding season starts, aggressive interactions between individuals increase (Turner and Iverson 1973). At this time, refuge group individuals make brief exploratory jaunts into the neighboring areas. Since the neighboring areas are at a very low density, exploring individuals have a low probability of encountering area residents. With increasing aggression levels in the refuge group and few neighboring residents, explorers may remain in the new area.

At low neighbor densities, there is a high probability that refuge group explorers remain in the neighboring area. The neighboring group is very permeable to immigrating individuals. This results in a high emigration rate from the refuge group and, thus, a low refuge group growth rate.

As the breeding season continues, population densities increase in both the refuge and neighboring areas. Refuge group explorers now have a higher probability of encountering neighboring residents. The explorer faces a problem. Aggression exists in its present group. However, avoidance, dominance-submission behavior and learned hierarchies reduce the amount of agonistic behavior between individuals within a social group (Eisenberg 1966, Poole and Morgan 1973). Aggression results when an explorer encounters unfamiliar individuals in neighboring areas. It is widely recognized that

aggressive interactions are more intense between unfamiliar individuals than familiar individuals (Scott 1966, Poole and Morgan 1973, Getz and Carter 1980, Charnov and Finerty 1980, Bekoff 1981).

The explorer confronts two opposing aggression sources, within the social group and between social groups. If the between-social-group aggression is less than the within-social-group aggression, the explorer will emigrate. If the between-social-group aggression is greater than the within-social-group aggression, the explorer remains in the refuge group.

When the density of the neighboring group is sufficiently high, between-social-group aggression dominates and inhibits emigration. The neighboring group has become impermeable to immigrating explorers. Basically, the neighboring group has "fenced" the refuge population. Since population growth of the refuge is no longer reduced by the emigrating explorers, the growth rate increases.

During the low phase, spacing behavior regulates the population through emigration (Fig. 1). However, the effectiveness of spacing behavior to regulate population densities decreases as the social impermeability of the neighboring groups increases. At high densities, the neighboring groups socially "fence" a population by blocking further emigration. Once emigration is blocked, population regulation is achieved by the operation of the next most sensitive regulation mechanism. The next most sensitive mechanism is resource exhaustion. When an enclosure is constructed around natural populations, spacing behavior is pre-

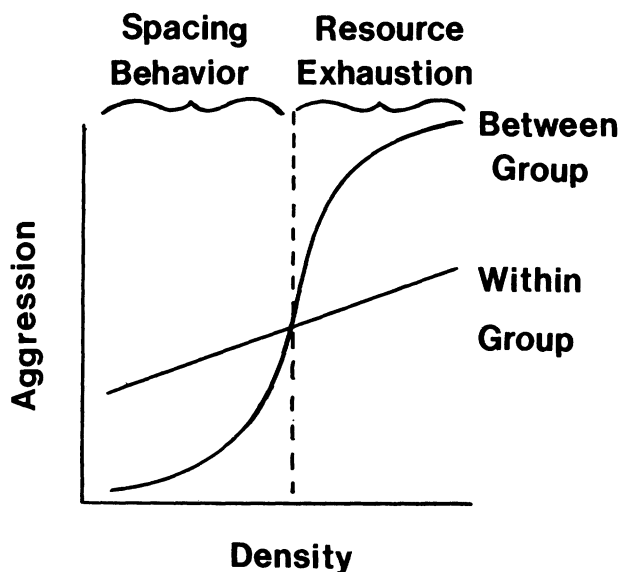


Fig. 1. When within-group aggression is larger than aggression between groups, spacing behavior regulates population densities. When between-group aggression is larger than within group aggression, population regulation is achieved through resource exhaustion.

vented and the population builds up to high densities, destroys the habitat, and declines. This "fence" effect has been observed in *Microtus ochrogaster* and *M. pennsylvanicus* by Krebs et al. (1969) and *M. townsendii* by Boonstra and Krebs (1977). However, if excess food is added to enclosed populations, the populations continue to increase and rise to densities higher than that obtained by unfed populations (Houlihan 1964, Ford 1978).

In order for the social fence to operate, two assumptions must be made. The first assumption requires that aggressive interactions between unfamiliar individuals are more severe than aggressive interactions between familiar individuals. Familiar individuals have previously established a dominant-subordinate relationship. Upon meeting, the subordinate automatically defers to the dominant individuals. If the individuals are not familiar, a dominant-subordinate relationship would not exist. The individuals would then fight and establish the hierarchy. Scott (1966) concluded that forced contact between unfamiliar individuals is a major factor inducing "destructive fighting". In the deer mouse *Peromyscus maniculatus*, individuals from adjacent home ranges showed less aggression than unfamiliar individuals (Healey 1967). Aggressive interactions between individuals declined exponentially as a colony of unfamiliar house mice, *Mus musculus*, developed a hierarchical social organization (Poole and Morgan 1973). Poole and Morgan (1975) also demonstrated that the dominant male in a hierarchical colony attacked male and female strangers ten and four times more frequently, respectively, than it attacked familiar subordinates.

The second assumption requires that social group size varies. Crook (1972) argued that an optimal group size should exist. However, if the surrounding environmental conditions change the optimal group size should also change. A varying social group size has been reported for the field vole, *Microtus agrestis* (Eisenberg 1966), the mountain vole, *M. montanus* (Jannett 1978), and the prairie vole, *M. ochrogaster* (Getz and Carter 1980). At very low densities social groups consisted of widely spaced pairs, while at high densities larger extended families developed.

Fitness and the social fence

The social fence hypothesis describes a process by which both dominants and subordinates maximize their fitness. The strategy which maximizes their fitness, however, changes as the refuge and neighboring group densities change. To best describe the changing strategy, the advantages and disadvantages associated with group membership must first be considered.

The disadvantages of group living largely result from increased predation, over-utilization of local vegetation, and reduced reproduction potential due to density ef-

fects. Predators have a higher probability of detecting groups of lemmings than solitary individuals. Pitelka (1973) has reported that highly mobile avian predators, the snowy owl and the pomarine jaeger, concentrate on high lemming densities. In fact, the presence of snowy owls is an indicator of locally high lemming densities (Pitelka 1973). Group living also increases predator capture success. Since local vegetation provides both food and cover, vegetational consumption reduces the cover needed to hide from predators. Group living reduces the amount of food resources available to each animal and therefore increases the likelihood of resource exhaustion. Batzli and Pitelka (1970) demonstrated that *Microtus* grazing at high densities reduced grass volume of major food plants by 85%. In natural enclosures, *Microtus* densities have reached high densities, overgrazed the vegetation and crashed (Krebs et al. 1969, Boonstra and Krebs 1977). Another disadvantage to group living is the decreased reproductive potential of subordinates within the group. Christian (1980) reported that partial or complete inhibition of reproductive function is correlated with increasing densities, and this response is much more pronounced in subordinate than in dominant individuals.

Group membership is advantageous when it lowers the intensity and frequency of aggressive interactions between individuals. If it is more difficult to enter a new group than remain in a present group, individuals remain in their present group. By remaining, inter-individual aggressive interactions are reduced and groups enlarge.

The strategy which maximizes fitness depends on whether the disadvantages or advantages for group membership dominate. When refuge densities are low to moderate (relative to carrying capacity) and neighboring habitats are at low densities, a dominant individual would maximize its fitness by expelling subordinates. Subordinates would maximize their fitness by dispersing into the low density neighboring habitats. At low to moderate densities, aggression levels within the social group are higher than between groups (Fig. 1). Spacing occurs and prevents larger groups from forming.

At high densities (relative to carrying capacity), neighboring areas are fully occupied. Since aggressive interactions between unfamiliar individuals are more intense than between familiar individuals, a subordinate minimizes aggressive interactions and possible severe injury by remaining with familiar individuals. The subordinate increases its chances of surviving, thus maximizing its fitness, by remaining in the present group and continuing to be submissive to the dominant. Since a dominant drives strangers from its home range, the subordinate also maintains a degree of protection from individuals potentially larger and more aggressive than itself. If subordinates are relatives of the dominant, the dominant maximizes its inclusive fitness by allowing the subordinates to remain within its home range. Ejec-

tion of subordinates into hostile areas could lead to the subordinate suffering severe injury. This reduces the subordinate's fitness and the dominant's inclusive fitness. When neighboring densities are high, aggression levels between social groups are higher than within a social group (Fig. 1). The group advantages dominate and groups form.

By becoming a subordinate at high densities, an individual lowers its reproductive potential relative to an individual which dispersed at low densities. However, the subordinate's reproductive potential at high densities is higher by remaining with the group than by entering a new group.

This mechanism is also valid if aggression of the dominant increases with density. An upper bound would exist on the intensity of aggression displayed by the dominant in expelling a subordinate if the subordinate is a relative. A higher upper bound would exist for aggressive defence of a home range against strangers. The defense upper bound should be higher than the expulsion upper bound, since the coefficient of relationship is lower between groups than within groups.

Discussion

Many alternate causal mechanisms have been hypothesized for the regulation of mammalian populations (see Introduction).

The social fence hypothesis is similar to both Lidicker's and Chitty's hypothesis when population densities are at low to moderate levels. At these densities, a spacing mechanism plays a significant role in population regulation.

During the low and increase phases of population growth, Lidicker (1975) hypothesizes, individuals emigrate into vacant regions. This emigration occurs well before the population reaches the carrying capacity and was thus referred to as presaturation dispersal. As long as vacant areas exist, presaturation dispersal continues.

According to the Chitty hypothesis, as modified by Krebs (1978), populations consist of increase and high density genotypes. Increase genotypes are adapted for reproduction and colonization, while the high density genotypes are adapted for conditions of mutual interference. As the population density increases, a genetically determined spacing behavior causes increase genotypes to disperse. Dispersal subsides as the proportion of increase genotypes decreases within the remaining population.

The similarity between Lidicker's, Chitty's and the social fence hypothesis ends as a population continues through the peak phase and into the decline.

The Chitty hypothesis, as modified by Krebs and Myers (1974) and Krebs (1978), incorporates a genetic behavior mechanism. Spacing behavior sorts out increase-genotype animals. A population reaches peak

levels once the population consists almost entirely of high-density genotypes, regardless of the actual density. The periodic fluctuations in numbers are generated by individual selection alternately favoring the increase and high-density genotypes. A density response time lag prevents the system from approaching a single equilibrium genotype.

According to the Chitty hypothesis, phenotypic differences between low and peak phase individuals result from genotypic differences. The low phase population has a high proportion of increase genotypes. The peak phase population consists almost entirely of high density genotypes. The social fence hypothesis, on the other hand, attributes phenotypic differences between low and peak phase individuals largely to environmentally induced effects instead of genotype.

Lidicker hypothesized that six factors, emigration, predation, competition, carrying capacity, physiological damage, and the onset of the wet season, are involved in explaining three to four year population fluctuations in the California vole, *Microtus californicus*. According to Lidicker, presaturation dispersal occurs at low densities. Once empty habitats are occupied, further presaturation emigration is prevented and population densities rise to peak levels. The increasing densities are stopped by a seasonally declining carrying capacity. The decline results from resource exhaustion, predation and saturation dispersal.

The social fence hypothesis differs from Lidicker's hypothesis in two ways. First, according to the social fence hypothesis, the emigration of individuals before a habitat has become saturated does not have a genetic basis. Lidicker (1962, 1975) suggested that presaturation dispersal may have a genetic basis and that a population may even be polymorphic for dispersal tendencies (presaturation and saturation). Second, the social fence hypothesis could explain population cycles if only the habitat carrying capacity and neighboring social group densities were known. Lidicker's hypothesis requires six factors.

Most of the remaining hypotheses on population regulation involve plant-herbivore interactions. The plant-herbivore hypotheses maintain that regulation occurs only when peak densities are reached. According to the social fence hypothesis, regulation through spacing also occurs at moderate densities. Once a social fence develops and inhibits spacing behavior, the local carrying capacity would then regulate population density.

Confusion concerning population regulation has resulted from the observation that many microtine populations do not fluctuate in the classic 3-4 year pattern. Insular populations commonly show annual fluctuations (Lidicker 1973, Tamarin 1977). Enclosed populations show annual fluctuations (Krebs et al. 1969, Boonstra and Krebs 1977). Also, many populations fluctuate irregularly (Garsd and Howard 1981).

Much of the between-population variation could be explained by the social fence mechanism if habitat

quality and spatial heterogeneity were considered. Habitat quality and spatial heterogeneity determine the speed required for the social fence to develop. Habitat quality has an important effect on a population's reproductive rate (Krohne 1980). The role of spatial heterogeneity is more subtle.

When good and poor habitats are adjacent, the population in the poorer habitat does not reach a sufficient density to inhibit emigration from the good habitat. The population is regulated by spacing and maintains a relatively constant, moderate density. A population of brown lemmings, *Lemmus trimucronatus*, on a six acre fertilized section of tundra did not cycle independently of the populations from surrounding areas (Schultz 1968). The lemming population would be regulated by spacing behavior. The increase in carrying capacity due to fertilization does not matter. On a two acre section of watered and fertilized short-grass prairie, prairie vole densities were moderate and fluctuated annually (Abramsky and Tracy 1979). Again, regulation would occur through spacing behavior and the artificially raised carrying capacity would not matter. In mountainous regions of Colorado and Utah, the preferred habitat of snowshoe hare, *Lepus americanus*, was very patchy. Dispersal of juveniles into surrounding low quality habitat maintained the snowshoe hare populations at stable, moderate densities (Dolbeer and Clark 1975). In all of these studies, the density of the neighboring social groups did not rise sufficiently to inhibit emigration from the best habitat. The artificially raised carrying capacity for the refuge group does not matter since regulation occurs through spacing behavior.

In large areas of uniformly good habitat, no difference exist between refuge and neighboring areas. All areas are permanently occupied. A social fence permanently exists and the population is regulated by the carrying capacity. The population has annual fluctuations. The amplitude of the fluctuation depends on the habitat quality. In Australia, very large areas of favorable habitat are present for rabbits, *Oryctolagus cuniculus*. Myers and Poole (1963) suggested that spacing behavior should regulate wild rabbit populations below the carrying capacity. However, spacing did not regulate densities in many rabbit populations throughout Australia. Populations behaved as confined populations. Despite density-related changes in fecundity, mortality, and social stress, rabbit populations repeatedly bred up to plague densities, overgrazed available vegetation and starved. Since favorable habitat existed over large areas, a social fence consistently existed. These rabbit populations were regulated by a seasonally fluctuating carrying capacity.

Insular populations are also regulated by the carrying capacity. In this case, spacing behavior is prevented by a physical barrier instead of a social barrier. This pattern has been observed in the Skomer vole, *Clethrionomys glareolus* (Jewell 1966), California vole, *Microtus*

californicus (Lidicker 1973), and Brewer's vole, *M. breweri*. These populations undergo annual fluctuations at densities above mainland populations.

In heterogeneous regions of good and marginal habitats, the form of population regulation varies. When only good habitats are occupied, spacing regulates the population. Dispersers from the good habitats move into adjacent marginal areas. Once the marginal habitats are fully occupied, social fences develop and the density rises to the carrying capacity. Resource exhaustion results and drives densities down. Since populations from marginal areas suffer greater losses, neighboring group densities drop below population densities in the good habitat. The social fence collapses and regulation is once again achieved through spacing. Populations in heterogeneous regions are alternatively regulated by spacing behavior and resource exhaustion.

When regulation alternates between spacing behavior and resource exhaustion, populations fluctuate between low and high densities. This mechanism depicts a classic microtine cycle. Pitelka (1957) described a single cycle for a population of brown lemmings at Barrow, Alaska. After a decline, the overall densities were extremely low and populations were highly localized. As the refuge populations started to grow, individuals moved into adjacent habitats until the neighboring populations contacted along broad fronts. Densities then rose to peak levels. With peak densities, "... virtually all herbaceous vegetation over vast acreages is cut" (Pitelka 1957: 14). Populations then declined.

The same pattern of early dispersal and subsequent population buildup, already discussed for microtines, parallels observations on the snowshoe hare, *Lepus americanus* (Keith and Windberg 1978, Wolff 1980). At low densities, hare populations survived only in local dense spruce or willow-alder refugia. As the refuge populations increased, individuals dispersed into neighboring, less favorable habitat. Spacing continued until hares were ubiquitous. Population densities then rose above the carrying capacity, destroyed the habitat, and declined.

In both the hares and the microtines, spacing behavior regulated the populations at moderate densities. Once neighboring areas became occupied, spacing was inhibited. Population densities then rose to the carrying capacity.

The relationship between snowshoe hare cycles and spatial heterogeneity has been observed by many authors (Howell 1923, Chitty and Elton 1937, Dolbeer and Clark 1975, Wolff 1980). The stability of snowshoe hare populations in the western United States has been related to areas with highly scattered preferred habitat. When habitat was more continuous, as in Canada, snowshoe hare populations were cyclic.

The spatial heterogeneity, population cycle relationship has also been noted in microtines. During the increase phase at Ahtiala, Finland, populations of field voles, *M. agrestis*, were concentrated in "permanent

production" habitats. At peak densities, the populations were more widely distributed over all habitat types (Myllymäki 1977). From his work in Central Sweden, Hansson (1977) noted that the relative distribution of habitat types regulated the total production of voles. Some landscapes have a low production while others have a high production.

Several predictions can be made from the social fence hypothesis. First, emigration from a central group, through the neighbor group and into a vacant area is inversely related to the density of the neighbor group. As the density of the neighbor group increases, the level of aggression associated with crossing the neighbor area increases. Once the crossing aggression exceeds the aggression promoting emigration, emigration from the central area decreases.

Evidence for an inverse density-dependent emigration has been reported. Calhoun and Webb (1953) stated that an inverse relationship between density and rate of invasion into the removal area existed in *Peromyscus*, *Clethrionomys*, *Blarina*, and *Sorex*. Krebs et al. (1978) demonstrated that Townsend's vole, *Microtus townsendii*, recolonized a removal area best when a central group was at a low density and undergoing growth. Recolonization was worse when the central-group density was high or declining. A 50 m strip separated the central and removal areas. At low densities, the neighboring group does not interfere with dispersal into the removal area, and recolonization would be good. At high densities the neighboring group inhibits dispersal, and recolonization of the removal area would be poor.

A second prediction from the social fence hypothesis is that a population will permanently be regulated by spacing if densities in neighboring areas are low or continually reduced well below a central population. Emigration regulated the central population of prairie voles at low densities continuously for four years (Abramsky and Tracy 1979).

Also, population regulation is predicted to result from resource exhaustion if neighboring densities are not sufficiently reduced below the density of a central population. Spacing did not regulate Brewer vole densities on Muskeget Island and the population fluctuated annually with resource availability (Tamarin 1980).

In an important philosophical advance, Lidicker (1978) adopted a multifactorial approach to the study of mammalian population regulation. The major benefit of Lidicker's multifactorial approach is that hypotheses need not be restricted to a single factor which must explain all phases of a population cycle. Lidicker's approach allows the integration of opposing ideas and, thus, the generation of entirely new hypotheses. The social fence is an example of a hypothesis generated from the multifactorial philosophy. In the future, I hope others also adopt a multifactorial philosophy.

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