1980

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The possibility of social regulation of wolf populations has been discussed in the literature for several years. Some of the first ecological studies of wolves indicated that their populations did not increase as rapidly as was theoretically possible, and that they reached a saturation point apparently not set by food. Subsequent captive studies demonstrated the existence of social mechanisms possibly capable of regulating population growth. However, the importance of these factors in wild populations has not been established. This paper has four objectives: (1) to evaluate the existing concept of "intrinsic limitation," (2) to propose that wolf population dynamics may be better understood by considering feedback between the prey resource and the wolf population, (3) to evaluate group selection explanations regarding evolution of "intrinsic limiting mechanisms," and (4) to propose an alternative explanation based on individual selection.

An overview of wolf biology is essential to understanding population dynamics of this species; the following summary is based on Mech (1970, 1972, 1977a). A wolf pack is a hierarchial, closed family group which maintains a territory. Wolves mate in February or March and 2 months later bear an average of five or six pups. Under good conditions, pups are full grown by autumn and accompany adults during winter. Some offspring may remain with the adults as successive litters are born; many die or disperse.

Usually, only one pair breeds in a pack, although wolves are not strictly monogamous, and several females may come into estrus within the group. Nonbreeding pack members help breeders in hunting and care of young. Wolves that disperse from packs usually wander over large areas and avoid packs (Mech and Frenzel 1971; Mech 1973 and

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unpublished). The mortality rate of these lone wolves is high (Mech 1977c). They do not reproduce until they are able to acquire a mate and a territory (Peters and Mech 1975).

Intrinsic Limitation

Four of the early ecological studies of wolves dealt with low populations that increased more slowly than was theoretically possible. Murie (1944) speculated that disease and intraspecific strife affected wolf mortality rates in Alaska and that productivity was reduced because only one or two females in a pack bred. In the Rocky Mountain National Parks of Canada, Cowan (1947) suggested that the low wolf density may have resulted from a disproportionate sex ratio. Intraspecific strife and low productivity were postulated as factors limiting a wolf population artifically introduced to Coronation Island, Alaska (Merriam 1964). This population showed only 10% of the growth theoretically possible. Increase of the wolf population in Alaska's Game Management Unit 13 was also comparatively slow, and Rausch (1967) cited poor pup survival, social restrictions on mating, and intraspecific strife as possible limitations.

Stable wolf populations were described in three studies. In northeastern Minnesota, the population in the Superior National Forest remained relatively stable from 1948 to 1953 (Stenlund 1955). Predator control programs and food supply were considered to be the major factors controlling wolf numbers. Stenlund also speculated that territoriality, disparate sex ratios, and a surplus of nonbreeders were important limiting factors in protected areas. On Isle Royale (Lake Superior) the wolf population remained relatively stable from 1959 to 1972, even though it was not exploited and prey populations were high (Mech 1966; Jordan et al. 1967; Wolfe and Allen 1973). Intraspecific strife and low pup productivity or survival on the island were the causes postulated for the stability.

During the same period, Pimlott et al. (1969) studied a recently protected wolf population in Algonquin Park, Ontario. This population increased and then stabilized despite an apparent abundance of food. Reviewing previous studies, Pimlott (1970, p. 66) concluded that

The density of wolf populations appears to be regulated by intrinsic mechanisms. In two areas where wolves had an abundant food supply and were

completely protected, the density stabilized at a level of approximately 10 wolves per 260 square kilometers (100 square miles). Over very large areas of Canada and Alaska, the density of the wolf population rarely exceeds 10 wolves per 2,600 square kilometers (1,000 square miles) and is often much lower (Mech 1966; Pimlott 1967).

This "intrinsic limitation" concept became generally accepted (Mech 1970). When food was abundant, populations were expected to increase to the density of about 10 wolves/260 km^2, a kind of "saturation point." Presumably at this density, social behavior would make space a limiting factor, and the population would remain relatively stable. According to this idea, the saturation point would occur at a level below where food resources would be adversely affected.

The concept of intrinsic limitation in wolves fit well with behavioral observations of captive packs. Schenkel (1947) had noted that generally only the dominant pair bred within a wolf pack. Six years of observations of the pack at Brookfield Zoo in Chicago confirmed this general rule, although there were a few exceptions (Rabb et al. 1967). Breeding was limited by strong mate preference, intrasexual and intersexual aggression, and immaturity.

Conjecture then arose as to whether the foregoing factors explained the low productivity of wolf populations in the wild (Woolpy 1968). Rabb et al. (1967), Woolpy (1968) and Fox (1971) used the terms "birth control" and "contraception" in discussing the behavioral conventions regulating breeding. To explain the high birth rate in exploited Alaskan populations (Rausch 1967), compared to the Isle Royale population, Woolpy (1968) speculated that birth control mechanisms had broken down when the social organization of the wolf population was destroyed by human hunting.

Ecological and behavioral information was integrated by Mech (1970) in a general discussion of the factors regulating pack size and number of breeding units in a population. He visualized (1) the growth of packs as regulated by social bonds and by competition for food and (2) the number of breeding units as regulated by territoriality and prey density. This theory strongly implied that upper limits of wolf populations were set by intrinsic social mechanisms.

The concept of intrinsic limitation in wolves, however, has yet to be critically evaluated. Is it accurate to speak of a saturated wolf density that is limited independently of food resources? Does intrinsic limitation mean more than just a low growth rate of the population? How

does the concept relate to population adjustments in response to fluc-tuating food resources?

For two reasons, we believe that the concept of intrinsic limitation has become outdated in view of recent information. First, there does not appear to be a universal saturation point determined by social be-havior but independent of food. Wolf populations in several areas reached almost twice the alleged saturation density of 10 wolves/260 km² when prey increased or became more vulnerable (Kuyt 1972; Par-ker 1973; Van Ballenberghe et al. 1975; Peterson 1979). In other stud-ies, summer food was an important factor in wolf pup survival (Van Ballenberghe and Mech 1975; Seal et al. 1975), even in the presence of abundant winter prey (Peterson 1977). Second, "intrinsic limitation" focuses on the role of social behavior in limiting population growth. We believe that social behavior is also important in population declines induced by food shortage. The mechanisms involved have been de-scribed by Zimen (1976) and Mech (1977c).*

Population Regulation

We define regulation of a population as a continual adjustment of num-bers to a level determined by critical resources. As vulnerable prey biomass declines, the wolf population declines. Feedback mechanisms exist that allow wolf numbers to increase as vulnerable prey biomass increases. The term "regulation" as used here describes two-way feed-back between components of the predator/prey system. Prey density affects wolf numbers, and wolves affect prey populations.

This approach is an intentional departure from the "equilibrium setpoint" view of population dynamics (Murdoch 1970). Theoretically, one can describe the components and their characteristics of the system (wolf and prey densities, age structure, health, vulnerability, etc.) and we can describe the relations influencing changes among the compo-nents. From this knowledge, one could predict how any given popu-lation would change with fluctuating resources. This approach con-trasts with the view that predator/prey systems tend toward equilibrium.

Editors' Note: The assumption that there is an intrinsic and constant upper limit to the population density of wolves should also be evaluated in the light of the observation by Terman that even under controlled laboratory conditions, rodent populations stabilize at irregular and unpredictable levels of density.

We adopted the concept of regulatory feedback in order to describe populations with fluctuating food resources.

The analytical questions to be asked using the concept of regulatory feedback are: (1) What events take place during adjustments in wolf populations (how do changes in resources translate into changes in reproduction, survival, and mortality)? and (2) How "tight" is the feedback between fluctuations in critical resources and population levels? The concept of tight versus loose regulation was elaborated by Murdoch (1970). A population shows tight regulation if it returns to a density determined by constant resources when displaced above or below that density. If regulation is nonexistent, a population would tend to persist at whatever level it is set, independent of fluctuations in critical resources (Murdoch 1970). Loose regulation may be identified by a lag in population change.

Eberhardt (1977) outlined a general progression of regulatory events that occur as mammalian populations encounter food shortages: (1) decreased survival of young, (2) delayed maturity, (3) reduced reproduction, and (4) increased adult mortality. In wolf populations, social behavior contributes to this same sequence of events (Mech 1977c). As a result, social behavior often seems to be the proximate cause of numerical change which is ultimately controlled by food.* We view the social factors that are independent of food as influencing the lag time, or tightness of population regulation.

Information from northeastern Minnesota and Isle Royale illustrate the feedback relations between wolf populations and their prey. The northeastern Minnesota wolf population appeared relatively stable from winter 1966–67 through winter 1968–69 (Mech 1977c). Maturing habitat, wolf predation, and a series of severe winters beginning in 1968–69 caused a drastic decline in deer numbers (Mech and Karns 1977). The wolf population increased by 32% in 1969–70, but then decreased annually until by winter 1974–75 it was less than half the 1969–70 level (Mech 1977c). Malnutrition of pups was evident from

*Editors' Note: This is the most explicit statement in the volume concerning the interaction of social and nutritional factors in population regulation. The paucity of such statements elsewhere reflects perhaps the absence of adequate information on the relation between population and food supply for most natural populations and the more specialized nature of most controlled studies. Since the wolf is a social carnivore, it is possible that the mechanisms by which wolves adjust to their food supply would be instructive in the study of another species often portrayed as a social carnivore, early *Homo sapiens*. The contrast between the conclusions of Packard and Mech and the issues debated by Cohen, Hassan, Ripley, and Lee should be noted.

1971 through 1973, causing 30% of the wolf mortality in those years, and by 1974, the number and sizes of litters had declined (Mech 1977c).

Several behavioral, social, and ecological changes became evident in the wolf population in response to the reduced consumption rate (Mech 1977a). Intraspecific strife increased as packs trespassed into other territories on hunting trips, and in 1974 and 1975, all the natural mortality in the study population of radioed wolves was caused by other wolves (Mech 1977c).

On Isle Royale the wolf population had also been relatively stable, averaging 22 individuals for 7 years, with one breeding pack (Mech 1966; Jordan et al., 1967; Wolfe and Allen 1973). In general, pup production appeared good in years when moose calf production was high, and poor when calf production was low (Peterson 1977). A confusing situation existed from 1966 to 1969 due to the breakup of the large breeding pack, immigration of a pack from the mainland, and possible emigration of some wolves from the island. As a result, in 1969 the population was at a low of 15–17 individuals (Wolfe and Allen 1973).

The Isle Royale wolves showed an immediate behavioral response to increased moose vulnerability from 1969 to 1972. They killed more moose and utilized them less completely (Peterson 1977). The wolf population, however, showed little numerical increase until about 1972 (Peterson 1977). By 1976 the population had increased to 44 animals, and the number of breeding units from one to three (Peterson 1979). During this period, the moose population had decreased from 1,300–1,400 in 1969 to 800–900 in 1976 (Peterson 1979). Moose malnutrition was high, calves were small, and the wolf kill of calves and weak yearlings was considerable. By 1977, the wolf population declined to 34 individuals. Probably the wolves had killed the most vulnerable moose, and were again faced with a food shortage.

The preceding discussion of the northeastern Minnesota and the Isle Royale wolf populations demonstrates that (1) food supply does critically affect wolf numbers over the long term, and (2) numerical response to changes in available prey biomass may lag a few years. We hypothesize that social factors directly and indirectly affect population size. Direct effects include intraspecific strife and limitation of the number of breeding females. Social factors interact indirectly with

nutritional factors in determining which segment of the population will be most influenced by fluctuations in food resources.

Social Factors

Territoriality and Intraspecific Strife

The theory that territoriality functions in the natural control of populations is long standing (Elton 1950). Murie (1944) was the first to observe intraspecific strife among wolves and to comment on its potential function in population regulation. He speculated that it would keep wolves at an optimum level in relation to prey resources. Since then, many observations of intraspecific strife among wolves have been recorded (Cowan 1947; Mech 1966, 1972, 1977c; Jordan et al. 1967; Mech and Frenzel 1971; Mahrenke 1971; Wolfe and Allen 1973; Van Ballenberghe and Erickson 1973).

Extensive studies in northeastern Minnesota have shown that the wolf population there is spatially highly structured. Reproductive packs occupy exclusive territories, with nonreproductive lone wolves occupying the buffer zones between territories (Mech 1972, 1973, 1977a). This spacing is maintained both by aggressive encounters and by advertisement of a pack's presence through scent marking and howling (Peters and Mech 1975; Harrington and Mech 1979). Such spacing in a saturated population makes it nearly impossible for new breeding units to become established unless major perturbations occur in the system. In a low-density population, new breeding pairs are able to establish territories (Mech unpublished).

If adjacent packs travel in the overlap zones between territories, they run a greater risk of encountering each other (Wolfe and Allen 1973). While prey was abundant in northeastern Minnesota, wolves were unlikely to kill deer in the buffer zones (Hoskinson and Mech 1976; Mech 1977a,b). However, as prey became scarce, they appeared more likely to make kills in those areas, and to trespass into other territories, running a greater risk of fatal encounters with neighboring packs (Mech 1977c).

The amount of vulnerable prey biomass is probably important in determining the size of territories. For example, after having used most of Isle Royale for several years, the "West Pack" confined its travels

to one end of the island in 1971, when sufficient prey could be killed in that smaller area (Peterson 1979). This change seemed to fit the "elastic disc" theory of territoriality (Huxley 1934).

However, there seems to be enough flexibility in wolf consumption rates, activity levels, reproductive rates, and pack sizes that territory sizes are adjusted to food supply only within wide limits. In northeastern Minnesota, most wolf packs maintained their territories despite gross changes in deer numbers (Mech, unpublished). One wolf pack studied for 7 years occupied the same basic territory when it contained nine members as when it included only two, although size adjustments did occur along the buffer zones (Mech 1977a).

Thus, territoriality affects population size primarily by parceling a population's range into a limited number of areas, each supporting a reproductive unit. Secondarily, territoriality reduces wolf numbers through the mortality or injury that sometimes occurs when packs defend their territories.

Exclusive Breeding
Productivity of the population is regulated by the number of breeders per reproductive unit as well as the number of breeding units per area. Wolf packs sometimes contain 20–30 members, although they usually include 8–10 (Mech 1970). Nevertheless, usually only one or two females produce young each year. For example, in reviewing the research on Isle Royale, Wolfe and Allen (1973, p. 628) commented: "It has become increasingly evident during these studies that restrictions on breeding constitute an important factor in the regulation of wolf numbers on Isle Royale. Ordinarily only one or two females are actually observed to breed out of perhaps twelve females on the island."

Of 20 packs studied for from 1 to 8 years in northeastern Minnesota, Mech (unpublished) has never found evidence that more than one female in a pack bore a litter of pups. A few cases have been observed elsewhere of two females in a pack producing young in the wild (Murie 1944; R. O. Peterson, personal communication), and attempted breeding or pregnancy in more than one female in a pack has been reported in the wild (Jordan et al. 1967; Rausch 1967; Peterson 1977; Peterson and Allen 1976). However, in most such cases, extra litters probably fail to survive, as observed by Peterson (personal communication). In captive wolf packs, parallel observations have been reported (Rabb et

al. 1967; Lentfer and Sanders 1973; Altmann 1974; Zimen 1975; Klinghammer et al. 1977).

The effect of a breeding system in which only one female per pack usually reproduces successfully is obvious. In larger packs, there would be several females, and if all bred, the breeding potential of the population would be much higher than it is. On the other hand, this breeding system might also allow an extra female to breed and raise young successfully if food were in abundance.

Age of Maturity
An important reproductive parameter influencing population growth is age of maturity (Cole 1954). In wolves, females usually do not mature until their second or third year. From examination of 246 pup reproductive tracts, Rausch (1967) concluded that ovulation was extremely rare in pups. In the Brookfield Zoo pack, females born after the group was established did not breed in their second year despite high social rank (Rabb et al. 1967; Woolpy 1968). Numerous other reports attest to the general rule that juvenile females rarely breed (Murie 1944; Young 1944; Lentfer and Sanders 1973; Zimen 1975).

However, under certain circumstances, the female wolf's reproductive system is capable of maturing at 10 months of age (Medjo and Mech 1976; Zimen 1975; Seal et al. 1979). This opens the possibility that ordinarily maturation is delayed through social suppression, poor nutrition, or some combination of these factors (Medjo and Mech 1976). Intriguing laboratory studies with rodents indicate that maturation may be delayed by poor nutrition or pheromones from grouped females, or may be accelerated by exposure to male urine (Vandenbergh 1973). If these effects occur in wolves, age of maturity could be a very important social factor helping to regulate wolf numbers.*

Some of the nonbreeding females observed in the wild and assumed to be socially suppressed (Wolfe and Allen 1973) may have been physiologically immature, since it is impossible in the field to reliably separate immature from mature wolves without physical examination.

Behavioral maturity may be just as important as physical maturity (Woolpy 1968). Behaviorally inexperienced young—even though

*Editors' Note: See Christian and Drickamer for further discussions of the mechanisms by which reproductive system maturation is accelerated or suppressed or delayed among rodents and primates.

physiologically mature—probably are at a serious disadvantage when competing sexually with their parents and/or older siblings. This inexperience may well explain the observations in the Brookfield Zoo pack cited above.

Dispersal

Wolves dispersing from a pack may facilitate a population decline in dense populations, and contribute to a population increase in sparse populations. In a saturated population, they are chased by resident packs (Mech 1966; Jordan et al. 1967; Mech and Frenzel 1971; Wolfe and Allen 1973) and have a decreased survival rate (Mech 1977c). They form a breeding surplus, ready to fill in openings that arise in packs (Mech unpublished). In addition, if two loners succeed in establishing a territory, they may form the nucleus of a new pack (Mech 1972, 1973; Peters and Mech 1975; Rothman and Mech 1979).

We know from the Minnesota studies that wolves may disperse at ages ranging from 9 to 28 months or more, and that some wolves born to a pack may remain with the group until at least 4.5 years of age (Mech unpublished). The effect of nutritional, social, and maturational factors on dispersal is still undetermined.

From captive studies, two types of dispersing individuals have been postulated—those which leave voluntarily, and those forced out as a result of intense sexual competition among siblings and between parents and offspring (Zimen 1976). In captivity, serious harassment of subordinate or dominant individuals, and severe dominance fights sometimes resulting in deaths, have been reported (Rabb et al. 1967; Zimen 1975, 1976; Packard et al. unpublished). Zimen (1976) postulated that dispersal may be negatively related to food availability. He found that oppression of subordinates increased and new rank relations were established as hunger increased. Low-ranking pack members were sometimes not allowed to feed. Perhaps they are more likely to leave voluntarily if hungry (Murie 1944; Mech 1970; Zimen 1976).*

Disparate Sex Ratios

Cowan (1947) was the first to suggest that "anything which upsets the 50:50 sex ratio in a monogamous species such as the wolf will exert

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Editors' Note: Compare the discussion of two types of dispersing individuals in rodent populations provided by Tamarin as well as suggestions by Freedman that there are also individual variations among human beings in their tolerance of density-related situations and their inclination to emigrate.

profound influence upon the reproductive potential of the population." He found a 15:10 ratio of males to females in the Rocky Mt. National Parks of Canada, and concluded that the unbalanced sex ratio along with natural mortality and disease were enough to hold the population at low levels. Stenlund (1955) reported an 18:10 sex ratio in Minnesota, and agreed with Cowan.

Mech (1975) found that higher percentages of male pups were produced, or at least survived, in Minnesota wolf populations with higher densities. As food resources declined in northeastern Minnesota, the percentage of males in the dense population rose even further. The importance of sex ratios in regulating populations may vary under different environmental conditions. Evidence is still scarce, but we would expect to find the following: (1) since males tend to disperse farther than females (Mech unpublished) in saturated populations, a preponderance of dispersing males would reduce the number of lone wolves in the local population; and (2) in populations faced with a food shortage, fewer females would result in fewer potential pairs to fill in vacant territories created when packs break up due to territorial strife. The degree of influence of these various social factors probably varies depending on the ecological balance between density of a wolf population and its food resources. As outlined in table 6.1, the reproductive success of individuals in different social categories may also vary.

Interaction between Social and Nutritional Factors

Social factors may slow the growth rate of an expanding wolf population, but they do not necessarily prevent malnutrition. We propose that social factors promote wolf population regulation in three ways: (1) they cause the actual rate of increase of a population to be considerably lower than the potential rate of increase; (2) they delay the numerical response of a population to major fluctuations in vulnerable prey biomass; and (3) they result in unequal distribution of food resources among pack members, predisposing certain segments of the population (low-ranking individuals) to malnutrition.

Compared to populations of nonterritorial, solitary species with comparable fecundity and mortality, wolf populations show a much greater discrepancy between potential and realized rate of increase. Territoriality limits the number of breeding units, and the dominance hierarchy limits the number of breeders within each unit.

Table 6.1. Differences among Reproductive Categories of Wolves with Different Densities and Prey Resources

High density/High resources	*High density/Low resources*
1. Dense stable population	1. Declining population
2. Intermediate pack conflict	2. High probability of pack conflict
3. Biders have moderate success depending on mortality due to intraspecific strife	3. Biders most successful since more breeding females killed in intraspecific strife
4. Dispersers unlikely to acquire territory	4. Dispersers unlikely to acquire territory
5. Low proportion of breeding females	5. High proportion of breeding females due to low productivity and high mortality of subordinates and loners
Low density/High resources	*Low density/Low resources*
1. Increasing population	1. Sparse, stable population
2. Low probability of pack conflict	2. Low probability of pack conflict
3. Biders less successful since death of breeder is unlikely	3. Biders less successful since death of breeder is unlikely
4. Dispersers most successful at establishing territories	4. Dispersers may establish territory but not raise pups because of malnutrition
5. Breeders highly successful	5. Intermediate to low proportion of breeding females since dispersers unlikely to breed
6. High proportion of breeding females, since dispersers establish new packs	

A lag in the numerical response to fluctuations in prey resources was apparent in the declining phase of the wolf population of northeastern Minnesota (Mech 1977c) as well as in both the increasing and declining phases of the Isle Royale population (Peterson 1979). Territoriality in a saturated population functions to buffer the decline of wolves in the initial stage of a food decline. Packs are "forced" to utilize kills more efficiently (Pimlott et al. 1969; Mech unpublished), when vulnerable prey are less available inside their territories. They can exploit previously protected prey found along the buffer zones between packs (Hoskinson and Mech 1976; Mech 1977a,b), and can switch at least temporarily to other prey (Mech 1977a).

Alternatively, a wolf population might lag behind an increase in prey if the prey remain in unhunted refuges between pack territories. Furthermore, a population may not respond to increased prey if the abundance occurs outside the pup-rearing season (Peterson 1979). Evaluation of food required for successful reproduction is very difficult (Mech 1977a), complicating clear discrimination of the role of social factors.

When food supplies become inadequate, the subsequent malnutrition of subordinate wolves has a strong social basis (Mech 1977a). Relative to a species where all females were affected equally by the nutritional deficit, productivity of wolves would not decline so rapidly because nonbreeders would perish before the reproductive capacity of breeding animals would be severely impaired (Mech 1977a,c).

In terms of predator/prey stability, the varied effects of social behavior described above would combine to produce a lag in the response of the wolf population to fluctuations in food. Such loose feedback would tend to foster predator/prey oscillations.

Earlier claims that wolf populations are limited by intrinsic social factors were partly correct, but the influence of food supply now appears to be more important than was previously recognized. The challenge for the future remains to delineate the precise conditions under which, and mechanisms by which, nutritional and social factors operate independently as well as together in regulation of wolf populations. This is one of the primary objectives of the continuing studies in northeastern Minnesota.

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