Social Organization in Deer: Implications for Localized Management

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ABSTRACT / Populations of white-tailed deer (*Odocoileus virginianus*) inhabiting many state and national parks and suburban areas have grown to the point that they conflict with human activities. Conflicts range from destruction of vegetation through browsing to public perception that diseases carried by deer pose threats to human health. Traditional modes of hunting to control populations are inappropriate in many of these areas because of intense human development and activity. This article explores an alternative approach for population reduction based on deer social organization. Female white-tailed deer are highly philopatric and female offspring remain near their dams for life. This suggests that a population expands slowly as a series of overlapping home ranges in a form analogous to the petals on a rose. Incorporating the rose petal concept into a model of population growth shows that removal of deer by family unit can potentially alleviate conflicts in localized areas for as many as 10–15 yr.

Populations of white-tailed deer have grown significantly in the past 35 years throughout the eastern United States. In most states, deer harvests during the 1980s were at record levels. Increases in deer populations on some areas not open to hunting, such as state and national parks, exceed 40/km^2 (Table 1). Similar densities are reported in suburban areas such as Chicago (Witham and Jones 1987) and Minneapolis-Saint Paul (Sillings 1987).

As deer populations have grown, they have come into conflict with human activities. Conflicts are often most pronounced in parks and suburban areas where management through population reduction is considered impractical or inappropriate. In suburban areas, deer cause extensive damage to ornamental plants and to flower and vegetable gardens (Connelly and others 1987, Witham and Jones 1987). In parks, browsing of vegetation by deer is causing significant changes in plant community structure and composition, which, in many cases, is in conflict with vegetation management objectives (e.g., Storm and others 1989, Underwood and others 1991).

There is also growing awareness of potential impacts of deer on public safety and health. Issues of public safety pertain primarily to the incidence of automobile collisions involving deer. For instance, deer using Gettysburg National Military Park comprised 15%–29% of all deer–automobile collisions ($\bar{X}$ = 312 total accident/yr, SE = 62) in South Adams County, Pennsylvania, from 1983 through 1987. The park and its immediate surroundings are 4% of the land area of the county (Storm and others 1989.)

Most of the public concern of the eastern seaboard is focused on the risk of Lyme disease. Connelly and others (1987) report that while most people in Westchester County, New York enjoy seeing deer, 72% are concerned about the role of deer in the prevalence of Lyme disease. The primary vector for the disease is the deer tick, *Ixodes dammini,* and deer serve as a primary host for the adult stage of the life cycle. While deer do not show clinical symptoms of Lyme disease and do not serve as a reservoir for the causative agent (Telford and others 1988), their role in the transmission of the disease is unclear (Wilson and others 1984).

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Table 1. Dispersal rates in white-tailed deer at different population densities

Density (/km²)	Dispersers/ marked sample	Reference
<0.4	7/35 A[a]	Nelson (1990)
26	9/53 Y	Dusek and others (1989)
3	4/74 A	HWF 1970s data[b]
7	0/75 A	HWF 1980s data[b]
28	1/48 A	Simon (1986)
39	4/73 Y	Hawkins and Klimstra (1970)
40	1/53 A	Underwood and others 1991
78	1/21 A	Kammermeyer and Marchinton (1976)

[a]Samples are drawn from females of all female age classes (A) or from yearling females (Y).

[b]Data collected by authors on the Huntington Wildlife Forest (HWF) in the central Adirondack Mountains of New York.

Coping with the economic consequences of vegetation and health problems poses a serious management dilemma. Estimates of the economic losses associated with deer in suburban settings have not been widely measured but appear to be very significant. Witham and Jones (1987) estimate the losses in Cook County, Illinois, average $1306/automobile collision. Connelly and others (1987) estimate losses due to deer browsing of ornamental plants in Westchester County, New York, during 1986–1987 to be $6.4 million to $9.5 million.

Given that hunter harvest of female deer regulates population size in most areas and that hunting is generally inappropriate in parks and suburban areas, how can deer populations be managed? This article synthesizes findings from 25 yr of study we have conducted on the behavior and ecology of white-tailed deer in New York and suggests that an understanding of the social organization of deer may offer a solution to this dilemma. We present a new hypothesis that merits testing: Direct reduction of deer populations, using social groups as the target for reduction, is possible on geographic scales appropriate to suburban areas and parks.

Background

Beginning in 1964, a series of research efforts were undertaken to examine the behavior and ecology of white-tailed deer on the Huntington Wildlife Forest (HWF) in the central Adirondack Mountains of northern New York State. The central Adirondacks are characterized by rugged topography and nearly contiguous forest. The HWF is a 6000-ha, privately owned experimental forest. Elevations range from 400 to 900 m; snow cover ≥380 mm persists an average of 75 ± 7 days ($\bar{X}$ ± SE, time period = 1965–1987). Vegetation is dominated by sugar maple (*Acer saccharum*), American beech (*Fagus americana*), red spruce (*Picea rubens*), and hemlock (*Tsuga canadensis*).

Population surveys for white-tailed deer were initiated in 1966 on the Huntington Forest using three techniques. Counts of deer observed along roads were recorded during the summer months. Tracks observed on roads within the first 24 h after the surface had been raked served as indices to population changes. Finally, deer drives were conducted to estimate population density (Behrend and others 1970, McCullough 1979).

Intensive radiotelemetry studies began in 1969. Investigations conducted during 1969 through 1977 examined seasonal movement patterns (Sage and others 1983, Tierson and others 1985). Beginning in 1985, more detailed studies of social behavior were undertaken. Radiotelemetry and genetic analyses were used to identify membership of family units and spatial location of individuals within these family units during the time they were on summer range (Mathews 1989).

In 1966, experimental deer harvest was undertaken on a 2086-ha unit of HWF. An adjacent 3000-ha portion of HWF was reserved from hunting as a control. The experiment represented the first harvest of any kind in this population since the early 1930s. Late summer deer populations during 1966–1968 on HWF and throughout the region were estimated to be 10–12/km² (Behrend and others 1970, Sage and others 1983). During 1966–1970, there was a total of 270 animals (132 males and 138 females) removed, with the 50% reduction in the population density being achieved after two hunting seasons.

Three consecutive severe winters, 1968–1969 through 1970–1971, reduced populations in the hunted area to <1 deer/km², and hunting was suspended after the harvest in the autumn of 1970. Deer densities on the unhunted portion of HWF were estimated at 5–7/km². Densities on adjacent state lands were believed intermediate to those on HWF. The deer harvesting experiment was resumed after the hunted population recovered to an estimated 3 deer km². From 1978 to 1984, an additional 122 deer (60 males and 62 females) were harvested.

Finally, the demography of the hunted and unhunted populations was explored. Long-term records on abundance, hunter harvest, weather, and forest management were used to identify the respective roles each of these played in shaping the population dynamics of deer (Underwood 1990).

The Gas Molecule Metaphor

There was concern that the harvest experiments would fail because of what might be referred to as the "gas molecule theory" of deer behavior. The concern stemmed from the belief that any reduction in density on a local area would result in rapid influx of deer from surrounding areas. Implicit was the idea that individuals would "diffuse" from more densely occupied habitat to less densely occupied areas until an equilibration of numbers was reached. This notion is analogous to the diffusion of gas molecules seeking equilibrium in a vacant space via Brownian movement.

The gas molecule metaphor for deer population expansion may originate from an application of general ecological theory. The analogy was first explored in a theoretical context by Skellum (1951) and has since been apparent in the concepts such as ideal free distribution in habitat selection (Fretwell 1972) and population sinks (e.g., Pulliam 1988). In application, the gas molecule metaphor seems to have served as the rationale for the development of wildlife refuges. As described by Leopold (1933, p. 196): "... the essential character of a refuge [is] namely a place which provides sanctuary, breeding ground, or some other essential service, and ... the result is always *an outflow* of breeding stock" [emphasis added]. It seems reasonable to infer that Leopold saw the refuge (where hunting was prohibited) as a place in which high densities of game animals would occur, and from which individuals would flow out to continually repopulate the vacant areas being created by sustained harvests.

Clues that the gas molecule metaphor might not be applicable to deer can be found in a variety of observations. Urbston (1967) reported that a population in South Carolina expanded out from a single nucleus of one to two dozen animals with little immigration from an adjacent population. The lack of significant interchange between the two populations was later substantiated genetically by Manlove and others (1978) and Smith and others (1989). Verme observed (1973, pp. 549–550):

> In effect, therefore, if massive die-off of deer from a certain [winter] yard occurs, these animals would not be available to occupy their ancestral summering grounds. Deer living on adjacent areas might gradually shift over to fill the vacuum. Field observations reveal that upland habitat of seemingly excellent carrying capacity has remained vacant....

More recently, Jordon (personal communication 1990) observed that a direct reduction of a deer population in the North Oaks suburb of Minneapolis-Saint Paul resulted in a persistent depression of the population for 5 yr after the reduction effort.

Studies of seasonal movements conducted in northern New York during the 1970s provided insight to why the gas molecule metaphor may be inaccurate for deer. Work by Tierson and others (1985) on the HWF showed deer established home ranges of approximately 225 ha in summer (May through November) and 135 ha in winter (December through April). Once an animal established a home range on summer and winter areas, it maintained a high degree of fidelity to these, migrating back and forth between them seasonally, but using the same areas each year.

Fidelity to a specific area was especially strong on summer ranges. The timber harvest and regeneration that occurred on HWF during the 1970s created significant improvements in habitat conditions in some areas. However, deer did not shift their summer home ranges to these areas. Tierson and others (1985) concluded that social factors were more important than habitat conditions in determining summer home range.

These observations in northern New York are corroborated by studies of the seasonal movements of deer in very different habitat conditions. Hawkins and Klimstra (1970) tracked 465 deer over three years in southern Illinois, an area characterized by a mixture of agricultural (45%), brush (25%), and oak–hickory (*Quercus–Carya*) forest. They observed that most females became permanent residents of the area of their birth.

In a preliminary study of the social organization of deer in southern Illinois, Hawkins and Klimstra supported the hypothesis that deer are matriarchal. They observed family groups of two to five females thought to be siblings or offspring of other members of the groups. Nelson and Mech (1984) followed 11 deer for up to 56 months in the mature coniferous forest environment of northeastern Minnesota. They observed that females tended to establish summer and winter ranges in close association to their doe parent.

The Rose Petal Metaphor

Our work on HWF confirmed and extended knowledge of this pattern of social organization. Movement data for 87 females during the summer months, in combination with genetic analysis, allowed delineation of eight social groups composed of at least three to ten individuals (Mathews 1989). Observations and intensive radiotelemetry of does and fawns over 4 yr, and the genetic data from these animals, suggested that social groups were apparently family units of primarily female offspring and siblings. Intensive analysis of the spatial orientation of individuals within these social

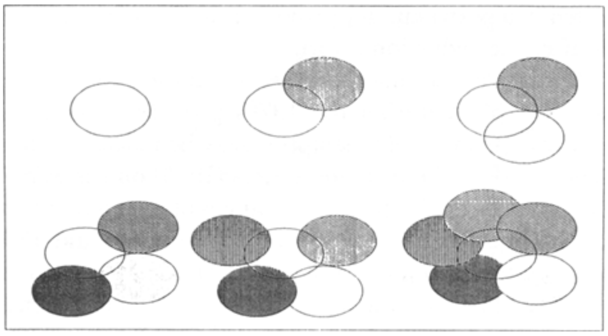

Figure 1. Family units of deer expand in a form analogous to the petals on a rose. Ovals represent the overlapping home ranges of female offspring of several generations surrounding the matriarch (after Mathews 1989).

groups showed substantial overlap of individual home ranges. The older (presumably dominant) females occupy a home range that is at the center of the group, with younger individuals occupying home ranges that overlap and extend the periphery.

These observations suggest a new metaphor of population expansion. Populations expand as an array of family units composed of females. As each new female is added to the unit, it establishes a home range that partially overlaps with that of its doe parent (Figure 1). These overlapping home ranges take a form roughly analogous to the petals of a rose (Mathews 1989).

Female deer rarely disperse. Technically, dispersal may be defined as the complete and permanent emigration of individuals from a previously established home range (Holekamp and Sherman 1989). Bunnell and Harestad (1983) provide a quantitative criterion, defining dispersal for black-tailed deer (*O. hemionus*) as movements >5 km out of a home range with no predictable return. Using Bunnell and Harestad's definition, data show that female dispersal rates are generally <5% from populations ranging in density from <3/km^2 (New York) to >70/km^2 (Georgia) (Table 1).

In contrast, studies on HWF and elsewhere suggest male dispersal is >80%, at similar densities. Males between the ages of 6 months to 2.5 yr disperse and establish new summering areas (Hawkins and Klimstra 1970, Nelson and Mech 1984, Tierson and others 1985). We contend that if dispersal in males is associated with breeding, males should establish new ranges in areas already occupied by females, thus adding little to the spatial expansion of the population.

Implications for Management

The rose-petal metaphor suggests that it may be possible to use a "surgical" approach to management of local deer problems, by focusing on the removal of family units. This has obvious implications to management because it implies that we can manage deer problems on much smaller spatial scales than those currently employed.

A variety of questions arise before implementation can be contemplated. Clearly, there are important political and economic questions associated with a management approach that includes direct reduction. These are beyond the scope of this article. However, the available data and theory can address three ecological questions that are key to management planning.

First, what is the minimum area to which this approach could be applied? Data from our studies and from a broad array of other environments show that the seasonal home range of a deer is <400 ha in size (e.g., Michael 1965, Larson and others 1978, Nelson and Mech 1984, Tierson and others 1985, Mathews 1989). If we assume some overlap in the home ranges of females within a family unit, the group home range might occupy 1500–2000 ha. Thus we believe the minimum area of application would be 400–2000 ha, depending on the size of the family unit.

Second, how many animals must be removed to eliminate deer in a given area? The ideal management action would be to remove an entire family unit, and thus the number of deer to be removed depends on the size of the family unit. In practice, this is not feasible because data on family structure within a deer population are rarely available. The alternative would be a removal effort that is applied continuously until deer are eliminated from the area designated for management control. This area may include one or more family units, each of which may be composed of one to perhaps as many as 15 females.

Third, how long will the void created in the population persist once the removal process ceases? Assuming the family units occupying the management area are removed completely, the answer to this question depends on three factors whose probabilities are not necessarily independent: (1) the rate of population growth, or more precisely, the rate of production of new females; (2) the probability of female dispersal from a group; and (3) the conditional probability that a female dispersing from another family group will find the void.

A model of population growth and expansion allows estimation of the time required for a colonizer to repopulate the area. For simplicity, assume an environment that is composed of a set of grid cells, each 1000 ha in size, and that each family group occupies a single cell (Figure 2). Deer have been eliminated from one of the cells through management.

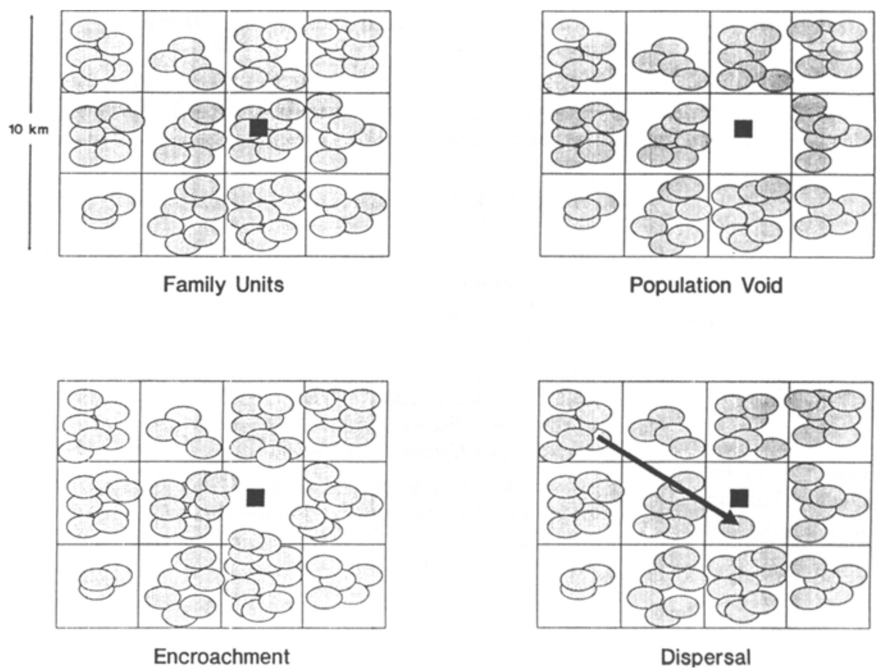

Figure 2. Hypothetical model of the distribution of white-tailed deer on a landscape. Each cell is 1000 ha. Shaded cells are occupied by a single family group and open cells are void of deer.

The persistence of this void will depend on whether or not our management area is colonized. Thus, we need to estimate not only the probability that a female will disperse, but also the probability that it will establish a new breeding range in the managed area. If the collective probability of a disperser leaving any of several family groups and immigrating to our cell is 1:10 (an arbitrary but probably liberal estimate), there is an even chance that no colonizer will arrive for at least 5 yr. The probability of the area being colonized will decline exponentially with distance to the source population (MacArthur and Wilson 1967).

Once a colonizer arrives, the area of the cell will be repopulated quickly. If the growth rate for the population (λ) is 1.6, and with each individual the family group home range expands by 225 ha, the entire cell will be reoccupied in about 5 yr.

The actual effect of the removal may be much longer lasting. First, the conflicts between deer and other management objectives may not occur until deer are relatively numerous. Second, the process of building a new population of 15 females could take as few as 4 yr (if more than one colonizer arrives in years 1, 2, or 3) or as many as 14 yr (if one colonizer arrives in year 10). Finally, precluding regrowth of the population requires removal of a few individuals, at most, each year (colonizers or their offspring).

Summary

In short, we believe that because of the social behavior and ecology of white-tailed deer, they are unusually well suited to alternative forms of management. Because deer populations are composed of family groups of females that are highly philopatric to ancestral group ranges, the removal of deer in areas of 400–2000 ha is hypothesized to create voids in the spatial distribution of deer populations. This suggests that highly localized or "surgical" management of deer populations by direct reduction (e.g., sharpshooting) should be considered in parks and suburban areas where other forms of management are inappropriate.

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