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Source: Wildlife Biology, 7(3) : 161-170

Published By: Nordic Board for Wildlife Research

URL: https://doi.org/10.2981/wlb.2001.020

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Population manipulations of North American deer *Odocoileus* spp.: balancing high yield with sustainability

Dale R. McCullough

McCullough, D.R. 2001: Population manipulations of North American deer *Odocoileus* spp.: balancing high yield with sustainability. - Wildl. Biol. 7: 161-170.

An array of models for sustainable harvesting has been proposed, and most are in some way dependent on a density-dependent response. I tested a subset of these models by manipulating three North American deer populations to reveal density dependence and determine population response to harvests. These were a white-tailed deer *Odocoileus virginianus* population on the George Reserve (GR) in southeastern Michigan, and black-tailed deer *O. hemionus columbianus* populations on Hopland Research and Extension Center (HREC) in Mendocino County, California, and on Fort Hunter Liggett (FHL) in Monterey County, California. The study areas represented a gradation in size, productivity, management control, and environmental stochasticity. The GR population showed a nearly linear density-dependent relationship of r on N. A mean maximum sustainable yield (MSY) of 49 deer/year was obtained at an N of 56% of K carrying capacity (KCC). A fixed harvest with stochasticity, however, reduced the sustainable MSY to 43 deer/year. A second population growth experiment 50 years after the initial introduction showed an equivalent growth rate. Analysis of harvest data from FHL showed buck harvest to be positively related to size of previous female harvests. From these results, a 'linked-sex harvest strategy' (LSHS) was proposed in which female harvest is sequentially incremented so long as buck harvest continues to increase, up to a presumed 'safe' female to buck ratio. At HREC, bucks were harvested in public bucks-only seasons. Buck harvest was monitored for 6-year pre- and post-treatment periods without female removals, and for a 7-year treatment period during which 20 females/year were removed for three years and 30 females/year for four years. There was no significant difference in pre- and post-treatment period buck harvests, so they were combined as a 'control'. There was a significant (25%) increase in buck harvest during the treatment period despite its coinciding with six consecutive years of drought. The combined-sex harvest was more than double that of the buck harvest alone during the control periods. The relevance of these studies to deer harvest management is discussed.

Key words: deer management, density dependence, harvest, maximum sustained yield, North American deer, Odocoileus spp., population manipulation

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Population dynamics, as observed in nature, is typically highly variable due to demographic and environmental stochasticity, community interactions (e.g. predation and competition), time lags, and the inherent difficulties of estimating population size and demographic rates (Sinclair 1989, McCullough 1990, 1999, Turchin

1995, White & Bartmann 1997). Consequently, time series need to be long in order to begin to evaluate population performance and, because of multiple uncontrolled environmental variables, it is usually difficult or impossible to sort out their effects (McCullough 1990, Dennis & Taper 1994, Sæther 1997). Determining changes depends on a strong trend in the time series, and causality may be confused unless, by chance, the course of nature has resulted in a reasonable experiment.

The relative role of density dependence in population response has also been much debated (see reviews of Sinclair 1989, Turchin 1995), and this issue is important to understanding population regulation and response to harvest. Harvest theory and practice is based on the assumption of density dependence (e.g. Ricker 1954, 1975, Beverton & Holt 1957, Caughley 1976, McCullough 1979). Early models were deterministic, so maximum sustainable yield (MSY) was produced by the population size (or density) that resulted in the maximum population growth rate (Ricker 1975, Caughley 1976, McCullough 1979). Walters & Bandy (1972) suggested that periodic harvests might increase yield over that of annual harvests, but the success of this approach is strongly dependent on the shape of the density-dependent function (McCullough 1979, 1992).

Most of the early models did not explicitly incorporate environmental stochasticity (but see Ricker 1958), which affects the sex and age classes differentially (Gaillard, Festa-Bianchet & Yoccoz 1998) and alters the conclusions about the effects of harvesting (e.g. McCullough 1979, Lande, Sæther & Engen 1997). Simulation models showed that fixed harvests of MSY in a fluctuating environment (virtually all environments) would inevitably lead to population extinction (McCullough 1979). Only harvests annually adjusted to the fluctuation in recruitment would result in an average MSY without population extinction.

More complex models (Getz & Haight 1989) with stochastic variation in environment, and sometimes in demography (Lande, Engen & Sæther 1995, Lande et al. 1997, Sæther, Engen & Lande 1996), have elaborated harvest theory. The models of Lande and colleagues are based on a threshold harvesting approach, i.e. the number above some threshold population is harvested. Their simulations suggest that threshold harvesting at K carrying capacity (KCC) maximizes the cumulative harvest before extinction, but maximizing the mean annual yield lowers the optimal threshold (i.e. the threshold is less than KCC).

Threshold harvesting has not been employed in management of North American deer species most likely because its formulation is relatively recent. Still, there are some inherent difficulties in implementing this approach; 1) There are practical problems in determining the size of the population with reference to the desired threshold; 2) Hunters are opposed to forgoing annual harvests; 3) As compared to more r-selected species, large mammal populations show relatively low shifts of population growth rate in response to environmental stochasticity; and 4) variance of population growth rate in large mammals is usually proportional to density rather than constant (McCullough 1979; see also Figure 6 in Messier 1994, which shows proportional variance in moose *Alces alces* on Isle Royale, Michigan). Optimal thresholds for annual harvests, therefore, would ordinarily be less than KCC (except, perhaps, in the most highly variable environments) and somewhat closer to the maximum growth rate population ('economic carrying capacity' of Caughley 1976, or ICC of McCullough 1979).

Translating optimal harvest theory into practical management, therefore, will be difficult. Inaccuracy of population estimation over realistic scales of management, in practice, often equals or exceeds the variation in growth rate due to environmental stochasticity. Indeed, if one has accurate population estimates, almost any kind of harvest scheme can be applied.

On the other hand, the traditional approach in North America of attempting to remove the 'harvestable surplus' (Leopold 1933), and the widespread practice of males-only hunting have, in general, resulted in highly conservative harvests. These practices grew out of the recovery programs that brought game species back from low numbers due to uncontrolled market hunting in the late 1890s. Sport-hunted game species have not been plagued by overharvest as have commercially important species. Cropping the harvestable surplus and bucks-only seasons minimize the likelihood of overharvest, but at the cost of low yields. The challenge facing harvest management of North American deer in the last half of the 20th century, therefore, was determining how to optimize a high annual yield while avoiding overharvest due to errors in population estimation (McCullough 1984, 1997, 2001, McCullough, Pine, Whitmore, Mansfield & Decker 1990). Stated in terms of thresholds, what is the threshold that maximizes annual harvest while avoiding population extinction? The threshold has to take into account environmental and demographic stochasticity, as well as errors in population estimation and difficulties of implementing the system through public hunting regulations.

The size and composition of the harvest itself is one of the easiest variables to measure in practice, which poses an additional question. Can the optimal thresh-

Table 1. Comparison of size, productivity, controlled and uncontrolled variables for the three study areas in which deer populations were manipulated. Productivity is expressed as measured by estimated maximum sustainable yield (number of deer/km^2/year).

Study area	Size (km^2)	Productivity	Controlled variables	Uncontrolled variables
George Reserve, Michigan (GR)	4.64	10.58	All harvest variables, emigration/immigration, predation	Minor weather variation
Hopland Research and Extension Center, California (HREC)	21.49	4.52	Female harvest by collecting permit	Predation, emigration/immigration, weather, acorn crops, poaching
Ft. Hunter Liggett, California (FHL)	667.76	0.96	Number of antlerless permits issued	Predation, emigration/immigration, weather, acorn crops, fire, poaching, military exercises

old be approximated by changes in the size and composition of the harvest in response to changes in harvest effort or regulations? If so, then harvests can be managed without dependence on direct population estimation.

The research I review here on North American deer populations is based on deliberate manipulations of population size and sex composition in an attempt to reveal the workings of density dependence, and its consequences for harvest management. Manipulated populations, of course, are subject to the same environmental stochasticity as populations fluctuating naturally. However, by making the manipulation of population size (or density) sufficiently strong the effects of natural stochasticity can be exceeded to reveal the effects of the changes in population size or density.

When I began studies of white-tailed deer *Odocoileus virginianus* on the E.S. George Reserve in southeastern Michigan in 1966, the empirical evidence for density dependence was weak. Although there were many demonstrations of shifts in specific demographic parameters with changes in density, such data were piecemeal, so their ultimate population consequences could not be evaluated. Hypotheses tests, as currently understood, were virtually non-existent, and even systematically collected data rare. I concluded that the route to better understanding was to attempt reductionist science as specified by experimental design, more along the strong inference model of Platt (1969). Unfortunately, the scale necessary for large mammal population studies ruled out true experiment design replete with controls and replications, so I pursued the next best thing, purposeful manipulations of sufficient magnitude to override the environmental noise that was inevitable.

Here I review three manipulation studies to understand the density-dependent response of deer populations; study sites were the E. S. George Reserve (GR) in southeastern Michigan, Fort Hunter Liggett (FHL) in coastal California near Monterey, California, and Hopland Research and Extension Center (HREC) near Ukiah, California. The white-tailed deer was the study species at the George Reserve, and the black-tailed subspecies of the mule deer *O. hemionus* at the two California locations. The study areas represent a graded series in size, productivity, environmental stochasticity and degree of management control (Table 1). The GR is the smallest, highest in productivity, lowest in environmental stochasticity and highest in control; FHL is at the opposite extreme of these characteristics, whereas HREC is intermediate. I should emphasize that these manipulations were not true experiments, because they lacked spatial controls and replications. Nevertheless, the logic of an experiment was followed to the extent possible within the constraints of the specific area.

Results

George Reserve (GR)

The GR was nearly ideal for a population manipulation study. First, it was a closed population because a deer-proof fence eliminated immigration and emigration. Second, the area enclosed was sufficiently large to support a reasonably large deer population, so that sample sizes would be reasonable, but not so large as to be logistically difficult. Third, the University of Michigan held a game-breeders license from the state of Michigan, which allowed nearly complete discretion about management. Manipulations could be made according to timing and methods that would not have been acceptable on other lands or allowed under state-wide deer hunting regulations. Fourth, from earlier work there was a past record of deer numbers and harvest statistics, as well as a collection of lower jaws that could be used for age determination.

The history of the population (McCullough 1979, 1983) was characterized by a rapid buildup in numbers upon introduction of six deer in 1928, followed by a long period of downward adjustment by culling starting in the 1930s once impact on vegetation became apparent. Deer were uncommon at the time in most of North America because of overhunting, so it took some time for early biologists to comprehend how rapidly a white-tailed deer population could increase. The GR became a classic case history showing that deer would thrive if given protection. The long downward reduction by culling yielded the data that demonstrated density dependence (McCullough 1979, 1984; analyzed independently by White & Bartmann 1997). A population of 99, on average, would increase to 148, and 49 deer/year (maximum sustainable yield = MSY) would need to be removed to stabilize the population at economic carrying capacity (Caughley 1976), also called inflection point carrying capacity (ICC, McCullough 1979).

To sustain a removal of an average of 49 deer/year, however, required that the exact number of recruits be measured and removed each year, and that would require an accurate census method, clearly an impossibility for most populations. Model simulations using stochasticity in the environment showed that a fixed kill of 46 could be sustained, or if stochasticity in the hunting system similar to public hunting in Michigan were applied, that number was reduced to 43/year (McCullough 1979). Thus, removals of 33% of the pre-hunt population could be sustained, or if information were much poorer, around 30% (removal of 43 deer from a pre-hunt population of about 135, the higher equilibrium population at the lower removal rate).

Again, the GR became a model case history for how deer populations could be exploited for high yield, and this model was generalized to all white-tailed deer populations by Downing & Guynn (1985). The validity of generalizing from the GR can be debated, but there is little question that this study had considerable influence on the thinking about deer population management.

Because the density-dependent relationship shown by GR deer was not linear, MSY was obtained at an ICC of 56% of KCC, rather than 50% of KCC as assumed by the logistic equation (Fig. 1). Non-linearity is thought to apply broadly to large mammal populations (Fowler 1981, 1987, McCullough 1992). The effects of density become more pronounced as the population approaches KCC, and because the rate of increase is quite high at lower densities, overshoot of KCC is common (Leopold 1943, Caughley 1970, McCullough 1997). Consequently, the average KCC for the GR (176) was exceeded (222) following the initial introduction of deer to the area (McCullough 1979, 1983). This type of time-lag is the basis for the irruptive population paradigm proposed by Leopold (1943) and Caughley (1970; see review of McCullough 1997). One assumption of the irruptive paradigm is that KCC is reduced by 'damage' to the vegetation to a new and permanently lowered KCC.

The reduction of the GR population to 10 deer I made in 1975 was specifically designed to test this prediction. The vegetation of the GR had been modified in a number of ways over the years, including changes in species composition and, particularly noticeably, growth form. Some woody species such as red cedar *Juniperus virginiana* and hawthorne *Crataegus crusgali* were severely hedged at the bottom (within deer reach), and small plants whose tops were within reach were suppressed from further growth in height. The most impressive demonstration of deer feeding effects, however, was the differential appearance of two species of pine trees, red pine *Pinus resinosa* and white pine *P. strobus* that were planted in plantations in 1928. By 1982, red pines, which are resistant to deer browsing because of their high resin content (hence the specific name), were about 25 cm in diameter at breast height and formed a closed canopy, whereas the palatable white pines were about 0.3 m in height, virtual bonsai plants.

If deer feeding had 'damaged' the vegetation, and thereby permanently reduced the carrying capacity of the GR, one would predict that a second population growth 'experiment' should yield a lower growth rate than the original increase. This was the hypothesis tested by the reduction to 10 deer. With protection in the following years, the population grew at virtually the

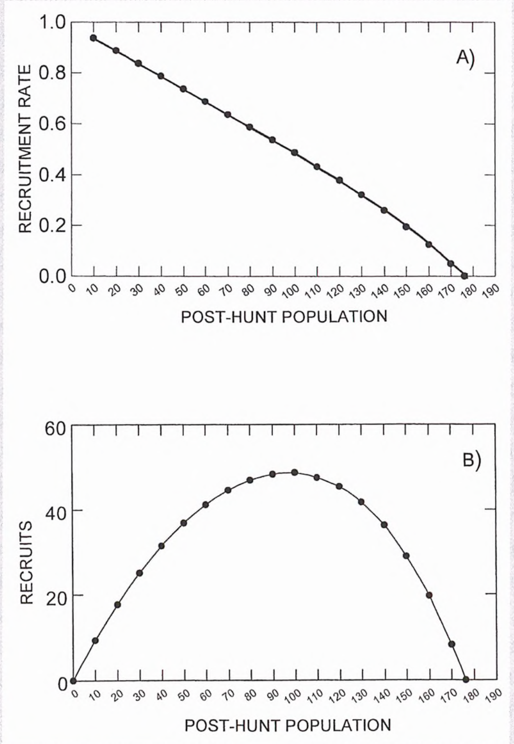

Figure 1. Recruitment rate (A) and number of recruits (B) on post-hunt population size for the GR white-tailed deer population. The density-dependent function becomes curvilinear at higher densities, so the numbers of recruits curve is slightly skewed to the right.

same rate as the initial introduction (McCullough 1982, 1983, Eberhardt 1985), reaching 212 deer before culling was re-instituted. This and other similar cases cast doubt on the generality of the irruption paradigm (McCullough 1997) and suggested caution in interpreting impacts on vegetation as 'damage'.

Fort Hunter Liggett (FHL)

Most deer herds in California have been managed for 'bucks-only' deer hunting. This has led to many populations at high density that are heavily skewed towards females, with small buck kills and low productivity. A notable exception is the consistent harvest of antlerless deer at FHL, a military base with heavy training activity, including live artillery firing (McCullough et al. 1990). It is a large area with tremendous natural and anthropogenic stochasticity (see Table 1). The deer herd has been subjected to antlerless hunting over a long time period, and the size of the antlerless kill has varied in consistent patterns, being lighter at some times and heavier at others (McCullough et al. 1990).

A retrospective analysis of 16 years of harvest data from FHL by age reconstruction methods showed that harvest of bucks lagged the removal of females by several years, but that buck harvest increased in response to female harvest (McCullough et al. 1990). Harvest of females was correlated with the number of antlerless permits issued. Thus, there were grounds to believe that incremental increases in the number of antlerless permits issued would lead to increased harvest of females, and in turn, increased harvest of bucks in subsequent years due to density-dependent increases in recruitment. McCullough et al. (1990) proposed the 'linked sex harvest strategy' (LSHS), which posits that harvest of females can be incremented in steps to increase buck harvest, and thereby total harvest.

Lubow, White & Anderson (1996) criticized LSHS on the basis of simulations with an age- and sex-structured model. Certainly LSHS is an unproven approach warranting criticism. Still, some of Lubow et al.'s model results are unlikely, such as: 1) long lag times, 2) lack of convergence tendencies of age structure of the sexes, and 3) different optimization points for the sexes. These irregularities bring into question whether their model is sufficient to evaluate LSHS.

The long time for their model to reach stability (over 200 years) is simply unrealistic. In my deer population manipulations at the GR no time lag could be detected between reductions made and the population response as measured by recruitment or yield (i.e. the lag was less than the methods could detect). Shifts in reproductive and survival parameters resulted in substantial density-dependent compensation despite only trivial shifts in age and sex structure, which did show a lag. I think this rapid, unlagged demographic response was attributable to high heterogeneity of the GR environment, and that individuals can quickly exploit resources released by reductions in density. This might be expected at GR because of the relatively rich habitat and the responsiveness of white-tailed deer. But buck kill also increased with a lowering of density of females at HREC, a moderately rich habitat with high environmental stochasticity (McCullough 2001), even though the treatment period (removal of females) covered only seven years, and the buck kill declined again in the 6-year post treatment period. At least in these specific cases, long time lags did not occur. Thus, the long time for Lubow et al.'s (1996) model to stabilize may not fairly represent many deer populations.

Convergence of age structures between the sexes with increased female harvest by a LSHS seems to be inevitable when beginning with a population near carrying capacity, a logical necessity of the LSHS. In such a population male mortality is due to both natural causes and harvest, whereas for females all mortality is due to natural causes. Because of high hunting mortality, survivorship curves of males are steep, and life span is short. Females, conversely, have comparatively long life spans and old age structures. I cannot see how it would be possible in a density-dependent population that the age structures between the sexes would not become more similar as previously protected females were subjected to harvest mortality. I would not expect complete convergence, but partial convergence as intended by McCullough et al. (1990) would seem to be inevitable as hunting mortality decreased female longevity and steepened survivorship curves.

Lubow et al.'s (1996) model gave different maximization points for the sexes. This could occur partly due to lack of complete convergence of age structures (as discussed above, natural mortality between the sexes is unlikely to be identical between the sexes under any condition), but more importantly due to unbalanced primary sex ratios. There is evidence of shifts in primary sex ratio with changes in population density in deer (Verme 1965, 1983, McCullough 1979), and clearly this could offset the yield curves between the sexes. However, whether or not this would undermine the logic of LSHS would depend on the direction of the shift. This can be seen in Figure 2 where recruitment curves derived from the shift in sex ratio of recruits with population size for the GR are plotted. Because the male peak is to the left of the female peak (see Fig. 2), incrementing female harvest to levels nearer male har-

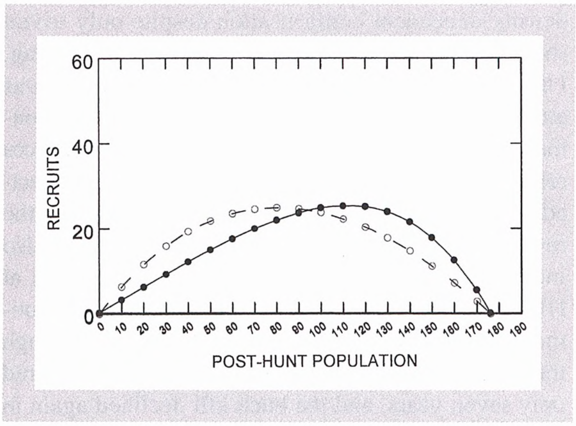

Figure 2. Number of recruits by sex (males: •,— ; females: ○,- - -) on post-hunt population size for the GR white-tailed deer population based on the shift in sex ratio on density reported by McCullough (1979). Peak recruitment of males occurs at higher population densities than does that of females

vest will result in convergence as proposed by the LSHS model. In this case, harvest of females would not be further incremented (in fact, it would be reduced some) if male harvest began to decline, and this would occur without overexploitation of females. This would remain true in any case in which the sex ratio shifts towards males as density increases. Only the reverse case would result in failure of the logic of LSHS.

Finally, one needs to appreciate that internal dynamics of the sex and age classes need to be consistent with an overall population density response, because these are inter-linked in the total plant-animal dynamic system. It may be that age and sex responses as modeled by Lubow et al. (1996) are not representative of shifts in sex ratio and age structure as they actually occur. Failure of a model to support LSHS, therefore, may be due to faulty structure of the model instead of unreliability of the strategy.

An age- and sex-model that supported LSHS could be constructed, but it would be no more proof of the usefulness of LSHS than would Lubow et al.'s model to reject LSHS. The proof lies in empirical tests, not in models. Lubow et al. (1996) are correct that LSHS has not been systematically tested. McCullough et al.'s (1990) attempted test at FHL in California was not carried through for reasons having nothing to do with LSHS. The untimely death of Don Pine, the local California Fish and Game Department biologist whose perseverance had assured continuity over the years, along with turnover in resource management personnel and the commander at FHL, resulted in loss of commitment to the LSHS plan. When six consecutive years of drought occurred in California in the late 1980s, the fort commander bowed to local hunter pressure and curtailed antlerless hunts. Kill statistics and field monitoring at the time indicated that the LSHS plan was on schedule, and the population was not showing negative effects of the drought. Nevertheless, politics prevailed over science.

Hopland Research and Extension Center (HREC)

My research at HREC was a test of the proposition that in dense deer populations near KCC (due to a past history of bucks-only hunting), imposing a female kill will increase subsequent buck harvest through density-dependent increase in recruitment. This, of course, is the logic behind LSHS. The study was designed from a retrospective analysis (McCullough 1984) of data from previous harvest and collections at HREC (Connolly & Longhurst 1975). This analysis supported the proposition that buck kill would increase with greater female removals, but as with all retrospective analysis, it was based on a correlation that may or may not have been due to cause and effect. The HREC manipulation study was designed to test the hypothesis and attempt to isolate density reduction as the cause of the effect, increased buck harvest.

As with the other studies reviewed here, the HREC manipulation was not a true experiment. There were no comparable areas to serve as controls or replications, and HREC was neither large enough to subdivide, nor were the different parts of the area equivalent. Consequently, controls in time were used by having a 6-year pre-treatment period during which no females were removed, a treatment period of seven years when females were removed (20/year for three years, 30/year for four years), and a 6-year post-treatment period during which no females were removed. The pre- and post-treatment periods were compared to evaluate drift in deer productivity that might have occurred due to background environmental changes. The measure of treatment effects was the buck harvest among the three periods during which the buck hunting effort was held constant. If the female removal influenced density-dependent recruitment of legal bucks (antlers with at least one fork), either through increased reproduction and/or reduced mortality, then buck harvest should be greater during the treatment period than during the control period(s).

The results of the HREC manipulation supported the hypothesis (McCullough 2001). There was no significant difference in the number of bucks harvested between pre- and post treatment periods ($P > 0.44$), so they were pooled as a control. A significantly greater ($P = 0.02$) number of bucks were harvested per year during the treatment period than during the control period (mean of 39.4 versus 27.9). Thus, the hypothesis was accepted.

Notably, the extended drought that led to curtailment of antlerless hunting at FHL occurred during the treatment period at HREC. The last six years of the 7-year treatment period coincided with the longest drought in the California rainfall record. Despite evidence that vegetation productivity (Murphy 1970) and deer productivity (Longhurst, Connolly, Browning & Garton 1979) are closely related to rainfall, the HREC deer population sustained increased harvests during the treatment (and drought) period. It was widely believed by hunters that deer populations in the areas surrounding HREC suffered pronounced declines. Deer hunting was all but abandoned on a private deer-hunting club property immediately adjacent to HREC. Population declines due to drought would be expected for populations near KCC with sex ratios highly skewed towards females because of bucks-only hunting. This is evidence that reducing density can dampen the effects of environmental stochasticity, and supports the suggestion of McCullough (1979, 1984) that variance in the density-dependent response may be proportional rather than constant.

Discussion

Density dependence and harvest systems

In North America, the harvestable surplus model of population management has held sway since publication of the influential textbook by Aldo Leopold (1933). In harvestable surplus, one first measures the annual increment, usually as the size of the youngest age class, and then sets seasons and regulations to remove this number. I refer to this as reactive management (McCullough 2001) because one first determines the 'excess' animals that can be removed, and then attempts to remove that number.

The shortcoming of this approach is that it assumes that the current population size is the desirable one and attempts to hold the population at that size. If the population is appreciably above the economic carrying capacity (or ICC), then recruitment of young is low, and the apparent harvestable surplus is correspondingly low (McCullough 1979). The reactive approach, therefore, does not recognize that increased yields might be obtained by taking advantage of the density-dependent response resulting from reduced density. It also overlooks that ungulate populations near KCC are subject to pronounced mortality during times of environmental stress, e.g. hard winters and droughts.

Conversely, using manipulations to reduce density to achieve increases in yield, which also buffers the population against environmental stochasticity, I have termed a 'proactive' approach (McCullough 2001). This same approach seems applicable to the management of European ungulates, which traditionally have been managed by prescribed harvest formulas to achieve goals, e.g. control of damage to forests or crops, and to achieve large antler and body size (trophy value) in males. This 'prescriptive' approach also uses density reduction to obtain certain ends that are deemed desirable.

Reactive systems are most conservative, and are immune to over-exploitation at the cost of lost yield and increased environmental impacts. Proactive and prescriptive systems differ mainly in that proactive systems are motivated primarily by the size of the harvest, and prescriptive systems by a desired state of the environment. They increase yield and reduce environmental impacts, but at the greater risk of overexploitation if population assessment is not adequate.

In application, none of the three, reactive, proactive, or prescriptive, systems has been pursued exclusive of the others; in each of these systems the ancillary consequences have been recognized, and either accepted or compensated for in some fashion. These are, therefore, idealized categories to highlight the different rationalizations for programs, and the separate goals and paradigms that have guided them.

The three population manipulation studies I reviewed here demonstrate the existence of density-dependent responses of North American deer populations and an underlying demographic process that resembles the yield or productivity parabola that has been hypothesized. Still, it is possible to over-exploit deer populations, so reliable measures of population size are advisable to monitor the effects of high harvests, and a margin of error retained as a hedge against errors. Furthermore, the results from FHL and HREC show that the density-dependent response is robust enough to be measured, and used to advantage in harvest program, in at least some environments with high stochasticity. Nevertheless, three cases are not sufficient. In the most extreme environments it is likely that stochasticity does overwhelm the density response to the extent that it is not a useful basis for harvest programs.

LSHS in the real world

Despite the criticism of Lubow et al. (1996), I still think that the LSHS is conceptually sound. The bigger question is whether LSHS can be applied practically in the real world. We proposed LSHS because reliable information is so difficult to obtain. I have long advocated that the first goal of a management program should be to develop reliable information if possible, and if management were informed by reliable information I would agree that LSHS is pointless. Nevertheless, for North American deer we have reliable information for only a few isolated research populations. Lubow et al. (1996) imply that 'traditional' ungulate management is based on reliable information. This is hardly the case. Caughley (1985) noted that deer management in North America in the early 1980s differed little from that practised in 1900. This may be an overstatement, but it is much truer of the current state of deer management than is the existence of all of the population data considered by Lubow et al. (1996) to be necessary for management.

The benchmark that LSHS has to exceed to be useful, therefore, is not reliable information, but rather, current management practice, a much less demanding standard. In fact, many agencies base ungulate harvest decisions on analysis of kill and herd composition counts. To some extent, LSHS rationalizes and implicitly states the premises of some commonly used practices. Nevertheless, agencies that believe they have reliable information, or are satisfied with conservative, risk-avoidance buck-only hunting programs have no need of LSHS. On the other hand, agencies that choose to, or are forced by constituencies to pursue aggressive harvest programs to utilize more of the potential yield should evaluate LSHS. LSHS involves risk, but in the absence of reliable information so do all approaches involving high yield management.

In some circumstances LSHS is doomed to fail. As McCullough et al. (1990) pointed out in their original monograph, LSHS will be useless for cases in which the population of interest does not conform to a density-dependent population model, or if the density-dependent population response cannot be sorted out from measurement error and environmental stochasticity. Conversely, if the population meets these requirements, LSHS may be useful. If all of the assumptions of LSHS are met, the population could be manageable as a black box with only harvest total, sex and age statistics. We did not recommend use of LSHS in this manner, which as an unproved method seemed excessively risky. We suggested that, at minimum, an index to the size of the manipulated population be obtained as well. LSHS is best pursued incrementally in a management experiment (McNab 1983) or as adaptive management (Walters 1986). The prospects for LSHS improve with increased quality of the habitat and are best in the most productive regions. Only when more experience supports the worth of LSHS should managers attempt black-box applications of LSHS.

Can LSHS be applied successfully to environments and situations where the necessary assumptions can be met? Neither argumentation nor modeling will resolve this issue, nor will one or a few empirical tests. A preponderance of evidence from a wide range of geographic sites and environmental circumstances will be required. Only then will we be able to say whether or not LSHS is a useful approach. It could hardly be otherwise given that the concepts LSHS rests upon, e.g. density dependence, carrying capacity, compensation, sustainable yield, are all subject to similar debates, and they all are tested simultaneously in LSHS management.

Acknowledgements - I thank the organizers of the Hunting Conference for inviting me to present this work. The GR studies were supported by a series of grants from the National Science Foundation; the FHL studies under contracts with the U.S. Department of the Army; the HREC studies under the California Agricultural Experiment Station, a contract with the California Department of Fish and Game, and the A. Starker Leopold endowed chair. I thank the many biologists with state agencies that I have interacted with over the years, and the faculty and graduate student colleagues who contributed directly to the field work. My predecessors at GR, Warren Chase, Earl O'Roke, Fredrick Hamerstrom, Arch Cowan and David Jenkins passed on records and advice. Literally thousands of people volunteered to participate in drive census counts at the GR over the years. Field assistants Paul Beier, John Bissonette, Terry Bowyer, Bruce Coblentz, Michael Fairchild, Dave Hirth, Dave Kitchen, Yvette McCullough, Greg Miller and John Simon shared the workload. At FHL, special thanks go the late Don Pine, and Bruce Elliot, Terry Mansfield and Dale Whitmore of the California Department of Fish and Game, and Bob Decker of FHL. At HREC, Paul Beier, Rand Evett, Gene Fowler, Bob Keiffer, Tom Kucera, Pam Mulligan, Al Murphy, Bob Timm, Floyd Weckerly and Bob Whittaker were particularly helpful in the field work, and Ken Mayer with California Fish and Game facilitated funding and the collecting permit required to remove females. Margaret Jaeger helped with the preparation of this manuscript.

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