



Density Dependence Special Section

Density Dependence: Applications in Wildlife Management

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ABSTRACT Knowledge of density-dependent processes is regarded as important for making decisions on the management of wildlife populations. Using published data on ungulates and upland game birds, we discuss density-dependent effects on population growth, harvest management under the logistic model, and management to increase or decrease survival and production. Empirical data show density-dependent growth for white-tailed deer (*Odocoileus virginianus*), reindeer (*Rangifer tarandus*), ring-necked pheasants (*Phasianus colchicus*), and northern bobwhites (*Colinus virginianus*), although the logistic model provided, at best, an approximation of growth. Managing harvest according to logistic theory is rare for ungulates and upland game; we suspect this owes to scarce data on population growth and complexity in density-dependent processes. Under density dependence, managing to increase production or survival may be self-defeating because an increase in 1 demographic variable entails a decrease in the other for sustaining populations ($\lambda = 1$). The problem can be addressed by providing space for population growth ($\lambda > 1$), at least until growth re-establishes the density-dependent response ($\lambda = 1$). © 2012 The Wildlife Society.

KEY WORDS density dependence, harvest, inversity, logistic growth, ungulates, upland game birds.

Emphasis on density dependence is very important to practical game conservation simply because it is counter-productive in any management programme to work against a density-dependent factor—the more work one does, aiming to increase numbers, the higher the mortality.—G. R. Potts (1986:184)

“Understanding the relative importance of density-dependent and density-independent feedback on population growth is essential for developing management strategies to conserve wildlife” (Fuller et al. 2007:1924). This statement reflects the accepted wisdom in wildlife management. Yet beyond such general assertions, which usually appear as justification for a study of density-dependent processes, what role does density dependence play in wildlife management decisions? Research on deliberately invoking density-dependent responses to accomplish management objectives seems to be rare. Of course, research on the nature and properties of density dependence delivers basic knowledge that is, at a minimum, important in understanding and explaining behavior of wildlife populations.

At this juncture, little doubt remains that density dependence is a common property of animal populations (Brook and Bradshaw 2006), though a good deal of variation may exist in the strength, seasonal timing, and life stages at which the phenomenon operates (McCullough 1990). Density de-

pendence is a key consideration in the theory of harvest management, including the special case of pest reduction. The logistic equation of population growth has been the standard model for developing theory on harvest management, given density-dependent population behavior; we will use the model as a point of reference in discussing the management implications of density dependence.

Density dependence also affects non-harvest aspects of wildlife management. For example, what we call the dilemma of sustaining populations (increased production entails increased mortality) may prevail under density dependence. The Potts (1986) quote (see epigraph) provides an example of the dilemma: “the more work one does, aiming to increase numbers, the higher the mortality.” By “sustaining population,” we mean one that does not increase through time but which may vary markedly among years. A sustaining population does not decrease through time by virtue of the modifier, “sustaining.” Readers need to keep this definition in mind to understand our arguments.

Using published information on ungulates and upland game birds, we provide an overview of density dependence as it relates to wildlife management. These taxa vary in population volatility and thus provide comparisons and contrasts of density dependence in species with lesser (ungulates) and greater (upland game birds) annual variability in population size. We begin with a brief review of population growth in the selected taxonomic groups and then discuss these findings relative to harvest management (including pests), management of survival and production rates, and habitat management.

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POPULATION GROWTH AND DENSITY DEPENDENCE

Ungulates

White-tailed deer (*Odocoileus virginianus*) released on the George Reserve in Michigan and reindeer (*Rangifer tarandus*) introduced to St. Matthew Island, Alaska (Klein 1968), represent examples for population growth in ungulates. In 1928, 2 male and 4 female deer were released into a 464-ha high-fenced deer-free enclosure in Michigan. Six years later, a drive count revealed that the population had grown to 160 (Fig. 1; McCullough 1979). In 1944, 29 reindeer introduced on the 35,705-ha St. Matthew Island in the Bering Sea, grew to an estimated 6,000 by 1963 (Klein 1968; Fig. 2). Both introductions took place in areas free of natural predators.

Density-dependent fecundity was evident in the George Reserve population. At low population densities, female fawns regularly bred and gave birth at just over 1 year of age. Average embryo counts for fawns at low post-hunt population sizes were as high as 1.82, but declined steadily as densities rose, falling to 0.00 at a post-hunt density of 100. Embryo counts for yearling and older females dropped from an average of 1.95 at low post-hunt densities to 1.42 at high ones (McCullough 1979). Mortality at the George Reserve was almost entirely due to human hunting under the University of Michigan's game breeding license and thus could not be tested for density dependence.

Age ratios suggested density-dependent fecundity for reindeer on St. Matthew Island. Ratios of fawns:yearlings:adults declined from 75:45:1.00 in 1957 to 60:26:1.00 in 1963. Further indirect evidence of density dependence during the same period was shown through body mass declines for yearling males from 103 kg in 1957 to 68 kg in 1963 (Klein 1968).

These examples and the one from Protection Island below are cases in which emigration was not possible. Under such conditions, the effects of density dependence are more obvious as they tend toward irruptive behavior (McCullough 1999).

Three unconfined populations of white-tailed deer in South Texas were tested for density dependence by 2 meth-

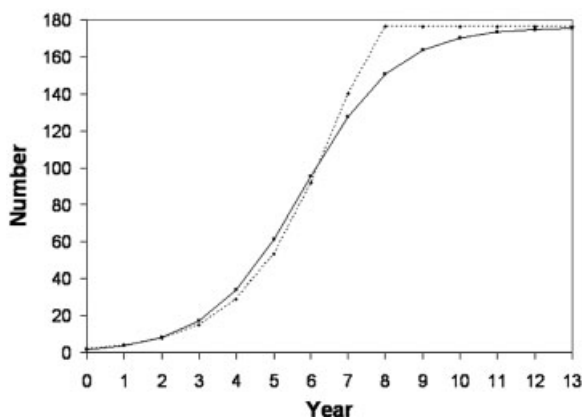


Figure 1. Predicted (logistic equation, solid line) and observed (dashed line) population growth of a white-tailed deer population on the George Reserve, Michigan, USA (McCullough 1979).

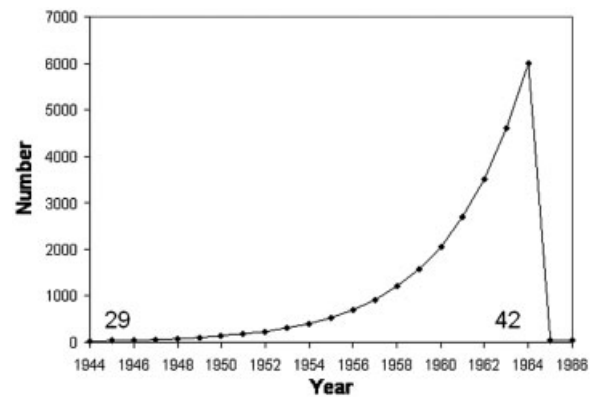


Figure 2. Assumed population growth of a reindeer population on St. Matthew Island, Alaska, USA (Klein 1968). The numbers 29 and 42 represent starting and ending populations.

ods (DeYoung et al. 2008). Density dependence was detected in 2 of the 3 populations, those of the Welder Wildlife Refuge and the Chaparral Wildlife Management Area. The third population, that of the Faith Ranch, did not show density dependence, possibly because it was more arid with more variable precipitation, a condition that makes detection of density dependence more difficult (DeYoung et al. 2008).

Upland Game Birds

Ring-necked pheasants (*Phasianus colchicus*) released on Protection Island, Washington (Einarsen 1945) and northern bobwhites (*Colinus virginianus*) released on Great Island, Massachusetts (Cookingham and Ripley 1964) provide examples of population growth and associated density dependence for gallinaceous birds. Two cocks and 8 hens (2 subsequently died) obtained from a game farm were released on Protection Island (158 ha) in 1937. The island had practically no mammalian predators and normal compliments of migratory hawks and owls. The population on the island grew from 40 pheasants in fall 1937 (after 1 production season) to 1,898 in fall 1942. Growth followed a sigmoid curve (Fig. 3); Einarsen conjectured the population

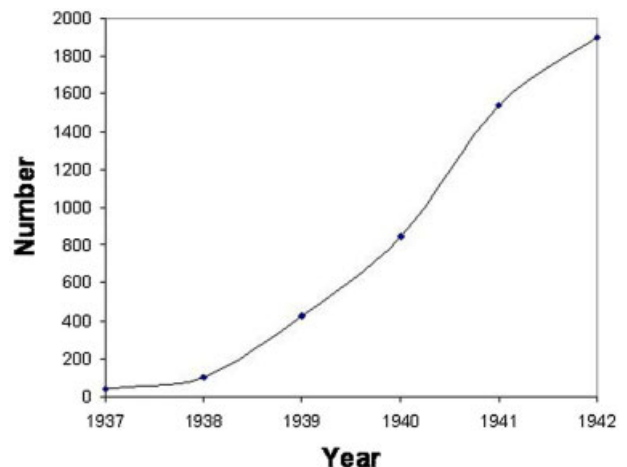


Figure 3. Growth of a ring-necked pheasant population on Protection Island, Washington, USA (Einarsen 1945).

would have leveled off in another 2 years because the spring-to-fall increase (%) was declining towards 0.0. The pheasant experiment ended when the military took over the island during World War II.

On Great Island (153 ha), biologists released 2 coveys (10 and 7 birds) of wild-trapped bobwhites in 1954. The island previously had had a population of bobwhites. The introduced population grew to a peak and then declined and growth did not follow a sigmoid curve (Fig. 4).

Einarsen (1945) and Cookingham and Ripley (1964) both observed density independence in winter survival and density dependence in production. Einarsen's (1945:5) observations show density-dependent effects at extremely high densities of pheasants (24/ha at peak):

Cock birds have been seen persistently molesting hens and chicks. As the population increased, single eggs dropped at random were more frequently found. Hen pheasants established community nests, which resulted in many wasted eggs, as no attempt was made to incubate them. Abandoned nests containing from 18 to 38 eggs were frequently recorded. Often community use of a nest by several hens resulted in abandonment even when only a few eggs had been laid. This did not occur when pheasant populations were smaller.

Cookingham and Ripley (1964) observed that the Great Island bobwhites followed Errington's (1945) Principle of Inversivity.

Errington (1945) observed bobwhite dynamics in Wisconsin and Iowa and ring-necked pheasant dynamics in Iowa. He found that percent summer gain tended to be in inverse ratio to spring densities (hence, the Principle of Inversivity or density-dependent production). With assistance from F. A. Brandner, Department of Mathematics, Iowa State University, Errington modeled the relationship with a reverse logistic equation.

Errington's (1945) classic paper established density-dependent production in the thinking of upland game bird managers on the basis of description and induction with undetermined cause. Errington (1945:32) speculated that some sort of cosmic influence that modified intraspecific toleration of individuals might be involved. Bergerud

(1985) hypothesized that increasing breeding density forces use of more marginal combinations of cover and space, thus depressing relative productivity as populations increase. Other hypothesized causes of density-dependent production in upland game include variation in resources per individual as density varies, density-dependent predation, heterogeneous fitness, and adaptive learning (Guthery 2002).

APPLICATION IN MANAGEMENT

The brief review above sets the stage for discussing the management implications of density dependence. Perhaps the main potential application is in harvest management, including lethal control of pests. The logistic equation provides a classic, if simplistic, point of reference for developing theory of harvest management.

Harvest

The differential form of the logistic equation is a parabola that plots rate of population change on the y -axis and population size on the x -axis. The differential form gives the derivative, or rate of change (slope) of all points along the S-shaped curve; whereas the integral form is the classic S-shaped curve. The parabolic relationship reveals that a single population size maximizes sustained yield and this occurs at one-half of carrying capacity (K). The relationship also implies that a given yield (excepting maximum) may be attained at 2 different population levels. This deduction might be useful in managing for optimum sustained yield, that is, a sustained take, usually lower than maximum, that addresses auxiliary objectives such as viewing opportunities for nonconsumptive users. A manager could, for example, maintain lower or higher numbers, as management objectives dictate, while still harvesting the same number of animals.

Managers should be properly skeptical of implications from the logistic curve. It may at best approximate population growth and at worst provide an inaccurate model (Figs. 1–4). We do not know of a biological reason why maximum yield should occur at $1/2K$. Neither does any theory imply general reliability of the logistic curve in comparison with other models. Mathematical versions of the normal curve, Weibull curve and Gompertz curve, among many others, show y to be a sigmoid function of x (Banks 1994). Obviously, managers who wish to apply sigmoid theory in harvest management should check their data against the logistic curve to determine whether they should evaluate other population growth models. However, the logistic curve fits many relations involving such matters as adoption of technologies, product replacement, cumulative density of various variables, and growth of animal populations.

Given satisfactory performance of the logistic model and reliable estimates of carrying capacity, trend in population size (N_t), and intrinsic rate of increase (r), managers will be able to estimate through logistic modeling the population level that maximizes or optimizes sustained yield. Exacting a target yield from a population requires knowledge of the relation between harvest and non-harvest mortality (additive, compensatory). Caughley (1977) discusses how to mathe-

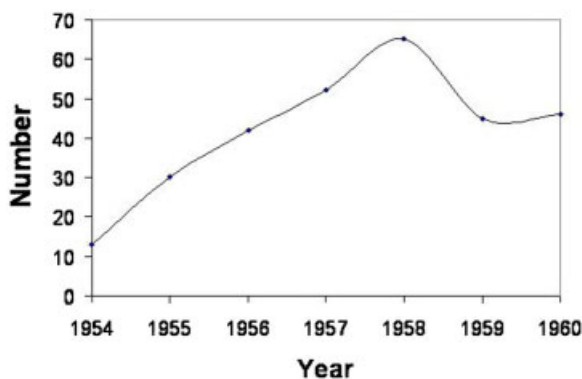


Figure 4. Growth of a northern bobwhite population on Great Island, Massachusetts, USA (Cookingham and Ripley 1964).

matically incorporate competing sources of mortality into harvest management based on the logistic curve.

A specified harvest also demands knowledge of the interface between hunters and quarry. How does one achieve the take of a specified number of animals consistent with estimates from a logistic model? This is a complex topic as exemplified by the theory of the hunter–covey interface (Guthery 2002). Harvest is based on a complex probability structure in quail hunting.

Lethal pest control may be viewed as harvest of sufficient intensity to reduce a population. However, because of density dependence, pest control might simply exact a sustained yield from a population, perhaps at the lower of the 2 levels along the yield curve that have identical gains. Knowlton (1972) reported that average litter size varied inversely with population density for coyotes (*Canis latrans*) in South Texas. Suppression of coyote density in this region entailed intensive programs that overweighed the density-dependent response in pup production.

Before discussing aspects of density-dependent population growth that aid in making correct management decisions not related to harvest, we wish to point out that data on population growth per se are not necessary to understand and manage density-dependent processes. An example is Errington's (1945) discovery of a reverse logistic (backward S) relationship between breeding density of northern bobwhites and ring-necked pheasants and percent summer gain (Fig. 5). The summer gain model can be modified to show absolute summer gain as a function of breeding density (Fig. 5). Thus, maximum and optimum gains can be estimated. Note that the gain curve has a maximum and 2 levels of take that will hold a population constant from year to year, but the curve is not symmetric as in the logistic model. A common feature of sigmoid curves is that the derivative will reveal a single maximum sustained yield and 2 population levels that support the same sustained yield below maximum yield. The apparent increase in absolute gain on the right tail is an artifact because percent summer gain has become a constant (asymptote) multiplied by increasing density.

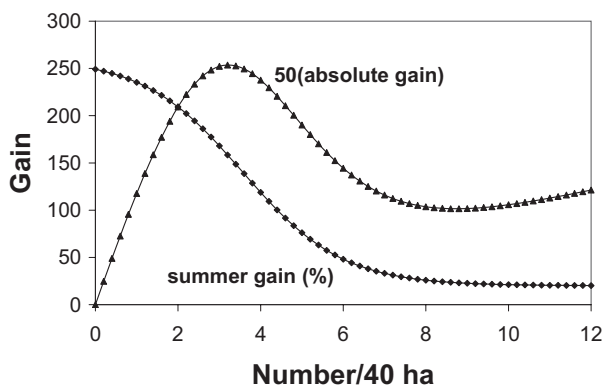


Figure 5. Reverse logistic relationship between spring density and percent summer gain and derived absolute spring-to-fall gain ($\times 50$) of pooled northern bobwhite and ring-necked pheasant populations during 1930–1943, Wisconsin and Iowa, USA (Errington 1945).

Managing Survival and Production: The Dilemma

A frequently stated objective of management research is to test methods of increasing the survival or productivity of members of a population. In this section, we will argue that such objectives may be fanciful in sustaining, non-increasing populations subject to density-dependent processes. If we are correct, the 1 objective inevitably countermands the other such that managing a demographic variable (even successfully) does not result in an increasing population.

Consider a simple difference equation that applies to a species with simple dynamics,

$$N_{t+1} = S_t N_t (1 + R_t)$$

where N_t , number of animals in the population in year t ; S_t , probability of survival in year t , and R_t , relative production (juveniles/adult) in year t .

The equation states that next year's population is equal to surviving individuals from this year's population plus their production. The equation is a tautology and thus inevitably true. The equation does not need empirical verification.

A population growth multiplier (λ_t) is defined as the ratio of next year's population to this year's population:

$$\lambda_t = N_{t+1}/N_t = S_t(1 + R_t)$$

For example, if next year's population is 750 and this year's is 500, $\lambda = 750/500 = 1.5$. If a population declines from 500 to 250, $\lambda = 250/500 = 0.5$. If $\lambda < 1$, a population declines; if $\lambda = 1$, a population stays the same; and if $\lambda > 1$, a population increases between years. In a sustaining population that shows no trend, though it may fluctuate markedly from year to year, the average value of the growth multiplier will be near 1.0. If a growth multiplier is >1 for several years a population will increase geometrically over time and this is not sustainable. Conversely, if a growth multiplier is <1 for several years a population will decrease geometrically and this is obviously not sustainable. The population will go extinct.

Suppose management in a sustaining quail population increases the annual survival rate from 0.20 to 0.25 in a population with relative production of 4 juveniles/adult. Then we have

$$\lambda = 0.25(1 + 4) = 1.25$$

The resulting growth multiplier is not sustainable because it exceeds 1.0 (i.e., with $\lambda = 1.25$, the population increases geometrically). For the population to be sustainable at an annual survival rate of 0.25, relative production must decrease to 3 juveniles/adult. At annual survival of 0.25 and relative production of 3 juveniles/adult, $\lambda = 1$, which is sustainable.

Three outcomes relative to sustaining populations (as defined) are apparent from the preceding arguments: 1) an increase in survival necessarily entails a decrease in production, 2) an increase in production necessarily entails a decrease in survival, and 3) increases in both survival and production are impossible over time. In other words, the wildlife manager who aspires to increase production or survival in a sustaining population cannot win for losing. This is

the dilemma of sustaining populations, which is consistent with the density-dependent processes discussed above and the observation of Potts (1986, epigraph). In a declining population, however, or one that has not occupied all of available space that may be occupied, managing for increased survival, production, or both is at least feasible. Whether such management will be successful is open to question. At least such management is worth trying, in contradistinction to the case with sustaining populations.

Habitat Management

Density-dependent processes may cause habitat management to be ineffective. A case in point is provisioning common goldeneyes (*Bucephala clangula*) with nest boxes (Pöysä and Pöysä 2002). In comparison with the control, the number of goldeneye pairs increased with additional nest boxes on experimental areas. However, the number of broods and the number of fledged birds did not increase. The authors observed negative density dependence in the number of broods and fledged birds. Thus, a density-dependent population process thwarted the effect of a management measure. Pöysä and Pöysä (2002) hypothesized that the density-dependence effect might apply to other cavity-nesting birds.

DISCUSSION

We return to the general justification for studying density dependence in wildlife populations: to “properly manage and conserve these populations.” Yet, in harvesting populations, we found no empirical research where managers maximized or optimized harvest under logistic or related density-dependence theory, at least for ungulates and upland game birds. However, Guthery (2002) provided theory for managing harvest of bobwhites under density-independent fall–spring mortality and density-dependent production.

Why is empirical application of density-dependence theory in harvest management lacking for ungulates and upland game birds? We suspect several factors weigh against its application:

1. Estimation of parameters (K , r) requires a long-term data set on a growing population, the relationship between breeding density and fall density, or the relation between fall density and overwinter mortality. Such data sets are in short supply.
2. An estimate of the number of animals to harvest from logistic theory entails knowing how to exact the specified harvest on management areas (season length, hunting pressure, bag limits, and other variables). Reliable estimation here also requires long-term data.
3. Logistic theory of harvest probably is not applicable at large scales (e.g., states). It is perhaps limited to specific areas such as game management areas or private holdings. Managers have little or no motivation to harvest under logistic theory at larger scales, where the motivations are to maximize recreational opportunity and conserve the resource. Of course, these motivations reflect an optimum sustained yield setting.
4. A more or less constant carrying capacity (K) associated with a more or less stable population is unlikely for

r -selected species such as quail, which show great annual variation in non-trending populations that may mask density-dependent responses. Derivation of yields using the logistic model simply does not work in this setting. It would seem to be more useful in decision-making for ungulates.

5. The logistic model may fail at the extremes of the r – K spectrum (Fowler 1981; D. R. McCullough, University of California, personal communication). Thus, a harvest of $1/2K$ might result in overharvest of K -selected species such as whales, a pattern that has empirical support.
6. Populations may, at some times, behave in density-dependent ways and at others exhibit density-independence. Even when density dependence is working, it may elude detection, particularly when environmental influences such as variance in precipitation are high (DeYoung 2011).
7. The processes involved in density-dependent population behavior are intricate and complex. Managers who appreciate this complexity might tend to skepticism over logistic theory and instead manage harvest adaptively by induction from experience.

Several factors increase the complexity of density dependence. For example, density-dependence relationships may change with time for North American duck populations (Murray et al. 2010) and with geographic locations for small game species (Williams et al. 2003). Density dependence may act on different sex-age groups; for ungulates, it may influence juvenile survival, age at first reproduction, adult fecundity, and adult survival (Bonenfant et al. 2009). To add to potential confusions, density dependence seems to operate at low populations for r -selected species and near carrying capacity for K -selected species (Fowler 1981). Given territorial predators, the rate of predation may decrease as the density of prey increases (Götmark and Andersson 2004), thus adding complexity by going contrary to general expectations.

Failure to appreciate the force of density dependence undermines the ability of state wildlife agencies to set better hunting regulations. McCullough (1987) noted that the relationship between harvest size and population density was not adequately understood by wildlife professionals, let alone licensed hunters. Sportsmen often do not understand that higher yields occur at lower population densities than are typical for deer in most states in recent years. For example, the Oklahoma Department of Wildlife Conservation has, since 1994, conducted 6 telephone surveys to random samples ($n \sim 1,000$ for each survey) of licensed deer hunters and asked the following question, “Which of the following choices is most important to you for a successful deer hunting experience?” The choices were 1) seeing many deer of both sexes, 2) seeing fewer deer but more bucks, 3) seeing even fewer deer, but more trophy bucks (Crews 2011). In each survey, between 62% and 70% of deer hunters chose the first option, when either of the other 2, if implemented, would result in higher yields, healthier deer, and reduced deer damage.

Perhaps the most important aspect of using knowledge of density-dependent processes to formulate sound management decisions involves the dilemma of survival and production in the presence of density-dependent responses; except in special circumstances, a manager cannot increase one without decreasing the other and vice versa. This circumstance apparently cuts across more specific (e.g., survival rate while foraging) and more general (e.g., survival rate during winter) activity and time frames. It implies that predator control to increase nest survival could, if successful, reduce fall-to-spring survival. The only way to deal with such quid pro quo demography is to provide additional space for a population to occupy. Then management to increase survival and-or production will be rewarded until the population occupies the additional space (reaches K) and density-dependent mechanisms take hold.

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