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THEORY OF THE HUNTER-COVEY INTERFACE

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ABSTRACT

We established mathematical models and explored the role of a learned response (avoidance behavior) to understand and manage the hunter-covey interface. Furthermore, we examined the dynamic nature of the probability of flush, given encounter, in a population that learned to avoid hunters as time passed. Learning rate was defined as the proportion of a covey that leaves the naive population and enters the experienced population per unit of hunter-covey contact. The conditional probability of flushing and shooting at a covey, given a covey encounter, declined through the season. This is because the probability of flushing was lower for experienced than for naive coveys and the population of experienced coveys grew with exposure. Thus, quality of hunting declined at a faster rate than quail population; i.e., birds became more wary as the hunting season progresses. The birds' ability to avoid hunters provided an explanation of the sudden reappearance of bobwhites contributing to reproduction in areas where hunters were unsuccessful the previous hunting season. Management can use our models to manipulate the interface and obtain a desired population following the hunting season.

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INTRODUCTION

Wildlife biologists and hunters have long recognized avoidance behavior by northern bobwhites (*Colinus virginianus*), i.e., trap shyness and flighty behaviors. Thorndike (1911), an early animal behaviorist, formulated this concept as the Law of Effect. It states "[O]f several responses made to the same situation, those which are accompanied or closely followed by satisfaction to the animal will, other things being equal, be more firmly connected with the situation, so that, when it recurs, they will be more likely to recur." In other words, a response followed by favorable consequences becomes more probable than a response followed by unfavorable consequences. Additionally, individuals that live in groups (e.g., bobwhite coveys) may have the opportunity to learn to recognize unfamiliar dangers by observing the responses of experienced individuals in the group. This behavioral concept is termed cultural transmission (Mainardi 1980, Curio 1988, Mineka and Cook 1988). Cultural transmission of information has been reported for several avian species, in which predator-naive individuals learn to recognize predators by observing the responses of experienced birds (Klopfer 1957, Curio et al. 1978, Vieth et al. 1980).

Several assumptions in animal behavior are: (1) all behavior is caused or determined in some way; i.e., all behavior obeys certain laws; (2) explanations of behavior based on internal causes and mental states are generally useless; and (3) the environment molds be-

havior. Animal behaviorists explain the cause of behavior by studying only those behaviors that can be observed and measured, without reference to unobservable mental processes.

Covey dynamics for northern bobwhites in southern Texas have been reported (Lehmann 1984). The nature of the behavior process, termed the hunter-covey interface, was explored because hunter-harvest data are commonly used in bobwhite density estimates, management, and establishing future hunting regulations. We used mathematical models to predict possible outcomes of the learning process on the hunter-covey interface. We started with a simple static model of daily harvest and generalized the model to account for avoidance behavior by bobwhites and site selection by hunters. The theoretical background for understanding the hunter-covey interface provides information that can be incorporated into harvest management plans.

METHODS

We first established and developed a static model of daily harvest. Under the static model 1 hunting party hunts 1 area on 1 day. The number of birds harvested (K) on any day is the product of coveys encountered times the number of birds shot per covey encountered. This statement may be expressed as

$$(1) \quad K = mp(N/s)$$

where

m = mean number of birds shot per covey flushed,
 p = probability of encountering a covey,

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N = total bobwhite population at the beginning of the day, and
 s = average covey size on the day.

The probability of encountering a covey (p) is of considerable practical and theoretical interest. Conceptually, we may view a given hunt as an area covered superimposed on an area hunted. Therefore, a hunt will effectively cover an area of some size within a larger area available for hunting. Assuming (1) hunting pressure is nonredundant, i.e., new space is hunted at each instant, and (2) coveys are randomly distributed in space on the hunted area, then the probability of encountering any covey is the area covered on the hunt divided by the area available for hunting,

$$(2) \quad p = a/A$$

where

a = the area (ha) effectively hunted on a day, and
 A = the area (ha) available for hunting.

The area effectively hunted increases with the speed of the hunters, the time spent hunting, and the effective width of the hunting zone. The relationship can be described as:

$$(3) \quad a = vhw$$

where

v = the velocity at which hunters travel (linear units/hr),
 h = hours spent hunting, and
 w = the effective width of the hunting zone (linear units).

The width (w) is homologous to effective strip width in line transect sampling of wildlife density. The time for hunting (h) is limited, and more or less fixed to morning and evening. However, the velocity may be increased by hunting from vehicles, horses, and/or by use of dogs. Rosene (1969:347) estimated a hunter on foot with dogs covers about 120 ha per day, whereas hunting parties using horses or vehicles cover 400–600 ha per day. If one assumes hunters using vehicles flush 3–5 times as many coveys as hunters on foot, then it is possible for low quail densities to be associated with high time-rates of flushing (coveys per hr) when hunters increase velocity and width.

The above arguments lead to a more general model of daily kill as:

$$(4) \quad K = m(vhw/A)(N/s).$$

This simple model holds under random distribution of coveys and nonredundant hunting pressures, which limits the model's application. More realistic models could incorporate avoidance behavior (learning) by coveys (Sisson 1996), which may be counteracted by hunters with selection of better habitat patches for hunting, baiting, or both.

Also, encountering a covey relates to how a covey responds (freeze, fly, run) when a hunting party approaches. The probability of flushing a covey also must address if it is within shooting range. The word flush, in the context of our paper, means hunters flush

a covey within shooting range. However, there will be a fraction of the coveys flushed because of avoidance behavior (all coveys encountered will not flush). Then the probability a covey flushes, given encounter, is defined as p_f . Under avoidance behavior, we revise the previous equation to:

$$(5) \quad K = m(vhw/A)p_f(N/s).$$

The above equation is subject to the assumption hunters do not preferentially select portions of areas for hunting and they do not bait. However, whether hunters bait, preferentially select hunting sites, or both, is not of concern in a more general conceptual model of daily harvest. Preferential site selection is conceptually similar to baiting in model development. We can define an area of size B which is preferentially selected and/or baited within the general area of size A . We specify all hunting occurs within area B and hunters show no preferential use within area B . Then the probability of encountering a covey becomes conditional on p_b , the probability a covey occurs in area B . Note that p_b relates specifically to the bobwhite population and not to area. The model for the daily kill now becomes:

$$(6) \quad K = m(vhw/B)p_f p_b (N/s).$$

This equation provides a deterministic estimate and therefore is best considered an average value under the conditions specified. Also, we realize that certain variables in the general model are dynamic. For example, scenting conditions for dogs vary with temperature and humidity (Gutzwiller 1990), which imposes variation in the effective width of the hunting zone (w). Populations decline through the hunting season as does the mean number of birds in coveys. And behaviorally, bobwhites may become more wary as time passes and exposure to hunting continues.

Next, we explored learning behavior leading to hunter-avoidance. In particular, we examined the dynamic nature of the probability of flush, given encounter, in a population that learns to avoid hunting parties over time (t). Naive coveys C_n were defined as not being exposed to hunting pressure. We assumed all coveys were naive at the start of the hunting season, and the probability of flush, given encounter, was lower for experienced coveys than for naive coveys; i.e., experienced coveys showed hunter-avoidance behavior. Individuals from naive coveys were lost through harvest, natural mortality, and emigration into the population of experienced coveys. The population of experienced coveys acquired gains from ingress of naive individuals and losses from harvest and natural mortality.

Population dynamics of the naive and experienced coveys can be modeled with similar natural mortality rates and harvest-loss rates per hunter-covey contact. The dynamic variable of interest is the mean probability of flush, given encounter, at some time t , defined as $p_{f,t}$. Since hunters are less likely to flush an experienced covey than a naive covey, this mean is a weighted average of p_{fn} and p_{fe} at time t ,

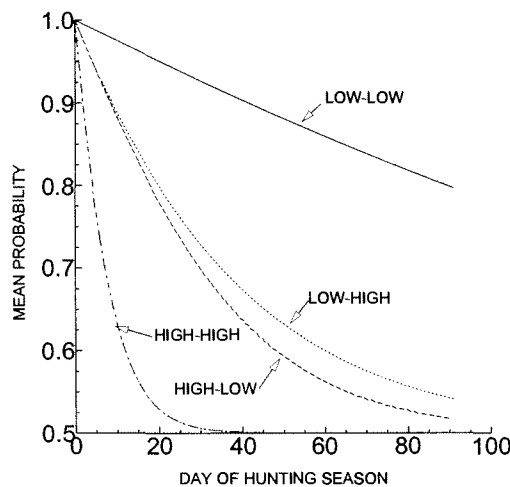


Fig. 1. Modeled trends in the mean probability of flush given an encounter for a bobwhite population consisting of naive and experienced coveys. Descriptors refer to hunting-intensity-learning rate; i.e., low-low indicates low hunting intensity and low learning rate. Experienced coveys have a lower conditional probability than naive coveys. The figure provides qualitative information on the dynamics of the mean probability.

$$(7) \quad p_{f,t} = (p_{fn}C_{n,t} + p_{fe}C_{e,t})/(C_{n,t} + C_{e,t})$$

where

$p_{f,t}$ = average probability of flush given encounter for a population containing naive and experienced coveys on day t ,

p_{fn} = probability of flush given encounter for naive coveys,

p_{fe} = probability of flush given encounter for experienced coveys,

$C_{n,t}$ = total population of naive coveys on day t , and

$C_{e,t}$ = total population of experienced coveys on day t .

The dynamics of naive and experienced covey populations may be defined in differential form as

$$(8) \quad \begin{aligned} C_{n,t+1} &= C_{n,t} - jpC_{n,t}H - kpp_{fn}C_{n,t}H - lC_{n,t} \\ &= C_{n,t}(1 - jpH - kpp_{fn}H - l) \end{aligned}$$

and

$$(9) \quad C_{e,t+1} = C_{e,t} + jpC_{n,t}H - kpp_{fe}C_{e,t}H - lC_{e,t}$$

where

j = the learning rate or rate at which coveys become experienced for each hunter-covey contact,

k = the loss rate to harvest for each hunter-covey contact,

l = the daily loss rate to nonhunting mortality, and

H = the number of hunting parties.

The coefficients may be considered as some fraction of a covey per unit of hunter-covey contact (j , k) or per covey (l).

RESULTS

The mean probability of flush, given encounter, initially declined as experienced coveys increased as a

proportion of the total population (Figure 1). It was possible for the mean to stabilize at some value under high hunting pressure and a high learning rate. This stabilization occurred when the population was saturated with experienced coveys; i.e., coveys that encountered hunters during the hunting season.

The dynamic model revealed several qualitative outcomes of the hunter-covey interface under avoidance behavior (Figure 2). The population of naive coveys may only decline, whereas that of experienced coveys may grow throughout the hunting season. Naive coveys declined more rapidly as hunting pressure and learning rate increased; conversely, experienced coveys increased more rapidly to peak populations during the season as hunting pressure and learning increased. Under high hunting pressures and learning rates, it was possible for a population to consist entirely of experienced coveys for a large portion of the season (see HIGH-HIGH graph, Figure 2).

Temporal trends in the daily harvest would be similar to those for the mean probability of flush given encounter (Figure 1). Under these models, the total population declined continuously because of natural mortality. Likewise, the daily kill would decline continuously (holding hunting pressure constant) because the kill represents some fraction of the total population. Trends in daily kill will appear flat with low harvest rates, learning rates, and natural mortality. Trends will appear more spiked as these variables increase.

DISCUSSION

Empirically observed values for m range between 1.5 and 2.0 birds downed per covey flushed. Bennett (1951) reported an average of 1.86 (SD = 0.076) for hunters in Missouri. Harvest data from a southern Texas corporate hunting lease, which included 2 hunters per covey flush, indicate $m = 1.68$ (SD = 0.572) (unpublished data).

The static model provides intuitive methodology for increasing or decreasing daily harvest or time available for hunting. This model predicts daily harvest declines as take per flush, velocity of travel, time spent hunting, width of the hunting zone, and the probability of flush, given encounter, decline (holding the population of coveys constant). Hunting time required to obtain a specified harvest on a given day varies inversely with the product of the 4 variables under management control, m , v , w , and p_f ; i.e., the time required to meet the specific harvest goals increases in a hyperbolic fashion as the product of these variables decreases linearly.

The model resulting in qualitative analysis of the dynamic interface between hunter and covey warns against general statements concerning the effects of avoidance behavior. According to the model, effects are contingent on the learning rate and hunting pressure (Figure 1). Trends in the probability of flush, given encounter, under LOW-LOW and HIGH-LOW regimes illustrate the potential effects of hunting pressure under identical learning rates. Moreover, the prob-

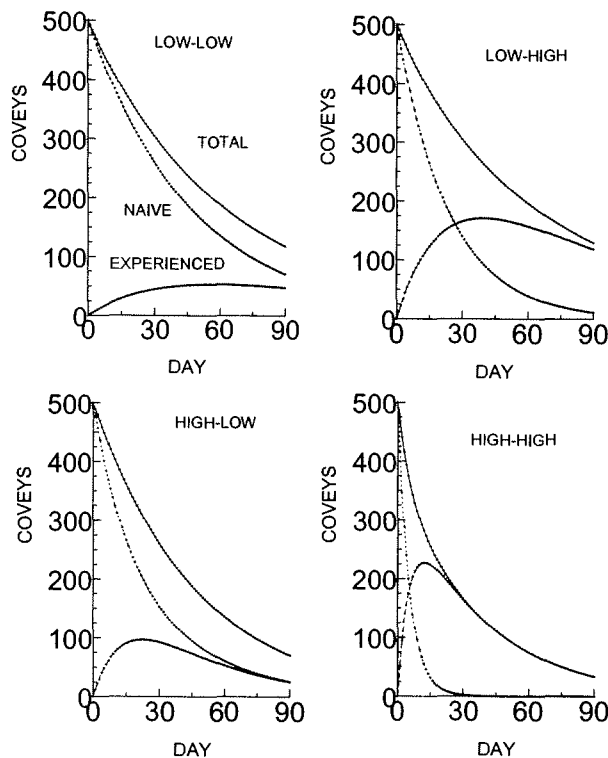


Fig. 2. Modeled trends in populations of naive, experienced, and total coveys under different hunting intensities and quail learning rates during a 90-day season. Descriptors refer to hunting intensity-learning rate. The figure provides qualitative information on covey dynamics because values of variables in the model are unknown.

ability of flush, given encounter, varies in a nonlinear manner over time. Under these models, the probability of flush, given encounter, was constant for experienced and naive coveys. Only the mean probability may vary with time, because of changes in the proportions of naive and experienced coveys. Therefore, there may exist periods within seasons where the mean probability of flush, given encounter, is unaffected by hunting intensity and learning rate (all coveys are experienced). This occurred at about day 45 in the hypothetical HIGH-HIGH regime (Figure 1). The mean probability changed imperceptibly after day 45.

MANAGEMENT IMPLICATIONS

If the assumption is that harvest makes no difference in population dynamics of quail, then there is no applied value in our models. However, if this is not the case, then the daily kill models illustrate several variables amenable to management action; velocity, time, width, baiting, and kill/flush. For example, the latter variable may be influenced by restricting hunters

to smaller gauge shotguns. Also, the models may be used to maximize recreation. That is, solving to maximize h could be attained by manipulating the remaining variables in the daily harvest model. Finally, knowledge of the dynamics of hunter-avoidance could be applied in managing harvest. One could start with naive hunters, say youth, to propagate wariness and then allow the more experienced hunters access. In theory, this would maximize recreation with some constraints on the total harvest.

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