EMPIRICAL TESTS OF HUNTER–COVEY INTERFACE MODELS

JASON B. HARDIN,[1] Caesar Kleberg Wildlife Research Institute, Texas A&M University-Kingsville, Kingsville, TX 78363, USA
LEONARD A. BRENNAN,[2] Caesar Kleberg Wildlife Research Institute, Texas A&M University-Kingsville, Kingsville, TX 78363, USA
FIDEL HERNÁNDEZ, Caesar Kleberg Wildlife Research Institute, Texas A&M University-Kingsville, Kingsville, TX 78363, USA
ERIC J. REDEKER, Caesar Kleberg Wildlife Research Institute, Texas A&M University-Kingsville, Kingsville, TX 78363, USA
WILLIAM P. KUVLESKY, JR., Caesar Kleberg Wildlife Research Institute, Texas A&M University-Kingsville, Kingsville, TX 78363, USA

Abstract: Quail hunting consists of a complex set of behaviors that involve humans, pointing dogs, and wild birds. The recent development of models known as Hunter–Covey Interface (HCI) theory provides an opportunity to analyze how we perceive, understand, and manage quail hunting. There are 2 groups of HCI models: static and dynamic. The static HCI model predicts daily hunting mortality based on the velocity of the hunt and area covered during a hunt. The dynamic HCI models estimate the probability of flushing a covey given a set of circumstances that revolve around the potential rate that quail learn to avoid hunters. We quantified the variables required to test whether the static and dynamic models of HCI theory provide meaningful results. We used spatial data on hunting velocity and area covered during >100 quail hunts, along with estimates of quail population density, mortality, and movements from 2 areas in south Texas, to evaluate output from HCI models. The static model predicted average daily harvest rates that ranged from 5 to 50 birds. This average is within the range of average daily bag of south Texas quail hunters in groups of 2–4. Output from the dynamic models suggested that quail populations on our study areas were subjected to relatively low hunting intensities with a corresponding low avoidance behavior and learning rate, which is a scenario that matched 1 of 4 predictions by Guthery (2002). We found it difficult to meet basic assumptions of HCI theory. For example, hunting pressure was potentially redundant, coveys were not always randomly distributed in space, and the extent to which quail are naive at the beginning of a hunting season was unknown. However, both the static and dynamic HCI models appeared robust to violation of these assumptions. Application of HCI theory may provide meaningful results that can be used to manage quail hunting pressure, optimize harvest, and sustain populations.

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Quail hunting is a process that involves dynamic interactions among humans, pointing dogs, and game birds. The tradition of hunting game birds with pointing dogs has a rich legacy (Stoddard 1931, Rosene 1969, Tapper 1992, Brennan 1993). Despite this long history and tradition, the actual processes of quail hunting, and how the components of the quail hunting process vary in space and time, are poorly understood. The way that people understand the dynamics of quail hunting is primarily based on perception, anecdotes, and opinions, rather than on quantified facts and data analyzed with predictive models and theory.

Behavior may be construed as movement. Quail hunting behavior is, therefore, a complex set of movements. To understand how the movements of hunters, dogs, and birds combine to form the quail hunting dynamic, it is necessary to (1) quantify each of these behavioral components in space and time and (2) organize these components as variables with unifying theory and models.

We conducted an empirical analysis of how quail hunting behaviors vary in space and time based on a theoretical construct known as the Hunter–Covey Interface (HCI; Radomski and Guthery 2000, Guthery 2002). Our specific objectives were to evaluate whether HCI theory provides meaningful results for quail (in this case, northern bobwhite [*Colinus virginianus*]) management by (1) identifying and quantifying quail hunting variables in relation to HCI theory, and (2) evaluating the assumptions upon which the HCI models are based.

The HCI theory makes predictions how aspects of quail hunting and quail hunting success change in space and time according to different variables. To date, empirical tests of the HCI theory have not been conducted. If the HCI theory generates realistic predictions about quail hunting dynamics, then quail managers and biologists will be in a better position to use HCI models for making informed decisions about how to orchestrate quail hunting pressure and achieve specific population management objectives.

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[1] Present address: Audubon Texas Quail and Grassland Bird Conservation Program, Texas A&M University-Kingsville, Kingsville, TX 78363 USA.

[2] E-mail: leonard.brennan@tamuk.edu

Despite progress from key publications by Errington (1945), Roseberry (1982), and Guthery (2002), a unified scientific basis for managing quail hunting pressure remains a critical gap in modern wildlife science. In general, the literature on quail harvest management is contentious, confusing, and often contradictory (Guthery 2002:95). Much of the confusion surrounding quail harvest management is related to early studies that provided empirical support for the doomed-surplus or full compensation hypothesis (Baumgartner 1944, Parmalee 1953, Campbell et al. 1973). The consistent theme of these studies was that hunting had no impact on the fall-to-spring mortality of quail populations. In contrast, more recent research has found that quail harvest mortality may be additive to natural mortality at some level (Roseberry and Klimstra 1984, Pollock et al. 1989, Robinette and Doerr 1993, Williams et al. 2004), especially during the later part of the hunting season (Roseberry 1982).

Much of the confusion surrounding quail harvest management also relates to the fact that few, if any, published studies on this topic were designed to prescribe a harvest rate that led to a specific breeding population density objective (Guthery 2002). If such an objective is identified, then it is theoretically possible to organize the components of quail harvest to achieve a management outcome. The HCI theory was designed as a tool to help managers obtain a threshold quail population breeding density by understanding and managing the primary components that influence hunting pressure and ultimately overall mortality during the nonbreeding season (Guthery 2002).

Theoretical HCI Models

The core of HCI theory is based on 2 sets of mathematical models: static and dynamic (Guthery 2002:115). The static model was constructed to provide information on how daily quail harvest varies in relation to hunting variables. The dynamic models were constructed to provide insight into how the probability of encountering a covey changes in relation to repeated hunting pressure and the presumption that quail learn to avoid hunters as the hunting season progresses.

Static Model.—The static model identifies daily kill (K) as a product of the mean number of birds harvested per covey flushed (m) multiplied by the probability of encountering a covey (p), all multiplied by the total quail population at the beginning of the day (N) divided by the average covey size on that day (c). The model appears as

$$K = mp\,(N/c). \tag{1}$$

The probability of encountering a covey (p) is a value found by dividing the area effectively hunted (a) by the total area available to hunt (A),

$$p = a/A \tag{2}$$

The area effectively hunted is a product of the velocity (v) of the hunt, the hours spent hunting (h), and the effective width of the hunting zone (w). This value is described as

$$a = v\,h\,w. \tag{3}$$

Therefore the more general formula is

$$K = m(vhw/A)\,(N/c). \tag{4}$$

The static model is further modified to include p_f that represents the conditional probability of flushing a covey, given an encounter,

$$K = mpp_f\,(N/c). \tag{5}$$

However, equation (5) assumes that an area is not preferentially selected for hunting and/or baited. To account for preferential selection of an area and/or baiting, the model can be modified further to include the probability of a covey occurring within the preferentially selected and/or baited area (P_b). The equation then appears as

$$K = m\,pp_fp_b\,(N/c). \tag{6}$$

Equation (6) can be used to adjust daily harvest by modifying the number of birds taken per covey, hours spent hunting, velocity of hunt, and/or effective strip width of the area hunted.

Dynamic Models.—In HCI theory, the dynamic models estimate the probability of a covey flush in response to encounters experienced by a quail population that learns to avoid hunters over time (Guthery 2002). Two dynamic models have been created. One describes experienced coveys (C_e) that were defined as coveys that have encountered a hunting party. The other dynamic model describes naive coveys (C_n) that were defined as coveys that have not been encountered by a hunting party. These models appear as:

$$\begin{aligned} C_{n+1} &= C_n - jpC_nH - kpp_{fn}C_nH - lC_n \\ &= C_n\,(1 - jpH - kpp_{fn}H - 1) \end{aligned} \tag{7}$$

and

$$C_{e+1} = C_e + jpC_eH - kpp_{fe}C_eH - lC_e \qquad (8)$$

where

j = learning rate,

p = proportion of the area hunted (as in the static model),

H = number of hunting parties,

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

l = daily loss rate to nonhunting mortality,

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

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

These models identify the day-to-day changes in population dynamics for the number of naive and experienced coveys. According to the first dynamic model (C_n), the population of naive coveys is expected to decline through the season. Decline is more rapid when the coveys experience high hunting intensity and high learning rates. In the second dynamic model, experienced coveys will initially increase and will do so at a more rapid rate with high hunting intensity and a high learning rate. According to the dynamic models, the number of naive coveys can only decrease; whereas, the number of experienced coveys will initially increase but can also decrease with time due to harvest and natural mortality. Guthery (2002:122) stated that, "similar harvest rates will be expected for both naive and experienced birds *if* experienced birds are encountered *and* flushed; however, hunters are less likely to flush an experienced covey than a naive one, given an encounter." Guthery predicted that under conditions of high hunting pressure and a high learning rate, it is possible for mean probability of flush given an encounter to stabilize. This will occur when the population consists entirely of experienced coveys that are extremely wary of hunters. The probability of a covey flush given an encounter with a hunter is expressed as:

$$P_{ne} = (P_{fn}C_n + P_{fe}C_e)/(C_n + C_e) \qquad (9)$$

where P_{ne} is homologous to p_f and is a weighted average between the probability of flushing a naive and experienced covey.

Assumptions

All scientific theories are based on ≥1 assumptions. Such assumptions, and whether they can be met under empirical conditions, are essential for assessing the veracity of a theory. However, theoretical constructs may also provide useful results when assumptions are either violated or not completely met. In such cases, the theory is considered robust, which may make it useful for application. Several assumptions of HCI theory must be tested under real-world conditions to determine if the predictions are meaningful for management. The most important assumptions of HCI theory are: (1) Hunting pressure is not redundant. The theory assumes that new space is hunted as the hunting events proceed through time (static and dynamic models). (2) Coveys are randomly distributed in habitat space on the hunting area (static and dynamic models). (3) All coveys are naive at the beginning of the hunting season (dynamic models). (4) The probability of flush given an encounter with a hunter is lower for experienced than for naive coveys (dynamic models).

The extent to which HCI theory, and the static and dynamic models, is robust to violations of these assumptions is unknown. Therefore, we evaluated whether the data used to generate predictions from HCI models met the 4 assumptions listed above.

STUDY AREAS

We conducted this study at 2 sites in south Texas, USA: Brooks and Duval counties. Details of climate, rainfall, and soils are available in Hardin (2003).

Brooks County.—This study site was on the 13,760 ha corporate San Tomas hunting lease on the King Ranch Encino Division within the lower Coastal Sand Plains. The San Tomas lease is in Brooks County approximately 32 km south of Falfurrias, Texas, USA. Howard (2005) provides an historical overview of this lease that has been managed for sustainable quail hunting since 1979. The primary woody vegetation was honey mesquite (*Prosopis glandulosa*), granjeno (*Celtis pallida*), and live oak (*Quercus virginianus*). Herbaceous cover consisted primarily of King Ranch bluestem (*Bothriochola ischaemum*), Bermudagrass (*Cynodon dactylon*), Gulf cordgrass (*Spartina spartinae*), sandbur (*Cenchrus incertus*), sunflower (*Helianthus annulus*), little bluestem (*Schizachyrium scoparium*), and croton (*Croton* sp.) (Hatch and Pluhar 1993). Cattle grazed pastures at this site under varying systems including the 3-herd, 4-pasture Merrill system, a switchback system, and a high-intensity, short-duration system, depending on the specific area.

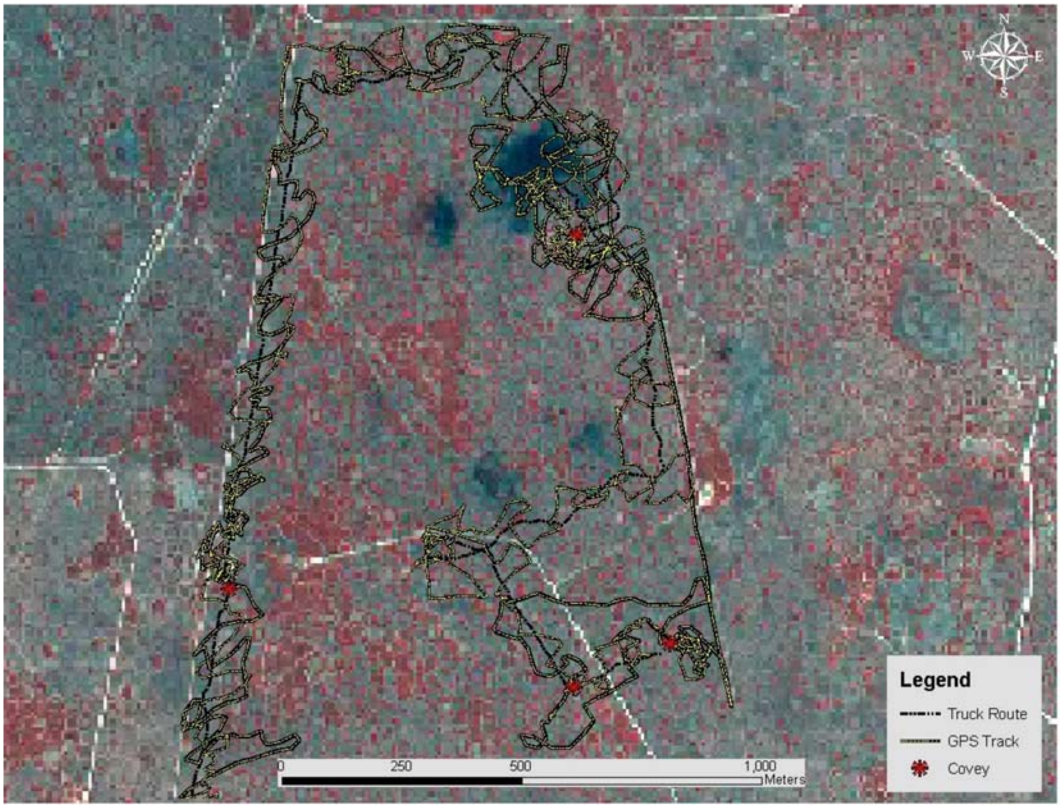

Fig. 1. Example of spatial arrangement of pointing dog (solid line) and hunting truck (dashed line) travel routes for quail hunts used to generate data for testing Hunter–Covey Interface models.

Duval County.—This site was on the 4,074 ha Temple Ranch in Duval County. This ranch was located in the brush country near the Bordas Escarpment approximately 24 km northeast of Freer, Texas, USA. The primary woody vegetation was honey mesquite, guajillo (*Acacia berlandieri*), and black brush acacia (*Acacia rigidula*) http://www.tnris.state.tx.us/DigitalData/data_cat.htm#. This study site had more woody cover and more diversity of woody species than the Brooks County site. The primary herbaceous species were buffelgrass (*Cenchrus ciliaris*), King Ranch bluestem, with other native species such as silver bluestem (*Bothriochloa laguroides*) and pink pappusgrass (*Pappophorum bicolor*; Hatch and Pluhar 1993). This site historically has been grazed by cattle but had been deferred from grazing since April 2000.

METHODS

Static Model

We observed quail hunts conducted from trucks that followed pointing dogs as they searched for quail (Fig. 1). We quantified the variables in Equation (6) to test the predictions of the static model.

Birds Harvested per Covey.—We assessed this variable by quantifying mean harvest per covey (m) from quail hunts on the 2 study sites and by examining published literature. As reported by Guthery (2002), the mean number of birds harvested per covey encountered typically ranges between 1.5 and 2. According to a recent survey, many ranches and leases in south Texas allow from 2 to 3 birds to be harvested per covey (Hardin and Brennan 2002).

Probability of Encounter.—We based the probability of encounter (p), for Equation (2) by using Global Positioning System (GPS) data collected on hunting vehicles and 37 pointing dogs during the 2 study seasons. We estimated the probability of encounter by dividing the area effectively hunted by the area available to hunt (a/A). To identify the area effectively hunted, as described by Equation (3), it was necessary to accurately determine the velocity that hunting dogs travel and the distance dogs hunted from the hunting vehicle. We determined the variables described in Equation (3) by fitting a GPS unit on pointing dogs during hunts.

We used 2 types of GPS units to collect hunting route data from dogs and vehicles. During the 2001 quail hunting season, a Garman Etrex Venture® (Garmin International, Olathe, KS, USA) GPS unit was wired to a Compaq iPAQ® 3650 (Hewlett-Packard, Houston, Texas, USA) computer using Starpal™ (STARPAL, Inc., Fort Collins, Colorado, USA) HGIS™ software. During the 2002 quail season, we used a NAVMAN (NAVMAN, New Zealand) GPS unit. The NAVMAN used for this project is a GPS receiver built specifically for the Compaq iPAQ®. All other data collection equipment from the 2001 quail season remained the same. These GPS units collect data at 1:12,000 mapping accuracy standards (Decker 2001). We downloaded data from the GPS with Garmin Mapsource® software (Garmin International, Olathe, KS, USA). We then exported the data to an Auto Cad DXF file and imported the files into ArcGIS® 8.3 (Environmental Systems Research Institute, Redlands, California, USA) as shape files.

All vertexes in the log file were collected at 7-second intervals. A 7-second interval was utilized for several purposes. First, our GPS units could collect data continuously for approximately 4 hours using a 7-second interval. This allowed for all the information from a single hunt to be collected on a single GPS unit. However, we also ran trials using longer and shorter intervals to make sure no data were lost. Second, turning angles of pointing dogs showed little to no difference at shorter time collection intervals Therefore, a 7-second collection interval optimized the collection effort for each hunt.

Small amounts of data were considered erroneous and removed prior to analysis. For example, if a GPS unit was turned on before or after a pointing dog hunted, those locations were removed. We analyzed the validity of data points by cross-referencing to a Geographic Information System (GIS) database. Points collected that obviously did not belong on the hunting path of the pointing dogs were identified and removed. Other erroneous data included speed measurements that were obviously out of the physical capability of the dogs. We used a Proc GLM procedure in SAS 8.1 to assess the variation in hunting velocity and area effectively hunted between hunting seasons and study sites.

We collected path data along pointing dog hunting routes and the corresponding routes the hunting truck traveled while following the dogs. We then converted these path data to an arc coverage using ArcGIS® 8.3. We subsequently used the near function in ArcGIS® 8.3 was to identify the distance that dogs traveled from the path of the truck during the hunt. We used a maximum distance of 500 m to correct for dogs that were not hunting with the vehicle (i.e., when they were lost). When dogs were >500 m from the hunting vehicle they were no longer considered part of the hunt. At such distances, the Hunter–Covey Interface ceased to exist, and activities typically shifted from hunting quail to searching for a lost dog. We therefore deleted vertexes greater than the established 500 m maximum distances for analyses of pointing dog routes and velocities. This resulted in the elimination of small amounts of data (0.2–2.6% of points used to delineate hunting dog routes) on approximately 20% of >160 hunts. We outlined the area for each hunt using the GIS and then calculated the hectares in each hunting area to determine (A), the area available to hunt.

We identified the hours spent hunting (h) from peripheral data collected by the GPS in the hunting vehicle. Each vertex collected along the hunting route included a measurement of time. This information gave us accurate time for the duration of each hunt.

Probability of Flushing a Covey.—We determined the probability of flushing a covey (p_f) given an encounter from radiomarked bobwhites on the Brooks County site. To predict the probability of flush given an encounter, we followed radiomarked coveys during hunts. If radiomarked coveys were within 100 m of the hunting vehicle, we considered them accessible to the pointing dogs. We classified these radiomarked coveys as either missed or pointed by the dogs.

Probability of a Covey being within a Baited Area.—Haines (2003) showed that baiting had no influence on a covey ranging more than 200 m from baited trails. Therefore, hunting routes were buffered 200 m, and area was calculated using ArcGIS 8.3. The area impacted by baiting, approximately 200 ha (Table 1), was similar to the area available to hunt. The baited areas were distributed evenly throughout all pastures available to hunt; therefore, the probability of a covey being within the baited area (p_b), as described in Equation (6), was probably of little consequence. Therefore, we used Equation (5) to calculate harvest.

Densities.—Bobwhite coveys are a dynamic social unit that maintain a more-or-less constant number of members during the winter (Williams et al. 2003). Thus, estimates of the number of coveys present and average covey size can be a practical method for estimating crude population density values.

We estimated the numbers of coveys (N/c) on the 2 study sites with morning covey call counts that followed protocols established by Seiler et al. (2002) and Wellendorf et al. (2002). We conducted morning covey call counts during the fall (Sep–Nov) to determine the pre-hunting season quail density. Morning covey call counts for quail are different from the point count techniques typically used to census land bird abundance. These covey call counts were designed to record the contact calls that take place among coveys of quail during a very brief (5–10 min) period during the first light of the day. Because of the brief duration of the calls, 1 observer can census only 1 point during a sampling session.

Morning covey call counts began approximately 30 min before dawn at each site and continued until about 15 minutes after sunrise, when the coveys finished calling. A calling covey was recorded with the time of the call, distance to the covey, and the direction to the covey. We assumed an area of 50.2 hectares was surveyed and that 78% of the coveys in the area surveyed called (Seiler et al. 2002). Therefore, the estimated number of coveys in the area surveyed was divided by a correction factor of 0.78. Then, we multiplied the corrected number of coveys by the average covey size observed during November quail hunts, and we divided that number by 50.2 hectares to calculate the number of birds per hectare.

We surveyed 8 morning covey call locations 2 times each (16 replicate samples) during fall 2001 at the Brooks County study site. We surveyed 9 locations, (3 locations in 3 different pastures) 3 times (27 replicate samples) during fall of 2002 at the Brooks County study site. We surveyed 5 morning covey call locations from 1 to 3 times (5 to 15 replicate samples) at the Duval County study site during fall of 2001 and 2002. All covey call surveys were conducted during periods of ideal sampling conditions when no wind or precipitation occurred.

Nonhunting Mortality.—We calculated natural (i.e., nonhunting) quail mortality during the hunting season (Nov 1–Feb 28) at the Brooks County site using the Kaplan-Meier staggered entry design (Pollock et al. 1989). During the 2001 quail-hunting season, we monitored 131 radiomarked birds. During the 2002 quail-hunting season, we monitored 58 radiomarked birds. We added birds caught and radiomarked after the beginning of the hunting season to the monitored population. We recorded the fate (natural mortality, hunter harvest, survival) of birds was recorded. For the purposes of calculating output from HCI static models, we assumed that nonhunting mortality was similar between the Brooks and Duval sites.

Table 1. Hectares available to hunt during the 2001–2002 and 2002–2003 quail hunting seasons at the Brooks and Duval counties, south Texas, USA, study sites based on a hunting route buffer of 200 meters.

	Study area	
Variable	Brooks County	Duval County
Mean	198.48	202.97
Standard deviation	65.39	70.35
Maximum	390.01	329.98
Minimum	93.34	93.62
Number of hunts	72	47

Dynamic Models

Similar to the static model, we estimated variables of the dynamic models as they appeared in Equation (7) and Equation (8). No empirical values for these parameters were available prior to this study. Data from radiomarked quail (such as response of birds to repeated encounters with hunters) were required to generate output from the dynamic models, thus analyses of dynamic models were limited to the Brooks County site.

Learning Rate Index.—Because Guthery (2002) considered the dynamic model predictions from a qualitative perspective, some kind of quantified value must be assigned to the learning rate so that model output can be assessed. Therefore, we assigned a categorical value of 1 as a learning rate index for all coveys that displayed evasive behavior by running from the pointing dogs on their first known encounter. Coveys that displayed evasive behavior upon their second known encounter with a pointing dog received a learning rate of 0.50, coveys that displayed evasive behavior upon their third encounter with a pointing dog received a learning rate of 0.33, and coveys that displayed evasive behavior upon their fourth encounter received a learning rate of 0.25. Coveys that never displayed evasive behavior were assigned a value 0. These learning rate index values essentially represented an exponential decay model, of which Guthery used several variants in his Fig. 8.4 (2002:123).

Portion of the Area Hunted.—The portion of the area hunted was equivalent to the area effectively hunted as described in the static model. Therefore, to quantify (p), we divided the area effectively hunted by the average pasture size at the Brooks County site.

Number of Hunting Parties.—We documented the number of hunting parties (H) by calculating the number of hunts conducted in a pasture and then dividing this value by the number of days in the season. This gave an average number of hunting parties per day.

There were 32 hunting areas on the Brooks County site. Each pasture had an average of 3 hunting areas. None of these areas were visited <2 weeks apart. Therefore, a single pasture could not have more than 3 hunting parties during a single day.

During a 120-day season at the Brooks County site, approximately 80 days were spent hunting. At the Brooks County site, there were up to 6 hunting parties per day; from 220 to 340 quail hunts occurred each season.

Loss Due to Harvest.—Loss due to harvest (k) is equivalent to the number of coveys impacted during a hunt. We calculated the values of (k) by dividing the number of birds harvested per covey by the average covey size.

Probability of Flushing a Covey.—The probability of flushing a covey (p_{fn}) given an encounter was described in the static model. The difference with this parameter in the dynamic models was that the history of how a covey responded to being hunted used to classify whether they were experienced or naive. As described earlier, we considered experienced coveys as those that were pointed by dogs during a previous hunt and naive coveys as those that had not yet been pointed by dogs. Then, the same process that was used for calculating the probability of flushing a covey were applied to experienced and naive coveys. The loss rate to nonhunting mortality was described earlier for the static model.

Evaluation of HCI Theory Assumptions

Assumption 1: Hunting is not redundant (*static and dynamic models*).—We examined the spatial distribution of hunting routes to assess the assumption that hunting pressure was not redundant during a given hunt.

Assumption 2: Coveys are randomly distributed over the hunting area (*static and dynamic models*).—We recorded covey flush locations using GPS devices to determine if they were randomly distributed. We used a nearest neighbor function (Nearest Neighbor Program, Ottawa, Ontario, Canada) in ArcMap 8.3 to determine the distances between covey locations. We generated random locations using the same areas in which coveys were flushed using ArcView 3.3. We used the nearest neighbor function to determine the distances between random locations and performed this analysis using Statistica (StatSoft®, Tulsa, Oklahoma, USA).

Assumption 3: All coveys are naive at the beginning of the hunting season (*dynamic models*).—We evaluated the impact of assumption that all coveys were naive at the onset of hunting season. This is an extremely difficult assumption to test because we have only a sketchy understanding of how quail react to and avoid predation whether such predators are wild animals or hunters (Brennan 1999). As a first approximation, we used juvenile: adult (or hatch year: after hatch year) age ratios to assess the extent to which a covey was composed of potentially naive or hatch year birds. Accordingly, juvenile birds would be considered naive and adults experienced. We also evaluated the behavior of radiomarked coveys during hunts in the context of whether or not they flushed or exhibited evasive behavior (e.g., running from the pointing dogs) based on their behavior during past encounters with hunters.

Assumption 4: There is a greater probability of flushing a naive covey than an experienced one given an encounter (*dynamic models*).—We evaluated the assumption that naive coveys are more likely to flush than experienced coveys by monitoring radiomarked coveys. Presumably, a covey is only naive until it has experienced hunting pressure.

RESULTS

Estimates of Variables for the Static Model

Birds Harvested per Covey.—We followed 162 hunts on the 2 study sites to collect data for estimating variables required to test the HCI theory. During the 2001 and 2002 seasons, mean harvest (m) ranged from 1.67 to 1.87 birds per covey. A mean of 1.77 (SD = 0.88, n = 461 coveys) quail were harvested per covey on the 2 study sites over the 2 seasons. We therefore used a value of 2 birds removed per covey to estimate daily harvest on the 2 study sites.

Probability of Encountering a Covey.—We collected more than 160,000 GPS locations from routes traveled by pointing dogs during 2 hunting seasons. We used these data to identify the area effectively hunted as described in Equation (3). Sixty-four dogs were used in the hunt; 37 were

Table 2. Descriptive statistics of seasonal pointing dog spatial efficiency during the 2001–2002 and 2002–2003 quail hunting seasons in Brooks and Duval counties, Texas, USA.

		2001			2002		
Variable	Site	*n*	Mean	SE	*n*	Mean	SE
Dog speed (kph)							
	Brooks	23	10.85	1.71	23	9.91	1.27
	Duval	14	9.72	2.22	14	8.38	2.03
	Pooled[a]	—					
Dog distance (m)							
	Brooks	23	34.96	8.75	23	34.89	10.52
	Duval	14	33.84	8.79	14	34.75	5.46
	Pooled	37	34.54	8.62	37	34.83	8.85

[a] Not pooled between sites because of a significant interaction.

used in both seasons. Mean dog velocity (9.7 kph) and distance (34.7 m) from the hunting vehicle were greater on the Brooks County study site than on the Duval County study site (Table 2). There was no difference in velocity or distance on the Brooks county study site between seasons. There was a difference of 1.34 kph in speed at the Duval County study site (Table 2). We calculated an average hunt time of 2.5 hours for both sites and used this value to calculate harvest (*k*) (Table 3).

Regression analyses indicated that dog velocity and the distances dogs hunted from the truck routes were independent, orthogonal variables.

Table 3. Duration of quail hunts at the Brooks and Duval counties, south Texas, USA, study sites during the 2001–2002 and 2002–2003 hunting seasons.

Duration of hunt:	Study area	
hours, minutes, seconds	Brooks County	Duval County
Mean	2:39:21	2:19:09
Standard deviation	0:47:54	0:44:54
Maximum	4:12:19	4:26:04
Minimum	0:59:09	0:57:07
Number of hunts	90	63

There was no significant predictive relationship between dog velocity and distance they hunted from the hunting vehicle (Fig. 2); r^2 values ranged from <0.0001 (Duval County 2002–2003, Fig. 2D) to 0.067 (Brooks County 2001–2002, Fig. 2A). Only the data from Brooks County during the 2001–2002 had a regression slope significantly > zero ($b = 2.42$, $P = 0.0004$; Fig. 2A); all other slopes of regression lines from data in Fig. 2 were not significantly different from zero (respective *P*-values ranged from 0.08 [Brooks County 2002–2003, Fig. 2B] to 0.98 [Duval County 2001–2002, Fig. 2C]).

Probability of Flushing a Covey.—Approximately 53.2% of radiomarked coveys were pointed during the 2001–2002 season. This value dropped to 31.3% during the 2002–2003 hunting season. Therefore, we used pooled probability of flush

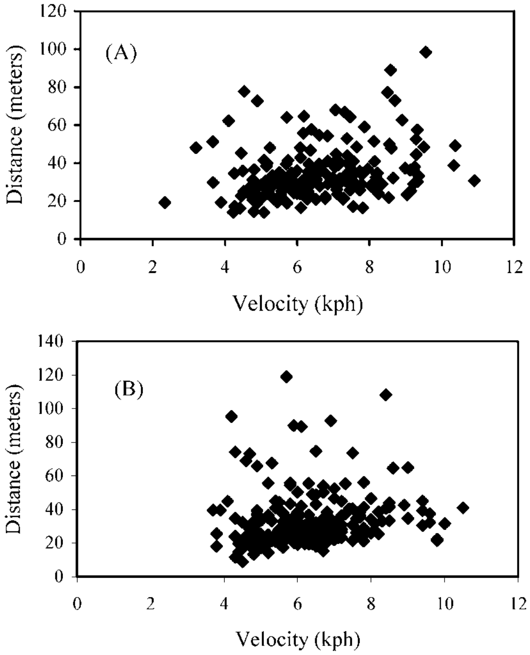

Fig. 2. Relationship between hunting dog velocity and distance from the hunting truck during the 2001–2002 and 2002–2003 quail hunting seasons at the Brooks County (A, B) and Duval County (C, D) study sites.

Table 4. Detectability of radiomarked coveys during the 2001–2002 and 2002–2003 quail hunting seasons, Brooks County, Texas, USA.

	Hunting season	
	2001–2002	2002–2003
Coveys encountered	47	32
Coveys detected	25	10
Percent detected	53.2	31.3

(0.44) for calculating output from the HCI static model (Table 4).

Densities and Nonhunting Mortality.—Population density (*N*) on the 2 study sites ranged from 1.7 to 3.0 birds per ha (Table 5). Nonhunting mortality was 24% and 21% during the 2001–2002 and 2002–2003 hunting seasons, respectively. Therefore, we incorporated a range of 10% to 30% natural mortality to adjust density and generate output from the HCI static model.

Covey size ranged from 8.2 to 11.4 birds per covey on both study sites. We observed an average of 9.7 birds per covey on both sites. Not all birds within radiomarked coveys flushed upon every encounter, which indicated that overall covey size was often slightly larger than 11 birds (an optimal covey size identified by Williams et al. [2003]). Therefore, we used a corrected value of 12 birds per covey to evaluate the static model.

Static Model Predictions

At the Brooks County site, probability of flushing a covey given an encounter differed by about 22% between the 2001–2002 and 2002–2003 hunting seasons (Table 6). Bobwhite density increased by about 70% from the first to the second year of the study, which was also reflected in an increase in covey size. The rest of the variables estimated from the Brooks County site varied slightly, or not at all, between the 2 years of the study. At the Duval County site, we observed an increase in density and covey size similar to the Brooks County site (Table 6). Hunting dog velocity was different between the Brooks and Duval sites, but the distance dogs traveled from the hunting truck did not differ between sites (Table 7).

Once all variables were estimated (Tables 6, 7) we used the static model to determine average daily quail harvest as a function of hunting velocity and amount of area covered during a hunt. As the speed of the hunt and the distance that the dogs traveled from the hunting vehicle increased, daily harvest increased in a linear manner on both sites (Fig. 3). The average daily harvest ranged from 5 to 50 birds, depending on the hunt velocity and amount of area covered by the pointing dogs (Fig. 3.)

Table 5. Birds per hectare estimated using morning covey call counts during Oct–Nov 2001 and 2002 at the Brooks and Duval county study sites, south Texas, USA.

	2001			2002		
Site	*n*	Mean	SE	*n*	Mean	SE
Brooks[a]	8	1.7	0.75	9	2.1	0.62
Duval[b]	5	1.9	1.05	5	3.0	0.65

[a] Eight call points were surveyed 2 times each in 2001 and 9 call points were surveyed 3 times each in 2002.

[b] Five call points were surveyed between 1 and 3 times during 2001 and 2002.

Estimates of Variables for the Dynamic Models

As with the static model, it was critical to accurately identify empirical values of the variables of the dynamic models as they appear in Equation (7) and Equation (8).

Guthery (2002) assumed that all coveys are naive at the beginning of the hunting season. Therefore, we examined the dynamic models based on this assumption. The average pasture size at the Brooks County site was 1,396 ha. During the 2 seasons at this site, an average of 1.8 birds existed per hectare (Table 5). With approximately 12 birds per covey, there was an average of 228 coveys within each pasture. Therefore, assuming all coveys were naive at the beginning of the hunting season, we used 228 naive coveys to begin iterative calculations of the dynamic models.

The learning rate index (a homolog to Guthery's learning rate, *j*) for radiomarked coveys at the Brooks County site over 2 hunting seasons indicated that 13 of 93 (14%) radiomarked coveys displayed evasive behavior. Of the 13 coveys displaying evasive behavior, pointing dogs missed 5 (38%) and pointed 8 (61.5%). Seven of the 13 (54%) coveys displaying evasive behavior did so upon their first encounter. Six of the 13 (46%) coveys displaying evasive behavior had been missed at least once during a previous hunting event.

To quantify the portion of the area hunted, the area effectively hunted was divided by the average pasture size (1,396 ha) at the Brooks County study site. This gave a value of 14% for the proportion of the area hunted.

The number of hunting parties (*H*) during a single day at the Brooks County study site never exceeded 6. We observed an average of 4 hunting parties per day distributed over 11 pastures. This site was composed of 32 hunting areas, none of which were visited <2 weeks apart, throughout

Table 6. Summary of parameters collected at the Brooks and Duval counties, Texas, USA, study sites during the 2001–2002 and 2002–2003 quail hunting seasons and used to calculate the Hunter–Covey Interface static model.

Area	Season	Variable	*n*	Mean	SD
Brooks County	2001–2002	Prob. of flush (*Pf*)	47[a]	53.19%	49.04%
	2002–2003	Prob. of flush (*Pf*)	32[a]	31.25%	54.98%
	2001–2002	Birds shot/covey (*m*)	91[b]	1.74	0.78
	2002–2003	Birds shot/covey (*m*)	206[b]	1.76	0.83
	2001–2002	Velocity (*v*)	23[c]	10.85[g]	1.71
	2002–2003	Velocity (*v*)	23[c]	9.91[g]	1.27
	2001–2002	Hours hunted (*h*)	44[d]	2:41:24	0:48:32
	2002–2003	Hours hunted (*h*)	46[d]	2:37:24	0:47:45
	2001–2002	Width (*w*)	23[c]	34.96	8.69
	2002–2003	Width (*w*)	23[c]	34.89	10.52
	2001–2002	Area hunted (*A*)	39[d]	202.52	59.10
	2002–2003	Area hunted (*A*)	33[d]	193.70	72.77
	2001–2002	Density (*N*)	15[e]	1.7	0.75
	2002–2003	Density (*N*)	27[e]	2.1	0.62
	2001–2002	Covey size (*c*)	197[b]	8.2	4
	2002–2003	Covey size (*c*)	351[b]	10.3	3.8
Duval County	2001–2002	Prob. of flush (*Pf*)	na[f]		
	2002–2003	Prob. of flush (*Pf*)	na[f]		
	2001–2002	Birds shot/covey (*m*)	49[b]	1.67	0.77
	2002–2003	Birds shot/covey (*m*)	151[b]	1.87	1.03
	2001–2002	Velocity (*v*)	14[c]	9.72[g]	2.22
	2002–2003	Velocity (*v*)	14[c]	8.38[g]	2.03
	2001–2002	Hours hunted (*h*)	27[d]	2:19:12	0:40:07
	2002–2003	Hours hunted (*h*)	36[d]	2:19:06	0:48:25
	2001–2002	Width (*w*)	14[c]	33.84	8.79
	2002–2003	Width (*w*)	14[c]	34.75	5.46
	2001–2002	Area hunted (*A*)	22[d]	204.21	75.38
	2002–2003	Area hunted (*A*)	25[d]	201.89	67.17
	2001–2002	Density (*N*)	12[e]	1.9	1.05
	2002–2003	Density (*N*)	11[e]	3	0.65
	2001–2002	Covey size (*c*)	130[b]	8.8	5
	2002–2003	Covey size (*c*)	236[b]	11.4	3.7

[a] Encounters with radiomarked coveys.
[b] Number of coveys flushed.
[c] Number of dogs hunting in both seasons.
[d] Number of hunts.
[e] Number of morning covey call counts used to determine density.
[f] Not applicable because no radiomarked birds were monitored on this study site.
[g] Brooks County velocity not significantly different between years, but a significant difference between years at Duval County.

the entire season. During each 120-day season, approximately 80 to 90 days were spent hunting. This hunting pressure was distributed evenly over the 120-day season. Typically, 3–4 hunting parties were in the field each day during 80 to 90 days for a range from 220 to 340 hunts during a season. Assuming each hunting area was visited 10 times, and each pasture could be potentially hunted 30 times. Calculating the dynamic model on a per pasture basis (30 outings), the number of hunting parties in a single pasture during a 120-day season is approximately 0.25.

Table 7. Range of values for dog velocities (kph) and distance dogs hunted from the hunting vehicle (meters) used to calculate daily harvest with the Hunter-Covey Interface theory static model.

Variable	Area	Season	–2 SD	–1 SD	Mean	+1 SD	+2 SD
Velocity (kph)							
	Brooks	2001–2002	7.5	9.2	10.9	12.5	14.2
		2002–2003	7.4	8.6	9.9	11.2	12.5
	Duval	2001–2002	5.3	7.5	9.7	11.9	14.2
		2002–2003	4.3	6.4	8.4	10.4	12.4
Distance (m)	Brooks and Duval pooled[a]	2001–2003	21.2	28.0	34.7	41.4	48.2

[a] Distances at Brooks and Duval County study sites were not significantly different and therefore pooled.

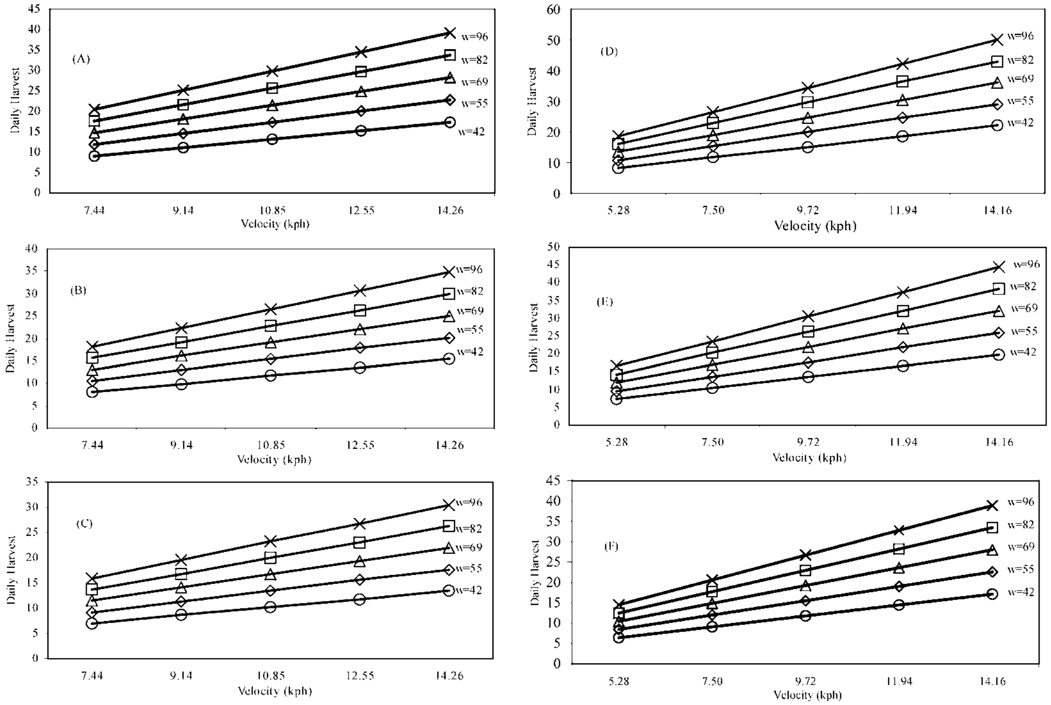

Fig. 3. Daily quail harvest at the Brooks County (A, B, C) and Duval County (D, E, F) study sites during the 2001–2002, and 2002–2003 hunting seasons calculated using the HCI static model with data from Tables 6, 7. (A, D) Density = 1.6 birds/ha (assuming 10% natural mortality), (B, E) Density = 1.4 birds/ha (assuming 20% annual mortality), and (C, F) Density =1.2 birds/ha (assuming 30% natural mortality). Mean harvest was 2.0 birds per hunter–covey contact and mean hunting strip width *(w)* = 69 m +1 SD = 82 m, +2 SD = 96 m, –1 SD = 55 m, –2 SD = 42 m.

Loss due to harvest (k) for each hunter–covey contact is similar to loss due to harvest (m) in the static model (Guthery 2002). However, (m) refers to the number of birds impacted by a hunter–covey contact whereas (k) refers to the number of coveys impacted by a hunter–covey contact (Guthery 2002). Therefore, on average 16% of each covey was impacted for each hunter–covey contact.

The probability of flushing a covey (p_{fn}) given an encounter was described in the static model. We categorized coveys as experienced or naive, based on whether we knew, from radiotelemetry, if they had been encountered by hunters. Then we used the same processes for calculating the probabilities of flushing a covey, given an encounter, were applied to experienced and naive coveys.

Hunters encountered 47% of the presumed naive coveys during the 2001–2002 hunting season. Experienced coveys had an encounter rate of 56%. During the 2002–2003 hunting season, hunters encountered 40% of the presumed naive coveys and only 18% of the experienced coveys. When these 2 years of data were pooled, the mean number of naive coveys encountered was 40% (Table 8), and the mean number of experienced coveys encountered was 47% (Table 8). These values were based on the assumption that all coveys are naive at the beginning of the hunting season. The values did not take into account that nearly half (46%) of the population were adults during the 2001–2002 hunting season and

Table 8. Detectability of radiomarked naïve and experienced coveys during the 2001–2002 and 2002–2003 quail hunting seasons, Brooks County, Texas, USA.

	Coveys encountered	Coveys detected	Coveys missed
Naive coveys[a]			
Total	50	8	12
Mean	2.00	0.80	1.20
Percent detection		40.00	60.00
Experienced coveys[b]			
Total	43	20	23
Mean	2.15	1.00	1.15
Percent detection		46.51	53.49

[a] Naive coveys are coveys that have not been pointed or found during a previous quail hunt.

[b] Experienced coveys are coveys that have been pointed or found during a previous quail hunt.

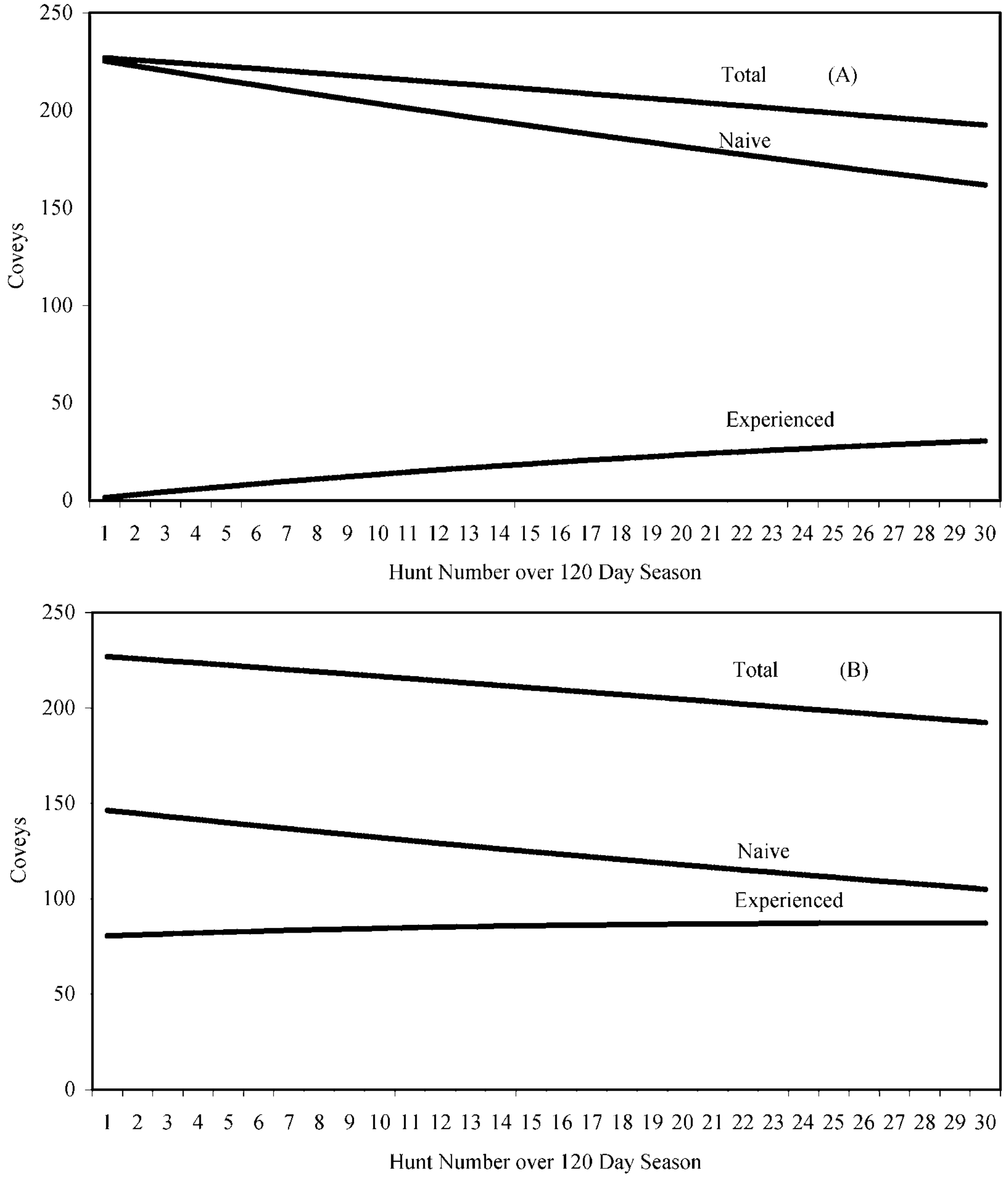

Fig. 4. (A) Dynamic model output trends for populations of naive, experienced, and total coveys during 30 hunts that took place over a 120-day season where all coveys at the beginning of the season are considered naive. (B) Dynamic model output trends for populations of naive, experienced, and total coveys during 30 hunts that took place over a 120-day season where 35% of the population was considered experienced at the beginning of the hunting season.

that approximately 25% of the population were adults during the 2002–2003 hunting season.

During the 120-day hunting season of 2001–2002, an average of 0.2% of the population perished per day due to nonhunting mortality. During the 2002 hunting season, 0.18% of the population perished per day due to nonhunting mortality. This is equivalent to a range of 0.08% to 0.25% daily loss to nonhunting mortality.

Predictions of the Dynamic Models

By combining the values for each variable into the dynamic models, we graphed the change in the population of naive and experienced birds (Fig.

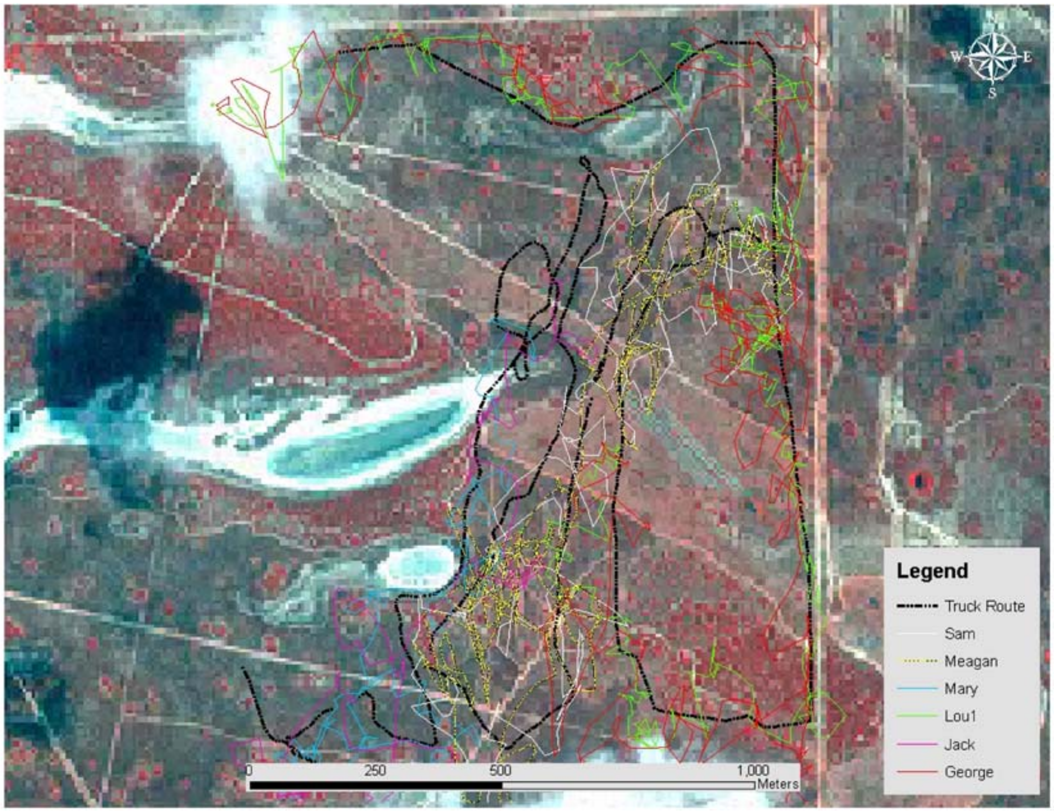

Fig. 5. Example of spatial redundancies exhibited by quail hunting trucks (dashed line) and pointing dogs (solid lines of various colors) during a quail hunt at the Brooks County study site. Different color lines denote different pointing dogs used during the hunt.

4A). Compared to Guthery's (2002:123, his Fig. 8.4) model, our results most closely resemble a low hunting intensity and a low learning rate (i.e., the Low–Low scenario). To further evaluate predictions of the dynamic models, we took the average hatch year (juvenile) to after hatch year (adult) ratios for the 2 study seasons and recalculated output from the dynamic models (Fig. 4B). Once again, the model output (Fig. 4B) most closely matched the low hunting intensity, low learning rate scenario identified by Guthery (2002:123, his Fig. 8.4).

Evaluation of Assumptions

Assumption 1: Hunting is not redundant (*static and dynamic models*).—We observed that quail hunting can be redundant within a given hunting event. Pointing dogs overlapped their own paths and the paths of other dogs during a single hunt (Fig. 5). We observed that routes taken by hunting vehicles could also overlap, sometimes to a large extent (Fig. 5).

Assumption 2: Coveys are randomly distributed over the hunting area (*static and dynamic models*).—Based on comparisons of nearest neighbor distances of random points and covey locations, we found that coveys were not randomly distributed over the Brooks County hunting area during the 2001–2002 hunting season (Fig. 6A). There was a 91-m (27.6%) difference between the mean nearest neighbor values of random (330.3 m) and covey (239.2 m) locations. In contrast, the distribution of coveys approximated a random distribution during the 2002–2003 hunting season (Fig. 6B); there was a 24-m (8.6%) difference between the mean nearest neighbor values of random (273.9 m) and covey (250.2 m) locations.

Assumption 3: All coveys are naive at the beginning of the hunting season (*dynamic models*).—This assumption is extremely difficult to test because we know virtually nothing about learning (or forgetting) rates in quail. Nevertheless, the value of addressing this assumption is that if nothing else, it identifies key weaknesses in our understanding of quail biology and points to potentially productive areas for future research.

Along with this assumption, one could also assume adult quail that have survived the previous hunting season may retain behavior that allowed them to avoid hunters. Harvest records showed an age ratio of 1.16:1 hatch year to after hatch year birds during the 2001 hunting season. These ratios were near 1:1, but they increased to >3:1 during the 2002–2003 hunting season. One could also assume that some portion (the adults with prior experience being hunted) of this population probably recognized hunting vehicles and hunters as danger and used evasive behavior to avoid them. Conversely, it may be possible that after coveys survived the hunting season they forget about hunters. If this is so, then Guthery (2002) is correct in assuming that all quail are naive at the beginning of the hunting season.

Assumption 4: There is a greater probability of flushing a naive covey than an experienced one given an encounter (dynamic models).—Experienced coveys during the 2001–2002 hunting season were encountered at a rate of 53% ($n = 32$). During the 2002–2003 hunting season, hunting parties encountered 40% of naive coveys ($n = 16$) but only 18% of experienced coveys ($n = 11$). However, once these values were pooled, there was a 40% chance of encountering a naive covey and a 47% chance of encountering an experienced covey. Therefore, our results show that there was not a greater chance of flushing a naive covey compared to flushing an experienced covey. These values were based on the assumption that all coveys are naive at the beginning of the hunting season. It does not take into account the fact that nearly half (46%) of the population were adults during the 2001 hunting season and that approximately 25% of the population were adults during the 2002 hunting season. Evidently, an unknown portion of the population that was considered naive was actually experienced.

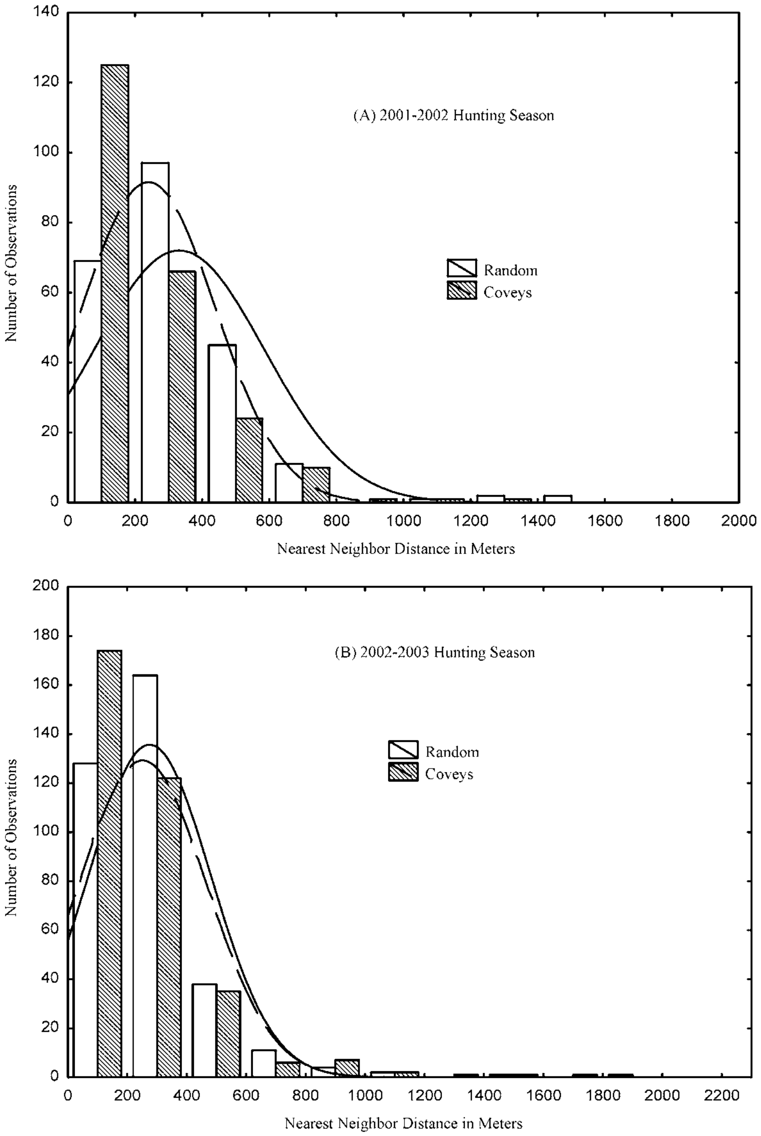

Fig. 6. Nearest neighbor distributions of random points and locations of radiomarked coveys on the Brooks County study site. (A) 2001–2002 hunting season, (B) 2002–2003 hunting season.

DISCUSSION

Static Model Predictions

The static model produced daily harvest values that were within the range of the daily bag of quail hunters in south Texas. This indicates that the static model seems to provide realistic output and meaningful predictions of daily harvest. Thus, the HCI static model may provide managers of quail hunting areas a tool for effectively managing quail harvest to achieve a specific population objective. By regulating the velocity of the hunt (i.e., driving the hunting vehicles faster or slower) and the amount of area hunted (by keeping the dogs relatively close to the hunting vehicle or letting them roam over a broader area), the static model can be used to modulate the level of daily harvest while also distributing hunting opportunities across a given area.

Brennan and Jacobson (1992) noted that even though harvest showed significantly decreasing trends, the number of hunting days remained constant, and in some cases, such as on public hunting lands in Mississippi, the trends increased. Typically, a few avid hunters account for most birds harvested on public lands (Hurst and Warren 1982). The HCI static model may be especially useful in areas experiencing high hunting pressure or relatively wide fluctuations in productivity. Furthermore, it is unlikely that density of the breeding population will be similar from year to year regardless of fall population (Errington 1945). Thus, variables that lead to hunter–covey contact and hunting mortality may also vary from year to year, even though there was consistency among other areas with respect to how many quail pointing dogs actually find. For example, Kellogg et al. (1982), and Sisson et al. (2000) observed that approximately 50% of the birds are missed during a quail hunt. This percentage is similar to what we observed (44%).

Once a manager decides how many quail can be harvested on an area during a given season, the static model can be used to determine the average daily harvest. Daily harvest can be adjusted by increasing or decreasing variables in the model (e.g., birds bagged per covey or the speed at which the hunt is conducted) to allow a maximum number of hunting days in relation to a predetermined level of harvest. Guthery (2002) provides the conceptual background and logic required for such an integrated approach to quail harvest management.

Predictions of the Dynamic Models

As described by Guthery (2002), the conditional probability of flushing a naive or experienced covey, given an encounter, is based on the assumption that all coveys are naive at the beginning of the hunting season. Based on this assumption and parameters estimated, we assessed the dynamic model. The predictions made when assuming that all coveys are naive at the beginning of the hunting season appear realistic.

After finding apparently realistic values for the dynamic model based on the assumption that all coveys are naive at the beginning of the hunting season, we ran the model based on the age ratios for the 2 study seasons. An average of 35% of the population was composed of adult birds. Therefore, we assumed that at least 35% of the population was composed of experienced coveys, holding all other variables the same. Although the population dynamics changed, the results were still realistic.

Compared to Guthery's (2002:123, his Fig. 8.4) scenarios of potential outcomes based on the dynamics models, our results most closely resemble a quail population subjected to a low hunting intensity that has a low learning rate (i.e., the Low–Low category in Guthery's graphic model). The model also produced meaningful results when the assumption that all coveys were naive at the beginning of the hunting season is ignored and after hatch year (i.e., adult) birds are assumed to be experienced. Compared to Guthery's (2002) model, our results, when not assuming all coveys are naive at the beginning of the hunting season, still closely resemble a quail population with a low hunting intensity and a low learning rate. This result is supported by the relatively low overall annual quail harvest rates at the Brooks County site that ranged from about 6% to 8% of the total population during the 2 seasons (R. Howard, San Tomas Hunting Camp, personal communication).

The dynamic HCI models were difficult to fully evaluate because we know virtually nothing about how, or what, quail learn or forget. The use of the learning rate categories to score the evasive behavior of known, radiomarked coveys is a crude, first approximation into quantifying the dynamic models. Veith et al. (1980) documented that birds are capable of sharing information that can be interpreted as predator avoidance behavior. However, progress with respect to understanding behavioral elements of predator avoidance by quail will be achieved only after a body of research on the magnitude and extent of quail learning abilities are determined using captive bobwhites or an adequate surrogate quail species.

Assumptions

We encountered difficulties with respect to meeting the assumptions of the static and dynamic models. Yet, the static model provided output that was within a realistic realm of values, and the dynamic models provided output that matched a low hunting intensity, low avoidance behavior learning rate scenario that was qualitatively predicted by Guthery (2002). The static and dynamic models seem robust to violation of their underlying assumptions.

The scientific literature contains examples of random and nonrandom habitat use by quail. Manley et al. (2000) identified that habitat use by bobwhites was disproportionate to availability and therefore nonrandom. Haines et al. (2003) identified changes in home ranges due to road baiting. Therefore, baiting potentially impacts the randomness of habitat use by quail. Both of the sites baited roads to concentrate birds. Guthery (1988) identified situations in which coveys were distributed randomly and not randomly. Our data showed that the degree of randomness exhibited by covey locations varied from year to year.

Roseberry (1979) and Lehmann (1984) noted that quail hunting is not conducted in a random manner. Hunters consistently preferentially choose a hunting course based on productivity. The manager at the Brooks County site noted that hunting guides typically want to return to areas that produce good hunts rather than spread hunting pressure evenly across a pasture (Howard 2005).

Future Research

Sensitivity analyses that assess HCI models by holding all variables but 1 constant and then calculate output based on a stochastic range of values for the remaining variable would be extremely informative. For example, our estimates of density were quite variable; 95% confidence intervals ranged from 20% to 50% of the mean values. If sensitivity analyses indicate that static and dynamic model output range widely in relation to minor variations in density, then managers will need to focus on collecting a relatively large number or replicate surveys to obtain precise density estimates when using HCI to manage hunting pressure.

Evaluation of HCI theory and models with data from other regions such as the pine woodlands of the Southeast or the agricultural landscape of the Midwest would be valuable. It will be useful to evaluate HCI theory in areas where animal-drawn vehicles or walking hunts are conducted. Presumably, hunting velocities and distances dogs travel from the hunter would be respectively slower and shorter than the estimates for variables used in this study. The study sites used for this research were larger than many other areas where bobwhites are hunted. Thus, evaluation of the HCI models on smaller areas and/or on public hunting areas where the quail population receives greater hunting pressure would be extremely useful for assessing their potential for management.

MANAGEMENT IMPLICATIONS

Quail managers typically practice harvest management based on intuition and trial and error rather than quantitative methods. If quail managers have the resources to collect data on quail density, nonhunting mortality, and estimate variables related to aspects of the hunt such as dog velocity and distance they travel from the hunting truck, then the HCI static model may provide an alternative to the trial and error approach for managing quail harvest. By following the concepts in Guthery (2002) and factoring in potential elements of density dependence, managers could potentially use the HCI static model to modulate quail hunting pressure to achieve a specific spring breeding density, which is an objective that presently eludes most attempts at quail management.

The management implications of the HCI dynamic models will remain unclear until more is learned about the capacity of quail to learn, or forget, predator avoidance behaviors. This knowledge gap represents a unique opportunity to conduct behavioral research on quail learning dynamics that will have profound implications for wildlife management

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