Heterogeneity in Observability of White-tailed Deer on Remington Farms

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Abstract: Population estimates of white-tailed deer (*Odocoileus virginianus*) based on marking individuals and resighting them at later times require assumptions about observability that are rarely verified. Yet the accuracy of estimates depends on meeting the assumptions. At Remington Farms on the eastern shore of Maryland, we tested accuracy of mark-resight population estimates from the heterogeneity model (M_h) of the CAPTURE program against a known abundance of a marked subpopulation of the herd. We also tested the assumption of heterogeneous capture probabilities. We conducted evening road counts to resight animals marked with collars and used radio-telemetry observations to estimate sightability of individual animals. Estimates of observability were biased high, and concomitant population estimates were biased low by between 25% to 35%. Estimates determined from radio telemetry of the observabilities of different individuals ranged from 0.04 to 0.45, an 11-fold difference. The overall effect of a substantial heterogeneity in observabilities is probably a positively biased estimate of average observability and thus a negatively biased estimate of population abundance.

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Mark-recapture methods (Pollock et al. 1990) have been applied to estimating abundance of white-tailed deer primarily by marking deer with visible collars and "recapturing" them by resighting marked and unmarked individuals (Downing et al. 1977, McCullough and Hirth 1988). These methods require explicit assumptions about "catchability" of individual animals. For example, catchability (1) is equal for all individuals (equal; M_O), (2) is different but constant for each individual (heterogeneity; M_h), (3) varies with capture occasion (time; M_t), and/or (4) changes after the first capture and remains constant there-after (behavior; M_b) (Pollock et al. 1990). The computer program CAPTURE is available to calculate abundance estimates using these models (Otis et al. 1978, White et al. 1982). However, in most applications it is impossible to verify if population estimates from a particular model are accurate.

The objectives of our study were to test: (1) accuracy of abundance estimates from the heterogeneity model by comparing model estimates to the known abundance of a marked subgroup of does in a deer population, and (2) the assumption of heterogeneous capture probabilities by determining "potential" observability with radio-marked individuals. We only marked and estimated doe observability because the majority (>50%) of the herd was does, does were easily captured and marked, and harvesting females is a management tactic used to obtain a desired level of annual recruitment and sustainable harvest (McCullough 1984, Lancia et al. 1988).

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Methods

Study Area

The study was conducted on Remington Farms, a 1,330-ha cash grain farm managed as a wildlife demonstration and research area. Remington Farms is located along the northeastern shore of Chesapeake Bay, 12 km southwest of Chestertown, Kent County, Maryland. The landscape is approximately 50% forest, predominantly upland hardwood swamp (Burger and Linduska 1967) with small scattered tracts of pine (*Pinus* spp.); 33% cropland; and 17% brushy wildlife cover. The latter includes hedgerows of multiflora rose (*Rosa multiflora*) and early successional areas managed for northern bobwhite (*Colinus virginianus*) and cottontail rabbits (*Sylvilagus floridanus*), man-made wetlands for waterfowl habitat, and farmsteads (Conner 1986).

Field Data

Marking.—Most deer were captured with a 21.3- x 21.3-m drop-net (Conner et al. 1987) during fall and winter between 1983 and 1986 as a part of studies by Conner (1986) and Wallingford (1990). Conner (1986) marked deer with neck collars made of 10.2-cm-wide black industrial belting. A unique alphanumeric and color code identified each deer. Only positive identifications of collars were included in the data analysis. In addition to the belting collar, Wallingford (1990) equipped additional females with radio collars (AVM, Livermore, Calif.) operating in the 150–152 MHz range. In both cases deer were immobilized with intramuscular injections of various combinations and doses of xylazine and ketamine, and in some cases immobilizations were antagonized with intramuscular injections of yohimbine (See Conner [1986] and Wallingford [1990] for details).

Road counts.—In 1984 we obtained visual observations of all deer, including collared deer, during evening road counts (Conner 1986) along 3 routes covering different portions of the farms. Counts were done in October through late November (prehunt) and December through January (posthunt), before and after a 1-week hunting season in late November–early December 1984. A complete count consisted of the combined observations from all 3 routes. Surveys began 0.75 hours before sunset and lasted 0.5–1.5 hours depending on number of deer observed. Surveys were conducted from a pickup truck traveling 5–10 km/hour. Individual deer were identified with binoculars or a 15–60x spotting scope. Deer were classified as antlered or antlerless during surveys.

Radio telemetry.—Radio-telemetry observations were made with a null-peak antenna system and a scanner/receiver (Telonics, Mesa, Ariz., or Advanced Telemetry Systems, Asanti, Minn.). Twin 4-element, yagi, rotating antennas were mounted on roofs of vehicles. Deer were radiotracked in 1986 during a 3-hour evening period from 2 hours before to 1 hour after sunset during the same pre- and posthunt periods as the road counts. Simultaneous azimuth readings from permanent receiver stations were taken (1) to achieve as near a 90° angle of intersection as possible to reduce size of the error polygon (Heezen and Tester 1967), and (2) to reduce error caused by animal movement (Schmutz and White 1990). Two to 4 animals were monitored at 10-minute intervals each evening.

Data Analysis

Observability estimates from road counts.—We used mark-recapture methods (Pollock et al. 1990) in the CAPTURE program (Otis et al. 1978, White et al. 1982) to estimate abundance of the known population of neck-collared does on Remington Farms. The known population was considered to be those individuals seen between the month before and several months after road counts, but not necessarily during actual counts. Population estimates from the "best fit" model of the model selection procedure of CAPTURE were compared to the known, marked population to evaluate accuracy and to generate a correction factor, $N/\hat{N}$, if necessary. One "trapping occasion" consisted of the combined observations from 1 complete morning and evening count conducted on the same day. Marked individuals seen on the first occasion were considered "marked" and those on subsequent occasions "unmarked."

We then applied the correction factor to observability estimates from CAPTURE. In most cases, counts of animals do not result in a complete tally of all animals in a particular area (Lancia et al. 1994) because the probability of observing animals (β) is generally less than 1.0. We can express the relationship between observability (β), counts C, and true population size N as:

$$E(C) = \beta N \tag{1}$$

where $E(C)$ denotes the expected value of count C. This is the basic relationship that underlies all population estimation techniques in which observability concerns predominate (Lancia et al. 1994). To translate counts of animals to an estimate of population size, β must be estimated; then the count is divided by the proportion counted, β, to yield a population estimate, $\hat{N}$:

$$\hat{N} = \frac{C}{\hat{\beta}}$$

Substituting in equation 1 yields:

$$\frac{N}{\hat{N}} = \frac{\frac{C}{\beta}}{\frac{C}{\beta_0}} = \frac{\beta_0}{\beta} \tag{2}$$

where β and β_0 are the "adjusted" and observed observabilities, respectively, and C represents in our application average number of does seen per complete road count. We consider this adjusted probability to be our best estimate of the "true" observability of does.

Assumptions that underlie this approach are: 1) the population of collared deer is closed, which in this particular application means that no deer considered to be part of the known population actually had died or had permanently emigrated; 2) no collars were lost; 3) collars were identified correctly, and 4) collared deer were a random sample of the doe population, if the observability estimates were to be applied to all does on the Farms.

Observability estimates from radio telemetry.—Radio-telemetry azimuth intersections and deer locations were estimated with XYLOG4 (Dodge and Steiner 1986). Because telemetry intersections have an associated areal error (Zimmerman 1990), we used a predicted error radius to generate a circular error area around telemetry intersections at the edge of open and closed habitat (Wallingford and Lancia 1991). This approach assumes a uniform probability distribution within the error area; the true distribution is likely more complex. Open habitat was considered any habitat absent overhead cover where deer could be seen during road counts, such as agricultural fields, food plots, marsh, and low brushy areas. Closed habitat was defined as wooded tracts with an overhead canopy where deer were not likely to be seen. The error radius (distance) was calculated with a regression equation derived from known location radio collars: $ED = -9.19DEV + 0.72DEV^2 + 0.21$ RECDIST, where ED = error distance, DEV = deviation of the observer-deer-observer angle from 90°, and RECDIST = average distance for 2 observers from the receiver to the estimated deer location. This equation accounted for 82% of the variation in the predicted error distance (Wallingford and Lancia 1991).

The circular error area was used to assign a probability to a particular telemetry intersection that the actual location of a radio-marked deer was in either open or closed habitat. Proportion of open habitat within the error circle for a given location was determined by plotting error circles on a habitat map of the Farms with a geographic information system (Computer Cartography Lab., N.C. State Univ.). Area of open habitat relative to area of the error circle was considered the probability that the true location was in open habitat and hence represented potential observability.

Telemetry data were combined over 3-hour evening tracking periods, and means and standard errors of the probability that an animal was in open habitat were calculated for each radio-marked animal and for all animals combined. The linear model of PROC GLM (SAS Inst. 1985) was used to test for homogeneity of slopes and to analyze data for effects or trends in time with respect to sunset. Analysis of covariance was used to predict slopes and *y*-intercepts for observability against time. The LSMEANS option was used to test for differences in observability among individual deer, after adjusting for the covariable time (Wallingford 1990).

Results

Road Counts

During pre- and posthunt periods, 76 and 69 collared does, respectively, were known to be in the population. The heterogeneity model in the CAPTURE program (M_h) was best fit for both periods. Population and observability estimates from CAPTURE were 56 ± 5.9 ($\bar{x} \pm$ SE) for prehunt and 55 ± 4.8 for posthunt, with observabilities (β_0) of 0.247 and 0.226, respectively (Conner 1986:38,39). These population estimates were biased low by a factor of $N/\hat{N}$ = 76/56 = 1.357 and 69/55 = 1.255. Substituting in equation (2) yields:

$$\beta = \frac{\beta_0}{1.357} = \frac{0.247}{1.357} = 0.182$$

and

$$\beta = \frac{0.226}{1.255} = 0.180$$

for the pre- and posthunt periods, respectively. Thus, observability estimates were biased high (e.g., $\beta_0 = 0.247$ versus an adjusted $\beta = 0.182$ for prehunt), and consequently, population estimates were 35% and 25% less than the known population of collared does for pre- and posthunt, respectively. However, adjusted observabilities were essentially the same in both periods.

Radio Telemetry

We recorded 291 locations of 9 does in the evening observations during the prehunting season and 519 locations of the 7 deer that remained alive during the posthunt period (Table 1). Telemetry-determined observabilities combined over the evening observation period ranged from a low of 0.04 to a high of 0.45, about an 11-fold difference.

Least significant means of observability adjusted for time indicated several overlapping groups of observabilities among individuals in the prehunt period

Table 1. Observability rates for adult female white-tailed deer determined by radio telemetry on Remington Farms, Maryland, October–November 1986 and December 1986–January 1987.

Observability							
Prehunt Period				Posthunt Period			
Deer Number	$\bar{x}$	SE	*N*	Deer Number	$\bar{x}$	SE	*N*
300A[a]	0.04	0.02	21	625A	0.13	0.03	60
625AB	0.15	0.05	33	786A	0.19	0.03	35
231ABC	0.16	0.03	68	1,343A	0.21	0.03	50
1,343BCDE	0.20	0.03	46	965B	0.37	0.04	77
786BCDEF	0.21	0.04	45	1,134B	0.38	0.04	89
965BCDEF	0.21	0.06	17	1,234B	0.39	0.04	97
1,234DEF	0.32	0.06	22	300B	0.45	0.04	111
732DEFG	0.33	0.07	13				
1,134G	0.45	0.06	26				
Combined	0.21	0.02	291	Combined	0.34	0.02	519

[a]Means within a period followed by the same letter are not different ($P > 0.05$)

and 2 distinct groups with different observabilities in the posthunt (Table 1). These patterns were indicative of substantial heterogeneity in potential observability during road counts.

A test between seasons of the homogeneity of slopes of observability for all individuals combined against time as a deviation from sunset indicated no difference ($P = 0.50$). The common slope of observability with respect to time from 2 hours before (+) to 1 hour after (−) sunset was −0.0013 ($P = 0.0001$), which indicates increasing potential observability as daylight diminished. After adjusting for the linear effect of time on observability, the *y*-intercepts, which represent observability at sunset, were 0.248 and 0.339 for the pre- and posthunt seasons, respectively. These potential observabilities were slightly larger than those estimated from mark-recapture data and substantially larger than adjusted observabilities. In contrast to the latter, potential observability apparently increased about 50% from pre- to posthunt seasons.

Discussion

There are several factors affecting observability that are reflected in differences between observability, as estimated by model M_h, and the telemetry data. The telemetry data estimated maximum potential observability of an animal; i.e., the probability that an individual was in open habitat during the time when road counts were done. If the individual animal was in open habitat it still might not be observed on a road count for several reasons. First, an animal could enter wooded habitat as the observer's vehicle approached during a road count. This behavior is known to occur (Conner 1986) and appears to be more common after the hunting season when deer are more wary than before the season.

Second, for surveys run in early evening, deer would be more likely to move into open habitat after the observer had passed because deer tended to move into open habitat at dusk. To account for this problem, we varied the starting and ending point on the surveys while covering the same area. Third, an animal could be in open habitat, but not visible to an observer. This situation could easily occur where terrain is not flat or where fields cannot be observed because of fencerows and hedgerows. Finally, group size affects observability (Conner 1986) with single deer being significantly less likely to be observed than deer in groups of 2 or more. Overall, these factors, and possibly others, reduced observability of deer seen on road counts to less than the observability estimated from radio telemetry.

Our estimates of heterogeneity in potential observabilities might have been affected by small sample sizes: 9 deer in the prehunt and 7 deer in the posthunt seasons. Nevertheless, these data suggest that observabilities can be very low, heterogeneity can be great, and observability can vary substantially, even for the same individual, over time. Sage et al. (1983:943) in completely wooded (closed) habitat found observabilities varied among radio-collared deer that were seen along forest roads. They also found some deer were essentially unobservable (e.g., 23 of 68 [34%] were not seen). McCullough and Hirth (1988:540) noted that "individual marked females showed great variation in likelihood of being observed." They found females with home ranges encompassing open areas were reobserved often, while those in wooded areas were seldom seen. Thus, we conclude that observability can be highly heterogeneous, which can result in estimates of average observability from the heterogeneity model of CAPTURE that are biased high and concomitant population estimates that are biased low.

We believe that our estimates of observability are applicable to white-tailed deer in areas of habitat that are similar to Remington Farms, are hunted intensively during a relatively short (about 1–2 week) season, and have a similar herd composition (>50% does). Thus, in Coastal Plain terrain that is about 50% forested and 50% open areas observabilities of does should be about 0.2. We expect that as proportion of open habitat changes, all else being equal, observabilities also would change.

We have shown that in the deer population we studied (1) potential observabilities of radio-marked deer are highly heterogeneous and (2) population estimates based on mark-resighting from the heterogeneity model of CAPTURE are biased low. Although we have no direct evidence that heterogeneous observabilities cause an overestimate in observability and hence an underestimate of population size, according to White et al. (1982:65) when animals have capture probabilities <0.05, M_h will be negatively biased. In our study only 53% and 62% of does in the pre- and posthunt populations, respectively, were observed during roadside counts. Hence between about 1/3 to 1/2 of the does were essentially unobservable.

Based on simulations (Otis et al. 1978:34), heterogeneity can lead to either over- or underestimates of population size depending on a variety of interplaying factors. In a simulation (Otis et al. 1978:34) where the range in observabilities was similar to our study, the population estimate was negatively biased by about 17%. Empirical studies of mark-recapture accuracy show overestimates (McCullough and Hirth 1988) or underestimates (Bartmann et al. 1987) of population size. Additional simulations might help clarify feasible possibilities, but further empirical studies are needed to estimate actual observabilities under field conditions in specific locations.

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