



## Original Article

# Hunter Cooperation With Requests to Avoid a Visibly Marked Ungulate

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**ABSTRACT** Studies utilizing radio tags to examine animal space use are widespread and often require the survival of marked animals over the entirety of a specified study period to answer movement-related questions. When studying the space use of game species, tactics such as applying visible markings to research animals and communicating with hunters may be needed to mitigate unwanted losses due to hunter harvest. Information regarding the effectiveness of visible markings and communication efforts in reducing harvest, as well as examples of hunter cooperation with requests to avoid harvesting marked animals, are lacking but could be quite useful when designing movement studies and planning capture efforts. Across 3 studies conducted during 2009–2015 on public and private land in the southeastern United States, adult white-tailed deer (*Odocoileus virginianus*) were captured and marked in 1 of 3 ways: via conspicuous (Global Positioning System [GPS]) radiocollar; conspicuous radiocollar combined with visible ear tags; or cryptic (very-high-frequency [VHF]) radiocollar. Hunters were asked not to harvest visibly marked deer (GPS radiocollars, with or without ear tags) and survival was compared with that of cryptically marked (VHF) animals. Visibly marked deer were less likely to be harvested than were cryptically marked individuals on private land, but collar types were treated similarly on public land. Additionally, visibly marked males were more likely to be harvested than visibly marked females and the likelihood of harvest increased with male deer age. Our findings suggest that hunter cooperation decreases with the opportunity to harvest a “trophy” and that cooperation is lower on public land compared with private land. Insight into hunter treatment of visibly marked deer can inform researchers and managers about expected losses when conducting long-term spatial monitoring of ungulates and other game species. © 2017 The Wildlife Society.

**KEY WORDS** Alabama, GPS, hunter cooperation, marking, *Odocoileus virginianus*, radiocollar, South Carolina, survival, ungulate, white-tailed deer.

Animal marking is a widespread approach for investigation of wildlife populations. Increasingly popular are studies that utilize radiotelemetry, often combined with Global Positioning System (GPS) technology, to examine the space use of marked animals (Cleveland et al. 2012, Jarnemo and Wikenros 2014, Latham et al. 2015, Marchand et al. 2015, Weterings et al. 2016). Among ungulates, as well as many other taxa of large terrestrial mammals, spatial monitoring is most commonly achieved by fitting a very-high-frequency (VHF) or GPS radiocollar around the neck of the animal. As with any form of animal marking, it is normally desirable for radiocollars not to influence the survival or behavior of the sample to ensure the validity of inferences made regarding

the unmarked population (White and Garrott 1990). When studying game species, unbiased hunter selection of marked animals is also important (Jacques et al. 2011). Aside from survival-based studies, however, a number of research topics pertaining to animal space use may require the survival and continual monitoring of radiotagged individuals through the entirety of the specified study period to obtain ample data sets or for comparison of space use across multiple seasons or years. Examination of seasonal home-range fidelity, for example, is not feasible without a sufficient number of marked individuals that survive and are given the opportunity to express the behavior of interest. In such cases, elevated rather than unbiased survival may be desired, and researchers may wish to limit hunter harvest of marked game animals.

A number of studies using VHF radiocollared white-tailed deer (*Odocoileus virginianus*) have documented that hunters often do not detect this type of collar prior to harvesting marked individuals (Fuller 1990, Mayer et al. 2002, Long 2005, Wallingford 2012), thereby contributing to unbiased hunter selection (Buderman et al. 2014). Conversely, highly visible markings can have the undesired effect of increasing

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hunting-related mortality among game species (Craven 1979, Caswell et al. 2012). When the goal of researchers is to minimize hunter harvest of marked animals, 2 steps must be taken: 1) ensure study animals are visibly marked; and 2) advertise among hunters that harvest of marked animals is highly discouraged.

Information on the success of these combined measures in minimizing harvest of marked animals is not well-documented. Although there is an abundance of literature that has demonstrated the effectiveness of incentive programs designed to increase hunter participation in research involving game species, such programs normally seek to increase the likelihood that hunters will take some desired action such as reporting harvests or completing harvest records (Bellrose 1955, Kilpatrick et al. 2005, Royle and Garretson 2005, Zimmerman et al. 2009, Souchay et al. 2014). Unfortunately, the same sort of incentive approach cannot be adopted by researchers to promote the voluntary restraint of actions such as harvesting marked research animals. Short of enforcing legal penalties, which is often not feasible in a research context, researchers are left with few options other than communication with hunters in an effort to gain voluntary cooperation. We examined the effectiveness of visible markings combined with advertisement efforts among hunters in minimizing harvest rates of radio-tagged white-tailed deer from 3 recently completed studies. We also determined the effect of sex and age of deer on hunter cooperation for consideration in future research efforts concerning the movement and space use of marked game species.

## STUDY AREAS

The 3 previous studies contributing marked deer to this analysis took place within Alabama and South Carolina, USA. One study was conducted across 2 public Wildlife Management Areas (WMAs) and 2 private holdings within Alabama, while the other 2 studies were conducted within the same private holding in South Carolina. Across all 4 study areas in Alabama, there was a 108-day deer hunting season during which one antlerless and one antlered deer could be legally harvested per hunter per day, with a maximum of 3 antlered deer harvests allowed per hunter throughout the season. On private land, 1 of the 3 antlered deer was required to possess  $\geq 4$  antler points ( $\geq 2.54$  cm) on at least one side. Additional restrictions for harvested, antlered deer applied on WMAs within Alabama, with each WMA having unique requirements. Study sites in Alabama included 1) Barbour WMA (BWMA; 11,418 ha), which was located in Barbour County and required that each antlered deer have  $\geq 3$  antler points ( $\geq 2.54$  cm) on at least one side to be legally harvested; 2) Oakmulgee WMA (OWMA; 18,009 ha), which spanned Bibb, Hale, Perry, and Tuscaloosa Counties and was split into 2 management zones approximately equal in size, one of which required that each antlered deer have  $\geq 3$  antler points ( $\geq 2.54$  cm) on at least one side to be legally harvested; 3) Rembert Hills Road (RHR; 6,880 ha), which was located in Marengo County and consisted of land owned by private individuals as well as land owned by a private company and leased to groups of

individuals for hunting; and 4) the Pioneer Cooperative (PC; 8,094 ha), which was located in Pickens County and consisted entirely of land owned by a private company and leased to individuals for hunting. In South Carolina, there was a 139-day deer hunting season during which one antlerless deer, and any number of antlered deer, could be legally harvested per hunter per day with no restrictions on antler size. The study site in South Carolina was Brosnan Forest (BF; 5,830 ha), which was located in Dorchester County and owned by a private company and hunted exclusively by company employees or by company invitation.

## METHODS

### Capture and Marking

As part of other studies, we captured adult ( $\geq 1$  yr old) male and female white-tailed deer during summers (May–Aug) from 2009 to 2015 using tranquilizer dart guns and radiotransmitter darts (Pneu-Dart, Inc., Williamsport, PA, USA). Darts contained a 2-cc mixture of Telazol (4.0 mg/kg) and xylazine–hydrochloride (2.0 mg/kg) administered as an intramuscular injection upon impact. To reduce capture-related stress, we allowed a minimum of 10 min to elapse before leaving the darting location to ensure full sedation of darted deer prior to our approach. We used a hand-held, 3-element yagi antenna and receiver (Mod R410; Advanced Telemetry Systems, Isanti, MN, USA) to detect dart transmitters and locate sedated deer. Upon capture, we blindfolded deer to further minimize handling stress. Darts were removed and a coagulant immediately applied to the wound to prevent blood loss.

We fitted captured deer with either a GPS radiocollar (Mod G2110D; Advanced Telemetry Systems) or a VHF radiocollar (Mod M2510B; Advanced Telemetry Systems), each equipped with a time-lapse mortality sensor. Initially, we sampled deer randomly from each population and fitted them with a predetermined collar type. Toward the end of the capture effort, we conducted sampling and collar assignment systematically to ensure sufficient representation of each sex, age class, and land ownership among both collar types. A subsample of deer with GPS radiocollars also received a 2-piece, yellow cattle ear tag in each ear (Y-TEX Corporation, Cody, WY, USA), and deer with VHF radiocollars received a small metal ear tag in one ear (Hasco Tag Company, Dayton, KY, USA). All GPS units were housed in a black, 189-cm<sup>3</sup> electronics box attached to a 3.8-cm-wide, fluorescent-orange strap, whereas VHF-only units had a black, 87-cm<sup>3</sup> radiotransmitter package attached to a 4.0-cm-wide, brown leather strap.

Brightly colored GPS radiocollars, alone or paired with yellow ear tags, were conspicuous markings intended to be visible to hunters at great distances and allow hunters to distinguish between GPS-marked deer (hereafter referred to as “visibly marked” deer) and unmarked deer. In contrast, the brown VHF radiocollars were comparably more cryptic (Fig. 1), and we assumed hunter treatment of VHF radiocollared deer (hereafter, referred to as “cryptically marked” deer) to be representative of the unmarked population (Buderman et al. 2014).



**Figure 1.** White-tailed deer marked with cryptic, very-high-frequency (VHF) radiocollar (top) and conspicuous, Global Positioning System (GPS) radiocollar and visible ear tags (bottom) during 2009–2015 in Alabama and South Carolina, USA.

We estimated the age of captured deer using a combination of tooth replacement and wear (Severinghaus 1949) and live body characteristics (Demarais et al. 1999) to maximize aging accuracy (Bowman et al. 2007). After processing, we administered a 3-cc intramuscular injection of tolazoline (2.0 mg/kg) as an antagonist to the xylazine–hydrochloride sedative. Deer remained under observation until they moved from the work-up location under their own power. All capture and handling methods were approved by the Auburn University Institutional Animal Care and Use Committee (PRN#s 2008–1489, 2013–2205, and 2013–2323), and followed the guidelines of the American Society of Mammalogists (Sikes et al. 2011).

### Advertisement

On all privately owned study areas (i.e., RHR, PC, and BF), a researcher or landowner spoke directly with each hunter

about the existing research in the area and possibility of encountering visibly marked deer with orange collars. Hunters were asked not to harvest deer with orange collars, regardless of deer sex or age, although this request could not be legally enforced. Hunters were frequently reminded about the presence of visibly marked deer, and requests to avoid harvesting them, often just prior to the start of each hunt.

On public study areas (i.e., BWMA and OWMA), researchers and wildlife agency personnel opportunistically spoke with hunters. In addition, signs with information about radiocollared animals and requests to avoid harvesting orange-collared deer were conspicuously displayed at entrances to, and major intersections within, WMAs as well as at WMA check stations and local deer-processing operations. Articles describing existing research, including the location of study areas and requests for hunters not to harvest orange-collared deer, were written and published on the Alabama Department of Conservation and Natural Resources (ADCNR) website, in an autumn issue of the ADCNR monthly magazine, and various other regional news and social media outlets. In addition, researchers created and periodically updated a discussion thread about existing deer research on a popular hunter forum in Alabama.

On study sites also occupied by cryptically marked deer (Table 1), researchers used the same methods of advertisement to inform hunters of the additional presence of these animals. Researchers asked hunters to treat “brown-collared” deer as any other uncollared deer, but to refrain from harvesting those with orange collars.

### Data Analysis

All deer captured in Alabama and included in our analysis were collared for the entire duration of the hunting season (i.e., 108 days) except in the case of death during that period. Because of the longer hunting season, data from deer captured in South Carolina included the first 99–108 days of the hunting season to maintain approximately equal exposure to the risk of hunter harvest for all deer. For all study areas, the hunting–exposure period included peak rut. We included in the sample as separate “individuals” any collared deer that

**Table 1.** Numbers of unique, radio-tagged white-tailed deer by collar type (Global Positioning System [GPS] or very-high-frequency [VHF]), sex (male [M] or female [F]), and study area during 2009–2015 in Alabama and South Carolina, USA.

Study area <sup>a</sup>	GPS		VHF		Total
	M	F	M	F	
BWMA <sup>b</sup>	3 (3) <sup>c</sup>	5 (5)	10	11	29
OWMA <sup>b</sup>	2 (2)	8 (8)	3	14	27
RHR	6 (6)	1 (1)	9	7	23
PC	6 (6)	5 (5)	10	14	35
BF	38	34	0	0	72
Total	55	53	32	46	186

<sup>a</sup> Study areas = Barbour Wildlife Management Area (BWMA), Oakmulgee Wildlife Management Area (OWMA), Rembert Hills Road (RHR), Pioneer Cooperative (PC), and Brosnan Forest (BF).

<sup>b</sup> Study areas that consisted of public land. Those not labeled were privately owned.

<sup>c</sup> Nos. in parentheses indicate individuals that also received visible ear tags.

survived their first full hunting season and were still alive and collared the next season, provided that they remained collared for the entire duration of the second hunting season or died during that period (DeYoung 1989). We included no deer in the study for >2 hunting seasons.

We calculated Kaplan–Meier survival estimates during the hunting season for all deer combined, as well as individually by sex and land-ownership type (i.e., public or private), and we calculated confidence intervals using a normal approximation (Kaplan and Meier 1958, Pollock et al. 1989). We determined cause-specific mortality rates from harvest-related deaths (i.e., legal harvest, illegal harvest, and unknown harvest) by censoring all non-hunting deaths ( $n = 8$ ) and then calculating mortality as  $1 - \text{survival}$  (Thayer et al. 2009). We examined hunting-related mortality rates for differences ( $\alpha = 0.05$ ) with a log-rank test using SURVDIFF in Program R 3.1.1 (R Foundation for Statistical Computing, Vienna, Austria).

Using the censored data set (i.e., non-hunting mortalities removed), we built 2 model sets—one for visibly marked and one for cryptically marked deer—to examine the effect of covariates on the probability of hunter harvest. We selected factors likely to influence the probability of hunter harvest as covariates for potential inclusion in model sets and included study area as a random effect to account for variation in the probability of hunter harvest due to deer location (Gillies et al. 2006). For both collar types, we generated a global, generalized linear mixed-effects model with a binomial distribution using GLMER, followed by an all model subsets analysis using DREDGE in Program R 3.1.1. We used Akaike’s Information Criterion adjusted for small sample size ( $AIC_c$ ) for model comparison and selection; competitive models were those with a  $\Delta AIC_c$  value  $\leq 2.0$ , provided the covariates in the top model were not simply a subset of those in competing models (Burnham and Anderson 2002, Devries et al. 2008, Arnold 2010). In the case of multiple competing models, we then proportionately redistributed model weight among top models and averaged coefficient estimates for multimodel inference (Anderson et al. 2000). We interpreted the effect of covariates on the odds of mortality from coefficient estimates and generated 85% confidence limits (CL) to maintain compatibility with the information-theoretic approach (Arnold 2010).

## RESULTS

Over 7 summers, we captured 186 (87 M, 99 F) adult white-tailed deer across 3 studies. Of these, 108 were equipped with GPS radiocollars, 36 of which also received visible ear tags. The remaining 78 deer received VHF radiocollars and a discrete ear tag in one ear (Table 1). Fifty-four radio-tagged deer (19 GPS, 35 VHF) remained collared and were monitored for a second hunting season for a total sample size of 240 deer included in our analyses. Estimates of age ranged from 1.5 to 6.5 years among males and from 1.5 to 8.5 years among females (Table 2).

Hunter harvest accounted for 12 (71%) of 17 hunting-season mortalities among visibly marked deer and 22 (88%) of 25 hunting-season mortalities among cryptically marked

**Table 2.** Samples<sup>a</sup> of radio-tagged white-tailed deer by land ownership (Public or Private), collar type (Global Positioning System [GPS] or very-high-frequency [VHF]), sex (male [M] or female [F]), and age (years) during 2009–2015 in Alabama and South Carolina, USA.

Age	Public				Private				Total
	GPS		VHF		GPS		VHF		
	M	F	M	F	M	F	M	F	
1.5	2	2	1	3	11 (1) <sup>b</sup>	2	1	3	25
2.5	3	5	7	8	13	11	10	1	58
3.5	2	8	7	6	16 (1)	8	9 (1)	8	64
4.5	1	6	2 (1)	8	9 (2)	14	3	7	50
5.5	0	1	0	9	4	5 (1)	2	5	26
6.5	0	0	0	7	1	0	1 (1)	2	11
7.5	0	0	0	1	0	1	0	2	4
8.5	0	0	0	0	0	2	0	0	2
Total	8	22	17	42	54	43	26	28	240

<sup>a</sup> No. of unique individuals, with the addition of 54 deer counted as separate “individuals” for a second hunting season.

<sup>b</sup> Nos. in parentheses indicate deer that died from unknown or natural causes during hunting seasons and were censored from the known hunter harvest data set.

deer (Table 3), with males experiencing greater harvest than that of females among both visibly marked ( $\chi^2_1 = 4.1, P = 0.04$ ) and cryptically marked groups ( $\chi^2_1 = 4.0, P = 0.05$ ). Hunting-related mortality among the entire sample of visibly marked deer was only 50% of that observed for cryptically marked deer ( $\chi^2_1 = 4.4, P = 0.04$ ). Considering land-ownership types independently, visibly marked deer again had less hunting-related mortality than cryptically marked deer on private land ( $\chi^2_1 = 4.1, P = 0.04$ ); however, collar types were treated similarly by hunters on public land ( $\chi^2_1 = 0.1, P = 0.70$ ). Visibly marked females experienced greater hunting-related mortality on public compared with private land ( $\chi^2_1 = 6.0, P = 0.01$ ). Similarly, visibly marked males experienced 79% greater hunting-related mortality on public compared with private land, though this was not a significant difference ( $\chi^2_1 = 0.8, P = 0.39$ ).

Among visibly marked deer, we selected 4 parameters for inclusion in model construction as factors that may influence the likelihood of hunter harvest (i.e., deer sex, deer age, land ownership, and visible ear tags), which resulted in 16 candidate models from the all-subsets analysis. Two models had  $\Delta AIC_c$  values  $\leq 2.0$  and together comprised 62% of the model weight (Table 4). The second-ranked model by order of increasing  $\Delta AIC_c$  differed from the top model by the addition of a single, uninformative ( $P = 0.42$ ) parameter and so we did not include it for multimodel inference (Devries et al. 2008, Arnold 2010). Based on the only remaining competitive model, we found 3 parameters to be important in describing the probability of hunter harvest among visibly marked white-tailed deer: deer sex, deer age, and land ownership (Table 4). Using coefficient estimates from the top model, we found that hunter harvest of visibly marked deer was 10.37 (3.05–35.18; 85% CL) times as likely for males as for females ( $P = 0.01$ ). We also found that for each 1-year increase in deer age, hunter harvest was 1.72(1.20–2.47; 85% CL) times as likely ( $P = 0.03$ ). Lastly, we found that hunter harvest on public land was 6.86

**Table 3.** Survival and hunting-related mortality rates of radio-tagged (Global Positioning System [GPS] or very-high-frequency [VHF]), male (M) and female (F) white-tailed deer by land ownership (Public or Private) during the 2009–2015 deer hunting seasons in Alabama and South Carolina, USA.

Land ownership	Survival <sup>a</sup>				Hunting-related mortality <sup>b</sup>						Proportion of mortality due to hunting		
	GPS		VHF		GPS			VHF			GPS	VHF	
	Rate	SE	Rate	SE	Rate	<i>d</i> <sup>c</sup>	<i>n</i> <sup>d</sup>	Rate	<i>d</i>	<i>n</i>			
Public													
M	0.75	0.13	0.65	0.09	0.25	2	8	0.31	5	16	1.00	0.83	
F	0.86	0.07	0.83	0.05	0.14	3	22	0.17	7	42	1.00	1.00	
Total	0.83	0.06	0.78	0.05	0.17	5	30	0.21	12	58	1.00	0.92	
Private													
M	0.80	0.05	0.65	0.08	0.14	7	50	0.29	7	24	0.64	0.78	
F	0.98	0.02	0.89	0.06	0.00	0	42	0.11	3	28	0.00	1.00	
Total	0.88	0.03	0.78	0.05	0.08	7	92	0.19	10	52	0.58	0.83	
Combined													
M	0.79	0.05	0.65	0.06	0.16	9	58	0.30	12	40	0.69	0.80	
F	0.94	0.03	0.86	0.04	0.05	3	64	0.14	10	70	0.75	1.00	
Total	0.87	0.03	0.78	0.03	0.10	12	122	0.20	22	110	0.71	0.88	

<sup>a</sup> Estimates were calculated following Kaplan and Meier (1958).  
<sup>b</sup> Mortality due to legal harvest, illegal harvest, and unknown harvest.  
<sup>c</sup> No. of hunting-related deaths observed during the hunting season.  
<sup>d</sup> No. of deer at risk for hunter harvest.

(2.21–31.31; 85% CL) times as likely as on private land ( $P = 0.01$ ). Though not an informative parameter in any of the top models, visible ear tags may have had some influence on harvest rates of visibly marked deer. In a comparison of deer with and without visible ear tags on private land, those without were found to be 2.10 (0.42–10.33; 85% CL) times as likely to be harvested as those with visible ear tags ( $P = 0.50$ ).

Because deer age was an important parameter explaining the probability of harvest among visibly marked deer, we further examined the effect of age by creating 2 additional models, one each for visibly marked males and females, containing only the deer age covariate with study area as a random effect. From these models, we found a positive relationship among male age and the probability of harvest. For each 1-year increase in adult male age, harvest was 1.83 (1.19–2.83; 85% CL) times as likely ( $P = 0.04$ ), meaning that a 5.5-year-old, visibly marked male was 11.25 times as likely

to be harvested as a 1.5-year-old, visibly marked male. Among visibly marked females, we also found a slight positive, though not statistically significant ( $P = 0.81$ ), relationship between deer age and the probability of harvest, where harvest was 1.12 (0.56–2.22; 85% CL) times as likely for each 1-year increase in age.

Among cryptically marked deer, we selected 3 parameters for inclusion in model construction as factors that may influence the likelihood of hunter harvest (i.e., deer sex, deer age, and land ownership), which resulted in 8 candidate models from the all-subsets analysis. Three models had  $\Delta AIC_c$  values  $\leq 2.0$  and together comprised 67% of the total model weight (Table 5). Of the top 3 models, the third-ranked model by order of increasing  $\Delta AIC_c$  differed from the top model by the addition of a single, uninformative ( $P = 0.55$ ) parameter and so was excluded from multimodel inference (Devries et al. 2008, Arnold 2010). Based on multimodel inference from the 2 remaining top models, only deer sex was important in describing the probability of hunter harvest. Using model-averaged coefficient estimates, we found that hunter harvest of cryptically marked deer was 1.94 (0.83–4.54; 85% CL) times as likely for males as for females.

## DISCUSSION

Despite efforts to limit hunting-related mortality through visible markings and advertisement, hunter harvest of visibly marked white-tailed deer occurred on both public and private land. Harvest of visibly marked deer was less than that of cryptically marked deer, however, suggesting that hunters were able to successfully identify visible markings and that some amount of hunter cooperation resulted in lower harvest rates than if nothing had been done to reduce mortality. Considering only deer on public land, we saw that there was no difference in hunting-related mortality between collar types, whereas visibly marked deer experienced lower harvest

**Table 4.** Ranking of top 5 models based on Akaike’s Information Criterion, with the addition of the null [ $S_{(.)}$ ] model, describing the probability of hunting-related mortality among visibly marked white-tailed deer during 2009–2015 in Alabama and South Carolina, USA.

Model	$K^a$	$AIC_c^b$	$\Delta AIC_c$	$w_i^c$
$S_{sex+age+LO}^d$	4	75.86	0.00	0.42
$S_{sex+age+LO+tags}^e$	5	77.30	1.44	0.20
$S_{sex+LO}$	3	78.48	2.61	0.11
$S_{sex+LO+tags}$	4	79.77	3.91	0.06
$S_{sex+age}$	3	79.82	3.96	0.06
$S_{(.)}$	1	82.54	6.68	0.01

<sup>a</sup> No. of estimated model parameters.  
<sup>b</sup> Akaike’s Information Criterion with small-sample bias adjustment (Burnham and Anderson 2002).  
<sup>c</sup> Akaike model wt.  
<sup>d</sup> Model variable LO = land ownership (i.e., public or private).  
<sup>e</sup> Model variable tags = presence of visible ear tags.

**Table 5.** Ranking of top 5 models based on Akaike's Information Criterion, which includes the null [ $S_{(\cdot)}$ ] model, describing the probability of hunting-related mortality among cryptically marked white-tailed deer during 2009–2015 in Alabama and South Carolina, USA.

Model	$K^a$	$AIC_c^b$	$\Delta AIC_c$	$\omega_i^c$
$S_{sex}$	2	112.51	0.00	0.36
$S_{(\cdot)}$	1	114.20	1.69	0.16
$S_{sex+LO}^d$	3	114.31	1.80	0.15
$S_{sex+age}$	3	114.64	2.13	0.12
$S_{age}$	2	115.51	2.99	0.08

<sup>a</sup> No. of estimated model parameters.

<sup>b</sup> Akaike's Information Criterion with small-sample bias adjustment (Burnham and Anderson 2002).

<sup>c</sup> Akaike model wt.

<sup>d</sup> Model variable LO = land ownership (i.e., public or private).

rates than did cryptically marked deer on private land. This suggests that efforts to communicate with hunters were less successful on public compared with private land, requests to avoid harvest of visibly marked deer were more frequently overlooked on public land, or greater selection for visibly marked deer on public land was a result of both factors.

Considering public and private land together, hunting-related mortality of visibly marked males was greater than that of visibly marked females, and mature, visibly marked males were more likely to be harvested than young males with visible markings. Greater hunter selection for visibly marked males and increased age suggests that hunters were less willing to honor requests to avoid harvesting deer with visible markings when presented with the opportunity to shoot a “trophy” male.

Antler restrictions were in effect on a portion or the entirety of 2 study areas included in this analysis. This could partially explain selection for older males given that antler size increases with age and, thus, older deer were more likely to meet antler criteria for legal harvest (Demarais and Strickland 2011). However, we were explicit in our request that all visibly marked deer, regardless of sex or age, not be harvested. The observed reduced harvest of visibly marked deer compared with those that were cryptically marked suggests hunters were able to successfully identify protected individuals, yet older males were consistently most heavily selected by hunters. Therefore, we suspect that selection was not driven by antler restrictions; rather, hunters were likely more willing to disregard harvest requests when presented with an opportunity to shoot a mature male. Further support for this rationale is provided by Jacques et al. (2011), who found that hunters were 144% more willing to harvest a radiocollared deer with large antlers than an antlerless, collared deer.

Model selection among cryptically marked deer, assumed to be representative of the unmarked deer population, identified deer sex as the only important parameter for describing the probability of hunter harvest, where males were more likely to be harvested than females. Notably, the second-ranked model was the null model, which accounted for 16% of the total model weight. This suggests that hunter selection of cryptically marked deer was independent of modeled covariates aside from deer sex, a markedly different

relationship than that of hunter selection among visibly marked deer. The effect of deer sex on selection of cryptically marked deer was not surprising, however, because adult males commonly experience greater rates of hunter harvest than adult females within hunted populations of white-tailed deer (Nelson and Mech 1986, Fuller 1990, Nixon et al. 1991, Van Deelen et al. 1997, Patterson et al. 2002). The absence of age in our top models for cryptically marked deer is consistent with some studies that found no difference in hunting-related mortality among age classes of adult deer (DeYoung 1989, Ditchkoff et al. 2001), but inconsistent with others (Dusek et al. 1992, Bowman et al. 2007). DelGiudice et al. (2006) documented an elevated risk of death from all factors including hunting among very young and old female deer, but observed relatively constant survival between ages 2–10, which encompassed nearly our entire sample.

Understanding reasons that hunters might harvest visibly marked deer, even when requested not to do so, requires consideration of the various factors that influence hunter motivation and satisfaction. Gigliotti (2000) identified 6 categories of hunters based on motivation for hunting. He found that the greatest proportion (32%) ranked enjoyment of nature as most important to their hunting satisfaction, while a lesser proportion (18%) were either meat or trophy hunters where a successful harvest was the primary contributor to satisfaction. However, the primary motivating factor among hunters can be highly variable and likely influenced by age, level of experience (Decker and Connelly 1989), and geographic region (Hayslette et al. 2001). Siemer et al. (2015) surveyed deer hunters in New York, USA, to determine the importance of various hunting objectives for overall satisfaction and found that “Opportunity to take big-antlered deer” was ranked second behind top-ranked “Opportunity to take at least one deer.” This indicates that having opportunities to harvest deer, including mature males, is an important contributor to satisfaction for some hunters and may explain our observation that hunters were often not willing to pass up a visibly marked deer, particularly if it was a mature male.

Our observed differences in treatment of visibly marked deer on public and private land were also likely a product of differences in hunter motivations. Stedman et al. (2008) proposed that private-land hunters have a stronger connection to the land they hunt and are more likely than public-land hunters to consider themselves land managers and act accordingly. This potentially includes adhering to harvest requests for the purposes of research and could explain the greater cooperation we observed on private compared with public land.

Visibly marked deer without yellow ear tags were twice as likely to be harvested as those wearing yellow ear tags on private land. Given that the desire to cooperate with research activities appeared to be high among private-land hunters, visible ear tags may have played a role in allowing hunters to identify research animals. Therefore, visible markings in addition to a brightly colored collar may help reduce hunter harvest of marked ungulates, particularly where hunter cooperation is high.

As long-term spatial monitoring of game species continues to be a focus of many global research efforts, so will be the need to understand the potential impact of hunters on the ability to draw inference from radio-tagged animals. Future studies could potentially benefit from employing additional visible-marking techniques and by conducting follow-up interviews with hunters to determine why visibly marked deer are selected for harvest. In this way, it may be possible to learn if certain marking techniques are more effective than others in allowing hunters to differentiate between marked and unmarked animals. In addition, follow-up information can allow researchers to further understand the motivating factors that influence hunter cooperation with research involving game animals.

Although efforts were made to achieve approximately equal representation of GPS and VHF radiocollars among each land-ownership type, sex, and age class, and have a sufficient sample in each group for meaningful comparisons, our samples were small compared with some survival-based studies (Nixon et al. 2001, DelGiudice et al. 2006, Brodie et al. 2013), but were comparable to others (Dinkines et al. 1992, Land et al. 1993, DePerno et al. 2000, Ricca et al. 2002, Brinkman et al. 2004). Limited samples may have contributed to our inability to identify differences between some groups, particularly those with vastly different hunting-season survival rates. In many comparisons of interest, however, statistical differences between groups were identified, indicating adequate statistical power despite a small sample (Johnson 1999).

## MANAGEMENT IMPLICATIONS

Researchers and wildlife professionals should be aware of how hunters treat visibly marked game species and implications this may have for studies intending to utilize radiocollars for long-term monitoring of animal space use. Our results indicate that visibly marked ungulates are more heavily selected by hunters on public compared with private land. Additionally, visibly marked males are more heavily selected than visibly marked females, with hunter selection increasing with male deer age. Therefore, some harvest should be expected in studies using radio-tagged ungulates, even when efforts are made to reduce the impact of hunters on survival. This is particularly true for research conducted on public land or if mature males are a component of the sample. Capture effort, target sample size, and project funding are some of the factors that may need additional consideration in light of expected losses.

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