VISIBILITY BIAS AND DEVELOPMENT OF A SIGHTABILITY MODEL FOR TULE ELK

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ABSTRACT: Tule elk (*Cervus elaphus nannodes*) are endemic to California, USA, and occupy habitats that differ greatly from those inhabited by many other elk populations. Because of the importance of demographic data to the conservation of this unique ungulate, we used telemetered animals to investigate factors influencing sightability of elk during aerial surveys. We determined if groups of elk known to be present in sampling blocks were observed or missed during survey flights. Stepwise logistic regression indicated that sightability was significantly affected by animal activity, habitat type, and group size. We developed a model to predict the likelihood of observing a group of elk, and provide recommendations for the use of correction factors for sightability during future surveys.

Reliable estimates of population size for large mammals are essential for assessing their status (Klein 1972), understanding factors related to their persistence (Berger 1990), and developing strategies for their conservation (Bleich et al. 1990b). Aerial surveys frequently are used to estimate size and other demographic parameters of wildlife populations, but visibility bias affects results from aerial surveys and varies among species and habitats (Caughley 1974). Consequently, visibility bias is a potentially important factor influencing estimates of population size.

Visibility bias is known to influence results from aerial surveys of large herbivores including elk (*Cervus elaphus*; Samuel et al. 1987), mule deer (*Odocoileus*

hemionus; Ackerman 1988), mountain goats (*Oreamnos americanus*; Strickland et al. 1994), Dall's sheep (*Ovis dalli*; McDonald et al. 1990), and mountain sheep (*Ovis canadensis*; Neal et al. 1993, Bodie et al. 1995). Survey results not corrected for visibility have many problems, including underestimates of population size, population estimates with large standard errors, and confidence intervals that do not contain the true population size (Steinhorst and Samuel 1989). A sightability model developed specifically for elk in a northern woodland ecosystem (Samuel et al. 1987) decreased bias when compared with surveys that had not been corrected (Unsworth et al. 1990). Modifications of that model recently have been applied successfully to elk

Alces

315

populations in Michigan, USA (Otten et al. 1993).

The tule elk (*C. e. nannodes*) is en-demic to California, USA, and occurs in 22 populations, most of which have been es-tablished by translocation (Koch 1987, McCullough et al. 1996). One of the largest of those populations inhabits the Owens Valley in Inyo County, immediately east of the Sierra Nevada. Aerial surveys for elk have been conducted in Owens Valley since 1943 (McCullough 1969). The purpose of those annual counts has been to establish the minimum number of elk present. Impor-tant management decisions, including those to translocate elk or initiate harvest, have been based on results of those surveys. Because of vast differences between habi-tat occupied by elk in Owens Valley and elk in more northern systems, and because of the importance of elk in Owens Valley for the conservation of this endemic taxon (Koch 1987, McCullough et al. 1996), we devel-oped a sightability model specifically for elk in Owens Valley. Additionally, we believe this model will be of value throughout the open habitats of the Great Basin in western North America.

Low-level aerial surveys to census large mammals are inherently dangerous (Bleich 1983, Heimer 1994). We sought to develop a technique that exposed the flight crew to fewer risks than that used previously to count elk in Owens Valley. Moreover, increasing costs and decreasing agency budgets (Bleich et al. 1982, Bildstein 1998) necessitated a methodology that was more cost-efficient than the established method. Further, an appropriate sightability model would yield more meaningful information on population size than would surveys intended only to determine the minimum number of animals (Unsworth et al. 1990). Thus, we adapted the technique of Samuel et al. (1987) to develop sampling procedures and a sightability model for tule elk in Owens

Valley. We hypothesized that an appropri-ate model would result in aerial surveys that were safer and more cost effective, and in demographic information (in particular, es-timates of the total population) that would be more robust than attempts to census the population from an airplane.

STUDY AREA

Owens Valley (36°30′N, 118°15′W) is located in Inyo County, in eastern Califor-nia, USA. That portion of the valley in-cluded in our study area ranges in elevation from 1,335 m at Bishop in the north to 1,160 m at Owens Lake in the south. Topographic relief on the valley floor is minimal, but the White and Inyo mountains to the east, and the Sierra Nevada to the west, rise abruptly from the valley to > 3,900 m. The Owens River flows southward through the valley, but most water has been diverted for agri-cultural and domestic uses.

Vegetation in Owens Valley is atypical of many habitats used by elk in North America, and consists largely of uplands dominated by saltbush (*Atriplex* spp.) and rabbitbrush (*Chrysothamnus nauseosum*), dry lowlands of alkali scrub that support greasewood (*Sarcobatus vermiculatus*) or saltgrass (*Distichlis spicata*), riparian ar-eas along the Owens River composed of stands of cottonwood (*Populus fremontii*) and willow (*Salix* spp.), tule (*Typha domingensis*) marshes in flooded lowlands, irrigated pastures, and agricultural fields. In general, shrub cover is low (< 20%) in these vegetation types and, with the excep-tion of riparian areas along the Owens River, visibility is high.

METHODS

We captured elk during September 1992 using a hand-held net gun fired from a helicopter (Krausman et al. 1985). We recorded the gender and relative age (year-ling, adult) of each animal, fitted it with

colored plastic ear tags and a color-coded telemetry collar containing a mortality sensor, and then released elk at the site of capture. To minimize potential biases associated with differential use of habitats by the sexes (Peek and Lovaas 1968, Bleich et al. 1997) and to ensure the widest distribution of telemetered elk throughout the study area, we placed a collar on a randomly selected animal from each group of elk encountered during our capture effort.

We divided the Owens Valley east of U.S. Highway 395 into 4 sampling blocks ($\bar{x}$ = 163 km², SD = 56 km², range 130-246 km²), the boundaries of which were easily recognizable from the air (Norton-Griffiths 1978). Each sampling block was inhabited by a distinct subpopulation, or herd (Bishop, Tinnemaha, Independence, Lone Pine; McCullough 1969), although limited movement by elk between adjacent sampling blocks occasionally occurs (McCullough 1969). Those subpopulations have formed the basis for contemporary strategies for elk management in Owens Valley (McCullough et al. 1996). We conducted aerial surveys of the sampling blocks during winter (January-March; n = 4), summer (June-September; n = 20), and autumn (October-December; n = 18). We did not conduct surveys during spring (April-May), when most males were without hard antlers, because of difficulty determining gender during that season.

We used 2 fixed-wing aircraft (Cessna 185), one with a telemetry crew (pilot and 1 observer) and one with a survey crew (pilot and 2 observers) on board, to obtain data for the sightability model. We defined a sightability trial as an effort by both telemetry and survey crews to detect elk in 1 sampling block on a particular day. The sequence of blocks to be sampled was determined randomly, and trials began at approximately 0800 h PST.

During the initial phase of each sightability trial, the telemetry crew located all groups of elk in a particular sampling block that contained telemetered animals and recorded the size, sex, and age composition (adult males, yearling males, adult females plus yearling females, or young—elk of either sex < 1 year old). We also recorded the time of each observation, and the vegetation type (uplands, alkali scrub, riparian, tule marsh, irrigated pasture, agricultural field) in which the group occurred. Additionally, we recorded activity (active or inactive) of the group. If no member of a group was standing, walking, or running, the group was considered to be bedded (inactive). If any member of the group was not bedded, the group was considered to be active. In addition, we recorded the vegetation type in which the group was located. Geographic coordinates (± 100 m) of groups containing telemetered animals were estimated with LORAN-C instrumentation in the aircraft (Oehler et al. 1996).

When the telemetry crew exited the sampling block (usually within 15 min), the survey crew began its effort to locate elk visually. The survey crew used a LORAN-C navigational device to fly low-level (≤ 75 m above ground), parallel transects, alternating between east-to-west and west-to-east, at intervals ranging from 360 to 870 m ($\bar{x}$ = 600, SD = 110). The distance between centerlines of transects was influenced strongly by speed and direction of wind, which often exceeded 15 km/h and came predominantly from the southwest. We began surveys randomly in either the south or north end of a sampling block. Surveys generally lasted ≤ 3 h and were completed by noon.

When the survey crew located a group of elk, they counted and classified individual animals, and recorded activity and the vegetation type in which the group was located. Presence or absence of collared animals was confirmed with a telemetry receiver,

Alces

because it was difficult visually to confirm the presence of collars from the air (Galea 1990). The survey crew also recorded the time of the observation, whether any of the crew was airsick, which crew member first observed the group, and the geographic coordinates of the location as estimated by LORAN-C. Observers for survey crews were selected in a manner that varied the amount of previous survey experience (whether they had participated in aerial surveys of any large mammal and the total number of prior aerial surveys for tule elk in Owens Valley in which they had participated).

Upon completion of the aerial survey, the pilot contacted the telemetry crew to determine if all groups containing collared animals in the sampling block had been located during the aerial survey. If not, the survey crew then used aerial telemetry to locate any groups containing collared animals they had not detected previously, and recorded demographic data, activity, vegetation type, time, and location.

We were aware that the aircraft could influence behavior and habitat use of ungulates (Bleich et al. 1990a, 1994). Nonetheless, during previous years we had not observed shifts in location or habitat type by elk during intense, low-level circling. Additionally, responses or movement by elk were observed only after multiple low passes. The telemetry crew also resighted ≥ 30 groups of elk 30 - 90 min after initially locating them, and determined that none had changed location, activity, or habitat type during the interim. Moreover, those parameters and the locations of groups located by the telemetry crew, and seen later by the survey crew, were the same as those recorded by the telemetry crew during their initial effort. Therefore, we assigned parameter values from telemetry flights to those groups that were located by the telemetry crew but not initially seen by the survey crew. We used all groups of elk that contained telemetered animals, whether observed or missed by the survey crew, to develop the sightability model (Samuel 1984).

We tested for possible relationships between particular variables and ability to see groups of elk. Using G-tests (Zar 1999), we examined associations between sightability and characteristics of the flight or observers, including distance between center lines of transects, direction of transect progression (north-to-south or south-to-north), previous aerial survey experience of observers, and observer condition (ill or not ill). Similarly, we used G-tests to evaluate associations between sightability and characteristics of elk groups (number of elk in a group, sex composition of the group, activity, and habitat type). Characteristics of the environment (cloud cover, temperature, wind velocity, season, year of survey, and sampling block) also were evaluated with the G-test.

We determined if a disproportionate number of initial observations could be attributed to where a member of the survey crew sat in the aircraft, using a χ^2 goodness-of-fit test (Zar 1999). We tested for possible differences in size of groups of elk first seen by the pilot, front observer, and rear observer with 1-way ANOVA. We examined whether particular variables, including group size, activity, habitat, and sex composition of groups, were related to each other using either the Mann-Whitney test (Snedecor and Cochran 1980) or the G-test. Further, we used the Mann-Whitney test to compare total time necessary to census elk with total time necessary to conduct sightability trials in the study area.

We used logistic regression (PROC LOGISTIC; SAS 1990) to develop models to predict the sightability of elk groups (Samuel et al. 1987, Bodie et al. 1995). Those multiple-regression models were based on a selected subset of predictor variables

(covariates) that had been suggested by the regression procedure; we used both stepwise selection and backward elimination of variables (Draper and Smith 1966, SAS 1990). All variables that individually had a significant association ($P = 0.05$) with sightability were candidates for inclusion. In addition, because a multiple regression model could use variables that were not individually significant, but might interact with other covariates to become significant (Dunn and Clark 1974), we initially considered as many variables as possible (Table 1). For stepwise selection, P-to-enter was set at 0.20. For both stepwise and backward elimination procedures, P-to-stay was < 0.06.

During the initial phase of model building, candidate variables were used without transformations. Categorical variables, such as vegetation type and activity, were converted to indicator functions with binary outcomes. Covariates were eliminated if the values of their coefficients were not significant.

After obtaining an initial subset of untransformed covariates using the regression procedure, we did further modeling where squares and interactions of variables from the subset were added as candidate variables. In addition, certain transformations of group size were considered, but we followed a modeling convention that would not allow the quadratic term to remain without the linear term (McCullagh and Nelder 1989). We tried the natural logarithm of group size, as Samuel et al. (1987) did in their modeling, and the square root transformation (Snedecor and Cochran 1980). We then allowed the logistic regression procedure to select the form of group size that best predicted sightability. We also considered squares of the discrete or continuous covariates from the subset, as well as certain interaction terms, such as (group size × habitat) and (group size × activity) as candidate variables.

The criteria for the final models were: (1) model parsimony (McCullagh and Nelder 1989); (2) low Akaike Information Criterion (AIC) and high gamma for the model (Agresti 1990, SAS 1990); and (3) each parameter had a significant coefficient value ($P = 0.05$). With our selected sightability model, we estimated the sighting probability for each group of elk using the observed values of covariates that characterized a particular group. The reciprocal of the sighting probability represents the correction factor for each group (Samuel 1984, Steinhorst and Samuel 1989, Otten et al. 1993, Bodie et al. 1995).

RESULTS

During September 1992, we placed telemetry collars on 25 elk (7 males, 18 females). During 1992-1995, we conducted 42 sightability trials, among which we observed a total of 2,330 elk in 127 groups ($\bar{x}$ = 18.3, SD = 18.5, range = 1-95) that contained ≥ 1 collared animal. The survey crew located 58.3% of 127 groups confirmed by the telemetry crew to be present during sightability trials. Length of time to census elk ($\bar{x}$ = 17.1 h, SD = 3.7 h, $n = 11$) was significantly greater (Mann-Whitney test, $P < 0.001$) than time necessary to conduct sightability trials ($\bar{x}$ = 10.2 h, SD = 0.7 h, $n = 7$) in the study area.

Number of sightability trials per sampling block varied because of occasional unsafe flying conditions or an absence of telemetered animals in a sampling block; 12 trials were conducted at Tinnemaha, 11 at Bishop, 10 at Lone Pine, and 9 at Independence. We observed no differences in the proportions of marked groups seen among years (G_3 = 0.72, P = 0.87) or sampling blocks (G_3 = 2.3, P = 0.51). Hence, we combined data across years and sampling blocks for subsequent analyses.

Season was significantly related to sightability (G_2 = 12.4, P = 0.002). Of 67

Table 1. Candidate predictor variables considered during initial model building for sightability of tule elk in Owens Valley, Inyo County, California, USA, 1992-95.

Variable	Type	Description
VEGWET	Indicator	0 if dry, dark background (uplands or alkali scrub); 1 if wet, green background (riparian, tule marsh, cultivated agricultural fields, or irrigated pasture)
GRPSIZ	Discrete	Total number of elk in observed group
ACTIVE	Indicator	0 if all elk are bedded; 1 if any elk was active (standing, walking, or running)
TOTSURV	Discrete	Total number of previous elk surveys by the observers
PREAIR	Discrete	Number of observers with any previous aerial experience
CENTDIST	Continuous	Average distance between centerlines of aerial transects
WIND	Continuous	Mean wind speed during aerial survey
TEMP	Continuous	Air temperature at beginning of aerial survey
CLOUD	Continuous	Percent cloud cover
NSICK	Discrete	Number of sick observers
YR	Discrete	Year of sightability trial
MNTH	Discrete	Month of sightability trial
SEASON	Discrete	Season of sightability trial
FEMALES	Discrete	Total number of female elk (adults and yearlings combined) in group
BULLS	Discrete	Number of mature males in group
YRLNGS	Discrete	Number of yearling males in group
YOUNG	Discrete	Number of young-of-the-year of both sexes in group
GRPCODE	Indicator	0 if single-sex group; 1 if both sexes in group
DIREC	Indicator	0 if started at north end of sampling block; 1 if started at south end
LONGDEG	Continuous	Longitude (degrees)
LONGMIN	Continuous	Longitude (minutes)
LATDEG	Continuous	Latitude (degrees)
LATMIN	Continuous	Latitude (minutes)

groups of elk available to be seen in summer, about one-half were sighted. During autumn, 51 groups were available to be seen and about two-thirds were sighted. Only 9 groups were available to be seen during winter, but all were sighted.

Four flight parameters were not significantly associated with whether a group was seen by the survey crew: direction of transect progression ($G_1 = 0.82$, $P = 0.36$), distance between centerlines of transects ($G_1 = 0.80$, $P = 0.37$), cloud cover ($G_1 = 0.82$, $P = 0.36$), and wind speed ($G_1 = 0.06$, $P = 0.80$). Ambient temperature, however, was related to sightability ($G_1 = 5.1$, $P = 0.02$); elk were more apt to be observed at cool temperatures ($\leq 15°$ C) than at moderate temperatures ($>15°$ C).

Several characteristics of the survey crew were not related to sightability. Whether one or both members of the crew had previous aerial survey experience (either with elk or another large mammal) was not related to the proportion of groups seen ($G_1 = 0.10$, $P = 0.75$). Also, different levels of survey experience for tule elk in Owens Valley were not related to sightability ($G_3 = 5.7$, $P = 0.13$). No significant difference in sightability occurred between 9 groups available to be seen when ≥ 1 observer was airsick and 118 groups available to be seen when no observer was ill ($G_1 = 1.6$, $P = 0.20$). Proportions of 127 groups observed initially by different members of the survey crew (pilot, 24%; front observer, 39%; rear observer, 37%) did not deviate significantly from the expectation that all members had the same probability of seeing a group of elk ($\chi^2_2 = 1.2$, $P = 0.54$). In addition, we noted no difference (ANOVA; $F_{2,71} = 0.42$, $P = 0.66$) among the mean ($\pm$ SD) sizes of groups seen by the pilot ($\bar{x} = 21 \pm 14.7$, range 3-47), front observer ($\bar{x} = 23 \pm 21.2$, range 2-95), and rear observer ($\bar{x} = 26 \pm 18.7$, range 1-83).

Groups of elk containing both sexes were more likely to be seen ($G_2 = 10.9$, $P =$ 0.004) than groups with only one sex (mixed groups, 73%; only females, 44%; only males, 47%). Groups with elk that were standing or moving were more likely to be seen ($G_1 = 38.3$, $P = 0.001$) than bedded groups (active groups, 88%; bedded groups, 35%). The type of habitat in which a group was located also was associated with sightability ($G_3 = 19.7$, $P = 0.001$). Sightability of groups was about equal for uplands and alkali scrub combined (53%), riparian (52%), and tule marsh (44%) habitats, but 100% of groups in irrigated pastures or agricultural fields was seen. There was a significant difference in visibility among categories of group size ($G_4 = 34.7$, $P = 0.001$) and the proportion of groups observed tended to increase with group size.

Mixed-sex groups ($\bar{x} = 28 \pm 19.4$) were larger (Mann-Whitney test, $P < 0.001$) than single-sex groups ($\bar{x} = 10 \pm 12.3$). A greater proportion ($G_1 = 11.8$, $P = 0.001$) of mixed-sex groups (60%) than single-sex groups (30%) was active. Active groups ($\bar{x} = 23 \pm 19.4$) were larger (Mann-Whitney test, $P = 0.001$) than bedded groups ($\bar{x} = 14 \pm 16.8$). In addition, groups located in dry, brown habitats (uplands or alkali scrub; $\bar{x} = 22 \pm 19.4$) were larger (Mann-Whitney test, $P = 0.01$) than those in wet, green habitats (riparian, tule marsh, agricultural field, or irrigated pasture; $\bar{x} = 14 \pm 16.6$). In contrast, habitat type was not associated with sex composition ($G_1 = 1.7$, $P = 0.20$) or activity ($G_1 = 1.5$, $P = 0.22$) of the group.

For logistic-regression modeling, we began with 23 candidate predictor variables (Table 1). Through both step-wise selection and backward-elimination procedures, we reduced the candidate variables to an initial subset consisting of activity, vegetation type (habitat), group size, temperature, and counts of females, adult males, yearling males, and young.

After further modeling, we arrived at a list of final models (Table 2). Model C had a smaller AIC than did models D or E, and

incorporated the natural logarithm transformation of group size. After inspecting regression diagnostics for model C, we eliminated 3 observations and resumed modeling using only the natural logarithm transformation of group size. Those results (models G and H) had the same covariates as other models that used the full set of observations (Table 2).

We believe model C had the best combination of model parsimony, low AIC, and high gamma. That model had as covariates activity, vegetation type, and the linear and quadratic terms of the natural logarithm of group size (Table 3). Moreover, model C included all 127 observations. Thus, the final model for predicting the probability (p) of sighting a group of elk during an aerial survey was:

$$p = (e^X)/(1 + e^X),$$

where, $X = -5.37 + 2.57x_1 + 1.46x_2 + 3.21x_3 - 0.48x_4$, and $x_1 - x_4$ are the predictor variables included in model C (Tables 2 and 3). Our model suggested a parabolic function for group size (Fig. 1); sightability tended to increase with group size up to about 30 elk, and groups consisting of > 30 animals tended to be less likely seen.

We determined a frequency distribution of sighting probabilities for the full complement of 127 observations. About one-third of groups required only mild correction factors because the sighting probability was ≥ 0.90. About 14% of the groups required very large correction factors, because the sighting probability was <0.10; those groups, however, were small (1-3 animals; Table 4).

Table 2. Candidate models for predicting sightability of tule elk in Owens Valley, Inyo County, California, USA, 1992-95, determined with the entire data set, and with outliers omitted. For each model, covariates (predictor variables) are listed in order of decreasing chi-square value: n = number of observations; AIC is the Akaike Information Criterion. Model C is recommended, because of low AIC, high gamma, and it is based on the full complement of 127 observations.

Model	n	AIC	Gamma
(A) ACTIVE[1] LNGRPSIZ[2]	127	119.6	0.730
(B) ACTIVE LNGRPSIZ VEGWET[3]	127	115.4	0.763
(C) ACTIVE LNGRPSIZ VEGWET LNSIZSQ[4]	127	110.7	0.785
(D) ACTIVE SQRTSIZ[5] SQRTSQ[6] VEGWET	127	115.7	0.759
(E) ACTIVE GRPSIZ[7] SIZSQ[8] VEGWET	127	126.5	0.733
(F) ACTIVE LNGRPSIZ VEGWET FEMALES[9]	127	111.2	0.788
(G)[10] ACTIVE LNGRPSIZ LNSIZSQ VEGWET	124	94.3	0.833
(H)[10] ACTIVE LNGRPSIZ FEMALES VEGWET	124	97.3	0.834

[1] 0 if all elk bedded; 1 if ≥1 elk not bedded (standing, walking, or running).

[2] natural logarithm of group size.

[3] 0 if habitat dry or brown (uplands or alkali scrub); 1 if habitat wet or green (riparian, tule marsh, agricultural field, or irrigated pasture).

[4] square of natural logarithm of group size.

[5] square root of group size.

[6] square of the square root of group size; equivalent to group size.

[7] total size of group (females + adult males + yearling males + young).

[8] square of group size.

[9] number of female elk in the group.

[10] 3 outliers omitted.

Table 3. Coefficients of predictor variables included in Model C, the model recommended for predicting sightability of elk groups in the Owens Valley, Inyo County, California, USA, 1992-95.

Covariate	Coefficient	SE of Coefficient	P-value
Constant	-5.37	1.30	0.0001
ACTIVE[1]	2.57	0.59	0.0001
VEGWET[2]	1.46	0.60	0.014
LNGRPSIZ[3]	3.21	0.99	0.001
LNSIZSQ[4]	-0.48	0.20	0.017

[1] 0 if all elk bedded; 1 if ≥ 1 elk not bedded (standing, walking, or running).

[2] 0 if habitat dry or brown (uplands or alkali scrub); 1 if habitat wet or green (riparian, tule marsh, agricultural field, or irrigated pasture).

[3] natural logarithm of group size.

[4] square of natural logarithm of group size.

DISCUSSION

Time necessary to conduct sightability trials was substantially less than time necessary to census elk populations. Sightability trials required, on average, only 60% of the time necessary to census elk and, as a result, flight crews were exposed to fewer risks. Similarly, fewer total flight hours reduced the cost of estimating elk populations when compared to costs for a census. Hence, we accept our hypotheses that development of sightability correction factors would reduce risk and decrease costs associated with demographic studies of tule elk. Tests of the third hypothesis, that sightability correction factors would yield more meaningful data, await the results of future surveys during which censuses will be compared with results corrected for visibility bias.

The reduced sightability of very large groups has a plausible explanation in the notion of contrast. Groups in dry, brown habitats (uplands or alkali scrub) generally were larger than those occurring in wet, green habitats (riparian, tule marsh, agricultural field, or irrigated pasture). Thus, larger groups would tend to have less color contrast with the terrain and associated vegetation than would smaller groups frequently associated with verdant areas.

The possibility that sightability is enhanced by contrast may be extended to activity as a predictor variable. For example, groups that were active (standing or moving) were more apt to be seen than those that were not. Active animals had a higher profile than bedded animals; hence, they were more likely to create shadows and, thereby, to contrast with the background color of the relatively flat terrain.
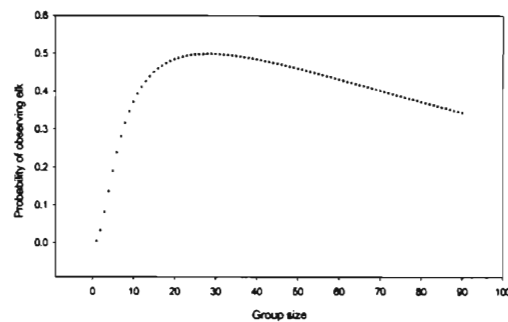

Fig. 1. Probability that a group of elk was seen as a function of the number of animals in the group. The probability that a group was seen was equal to: $\exp(y)/[1+\exp(y)]$, where $y = -5.37+3.21x-0.48x^2$ and $x=\ln(\text{group size})$ and is equivalent to Model C (Table 3) for elk bedded in brown, dry habitat in Owens Valley, Inyo County, California, USA, 1992-95.

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Table 4. Frequency distribution of sighting probabilities, based on model C, for 127 observations of groups of tule elk in the Owens Valley, Inyo County, California, USA, 1992-95.

Sighting probability	Frequency	Percent of total	Range of group sizes
0.0 - <0.10	18	14.2	1-3
0.10- <0.40	19	15.0	1-11
0.40- <0.50	23	18.1	4-60
0.50- <0.90	26	20.5	2-83
0.90- 1.0	41	32.3	5-95

Additionally, active groups tended to be larger than inactive groups, and probability of sighting a group increased with group size up to a limit (Fig. 1).

Whether groups were of mixed sex did not enter our model. The relationship of sex composition to sightability was likely accounted for by covariates (group size and activity) included in our model. Mixed-sex groups tended to be larger, and were more likely to be active, than groups containing only males or only females.

Signs of the coefficients in our recommended model (Table 3) were reasonable. The positive coefficient for activity indicated that active groups would more likely be seen than bedded groups. The positive coefficient for vegetation type indicated that elk located in wet, green habitat would more likely be seen than those in a dry, brown environment.

The sightability model of Samuel et al. (1987) included the natural logarithm of group size and percent vegetation cover as covariates. Similar to the model of Samuel et al. (1987), our model included the natural logarithm of group size: had our model contained only a linear term for group size, sightability would have increased no matter how large a group was. Samuel et al. (1987) did not, however, find activity (which they referred to as behavior) to be a significant covariate. In contrast, activity was the most significant covariate in our final models (Table 2). We hypothesize that the dense forest habitat in Idaho, USA, where Samuel et al. (1987)

developed their model, made a higher profile (standing versus bedded) of elk less of a factor there than in our study area.

Ackerman (1988) developed a logistic-regression model for sightability of mule deer in Idaho, USA. Although he considered the natural logarithm and square of group size, Ackerman (1988) reported that untransformed group size provided the best fit, which contrasted with our model and that of Samuel et al. (1987). The model of Ackerman (1988) included 3 covariates: activity, vegetation type, and group size. The covariates in his model were similar to ours, but he modeled activity with 3 categories, and vegetation type with 5 categories that resulted in 8 parameters, in contrast to only 2 parameters in our model, for those covariates. The use of indicator functions provided us with more parsimonious models, having far fewer parameters (McCullagh and Nelder 1989), than the final models of either Samuel et al. (1987) or Ackerman (1988).

We believe that data gathered during sightability trials over a period of 4 years included the probable values for covariates that would be experienced during aerial surveys of elk in Owens Valley. In particular, observed group sizes ranged from 1 to 95 elk. Moreover, our models were similar to those developed by Samuel et al. (1987) and Ackerman (1988). Currently, we suggest that corrections not be applied to a group if the probability of sighting that group is < 0.40. This should not be a serious issue,

because most groups used to develop our model that had a sighting probability < 0.40 were small ($\leq$ 11 elk; Table 4). We acknowledge that significant change in conditions of Owens Valley, such as group sizes > 95, will require additional modeling efforts.

ACKNOWLEDGEMENTS

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