Evaluation of a double-sample population estimation technique on elk inhabiting spring range in west-central Idaho

by Timothy Charles Ferguson

A thesis submitted in partial fulfillment of the requirements for the degree of Master of Science in Fish and Wildlife Management
Montana State University

Abstract:
A double-survey technique was evaluated for estimating elk (Cervus elaphus) population size from 1988 to 1991 in west-central Idaho. The method consisted of 2 closely spaced fixed-wing flights counting groups of elk. Population estimates were derived from a modification of the Lincoln index with groups observed on the first flight considered a marked sample available for resighting on the second flight. Thirty-one radiocollared elk were monitored in order to test the validity of the assumptions inherent in the technique and to determine factors influencing sightability. Information on spring distribution, habitat use, annual mortality, and grouping characteristics were collected concurrently. Population estimates were moderately consistent among replicates. One of 2 comparisons of population estimates with a helicopter survey technique were not statistically different. Changes indicated in the population over time were biologically feasible, but not all were reasonable. Coefficients of variation were low (4-11%) for all surveys. All assumptions associated with the use of the technique were violated, but deviations from 4 of the 5 assumptions were minor or could be corrected. The uncertainty in correctly identifying elk groups seen by both aircraft due to changes in position and group size could not be eliminated or accurately assessed. This failure indicates that the technique is a poor choice for censusing elk populations. The mean probabilities of sighting groups containing collared female and male elk were 67% and 63%, respectively. Sightability of radiocollar ed elk was significantly influenced by time of day, weather, vegetative cover, terrain, and aspect. Logistic regression analysis indicated group size, temperature, and topography significantly affected sightability of groups seen by both aircraft during double-survey tests. Observer skill and fatigue did not significantly affect visibility. Habitat types were used disproportionately by elk in spring. Timber was used more than in proportion to availability and grass was used less than in proportion to availability. Shrub cover types were used in proportion to availability. The annual survival rate for female elk was 0.70 (95% Cl, 0.56-0.86). Male elk had an annual survival rate of 0.51 (95% Cl, 0.33-0.79).

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This thesis has been read by each member of the thesis committee and has been found to be satisfactory regarding content, English usage, format, citations, bibliographic style, and consistency, and is ready for submission to the College of Graduate Studies.

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ABSTRACT

A double-survey technique was evaluated for estimating elk (Cervus elaphus) population size from 1988 to 1991 in west-central Idaho. The method consisted of 2 closely spaced fixed-wing flights counting groups of elk. Population estimates were derived from a modification of the Lincoln index with groups observed on the first flight considered a marked sample available for resighting on the second flight. Thirty-one radiocollared elk were monitored in order to test the validity of the assumptions inherent in the technique and to determine factors influencing sightability. Information on spring distribution, habitat use, annual mortality, and grouping characteristics were collected concurrently. Population estimates were moderately consistent among replicates. One of 2 comparisons of population estimates with a helicopter survey technique were not statistically different. Changes indicated in the population over time were biologically feasible, but not all were reasonable. Coefficients of variation were low (4-11%) for all surveys. All assumptions associated with the use of the technique were violated, but deviations from 4 of the 5 assumptions were minor or could be corrected. The uncertainty in correctly identifying elk groups seen by both aircraft due to changes in position and group size could not be eliminated or accurately assessed. This failure indicates that the technique is a poor choice for censusing elk populations. The mean probabilities of sighting groups containing collared female and male elk were 67% and 63%, respectively. Sightability of radiocollared elk was significantly influenced by time of day, weather, vegetative cover, terrain, and aspect. Logistic regression analysis indicated group size, temperature, and topography significantly affected sightability of groups seen by both aircraft during double-survey tests. Observer skill and fatigue did not significantly affect visibility. Habitat types were used disproportionately by elk in spring. Timber was used more than in proportion to availability and grass was used less than in proportion to availability. Shrub cover types were used in proportion to availability. The annual survival rate for female elk was 0.70 (95% CI, 0.56-0.86). Male elk had an annual survival rate of 0.51 (95% CI, 0.33-0.79).

INTRODUCTION

As human pressures on limited land resources increase, precise, cost effective estimates of ungulate population size will become essential for wildlife managers. Accurate information is necessary for determining optimum harvest levels (Caughley 1974), for setting appropriate hunting season lengths and regulations, and for monitoring changes in populations over time.

Aerial surveys are commonly used to assess ungulate numbers or population trends. However, many of these techniques lack adequate precision or are effort and cost prohibitive. Caughley and Goddard (1972), Caughley (1974), Cook and Martin (1974), LeResche and Rausch (1974), Norton-Griffiths (1976), Cook and Jacobson (1979), Mackie et al. (1981), Routledge (1981), Samuel and Pollock (1981), Pollock and Kendall (1987), Samuel et al. (1987), and Steinhorst and Samuel (1989) have indicated that aerial counts often underestimate numbers due to visibility bias. Surveys using helicopters (Unsworth and Kuck 1988, DeYoung et al. 1989, Unsworth et al. 1990) and techniques requiring restraint and handling of animals (Otis et al. 1978, White et al. 1982, Bartmann et al. 1987, McCullough and Hirth 1988, Bear et al. 1989, Pollock et al. 1990) are labor and cost intensive. An accurate population estimation technique that does not necessitate utilizing high cost equipment and requiring high levels of manpower is needed. A method that could fulfill these requirements is the double-survey estimate of population size (Magnusson et al. 1978). This technique utilizes less expensive fixed-wing aircraft, few personnel, and does not require capture or handling of animals.

The double-survey technique proposed by Magnusson et al. (1978) requires two independent surveys to determine the number of entities seen by both aircraft, the number seen by aircraft 1 but not by aircraft 2, and the number seen by aircraft 2 but not aircraft 1. Magnusson et al. (1978) identified 5 inherent assumptions necessary to insure the accuracy of population estimates:

1) The survey is conducted on a closed population.
2) Animals do not lose identifying marks during the survey.
3) All identifying marks are correctly identified and noted.
4) Each animal in the population has a probability of sighting greater than 0.
5) The surveys are independent.

Similar approaches have been used to determine tree crown density (Maxim et al. 1981) and to estimate the number of osprey (Henny et al. 1977), crocodile (Magnusson et al. 1978), and bald eagle (Grier et al. 1981) nests. Cook and Jacobson (1979) developed a double-survey procedure for mobile animals involving simultaneous counts by tandem observers. This technique was used to count emus (Caughley and Grice 1982), investigate observer bias for feral horses and donkeys (Graham and Bell 1988), and estimate the sighting probability of sea otters (Estes and Jameson 1988). Double-counts have also been proposed as a method to calibrate population indices (Eberhardt and Simmons 1987).

This study tested the efficacy of the double-survey technique for estimating population size of elk (Cervus elaphus) occupying open habitat during spring greenup in west-central Idaho. The long range electronic navigational system known as LORAN-C (Azure Technology 1989) was used to record positions of elk groups. The validity of the 5 assumptions was evaluated using radiocollared elk. Information on sightability, spring distribution and habitat use, harvest, annual mortality, and grouping characteristics was collected concurrently.

STUDY AREA

The 3,873 km^2 study area, located in the Snake and Weiser River drainages of Idaho Department of Fish and Game Region 3, was composed of Game Management Units 22 and 31 in west-central Idaho (Fig. 1). The Payette National Forest administered 40.4% of the study area with the remainder managed by private owners (36.2%), the Bureau of Land Management (14.6%), and State of Idaho Department of Lands (8.8%). Major land uses were commercial timber harvesting, livestock grazing, and recreation including hunting, fishing, sightseeing, and camping.

The climate of west-central Idaho is influenced by maritime air flows during winter resulting in moist, moderate weather. In late spring and summer, a continental climate dominates producing dry summers with variable temperatures. Annual precipitation at weather stations at 808 m and 899 m elevation averaged 51 cm and 66 cm, respectively, with 86% occurring from October through May. Mean annual temperatures were 8.5 C and 9.2 C for the 2 stations, respectively (National Oceanic Atmospheric Administration 1988).

Management Units 22 and 31 differ with respect to size, topography, and vegetation structure. Unit 22, the larger of the two (2,231 km^2), ranges in elevation from 805 m to 2,668 m with 19% of the area above 1,750 m. The physiography varies from

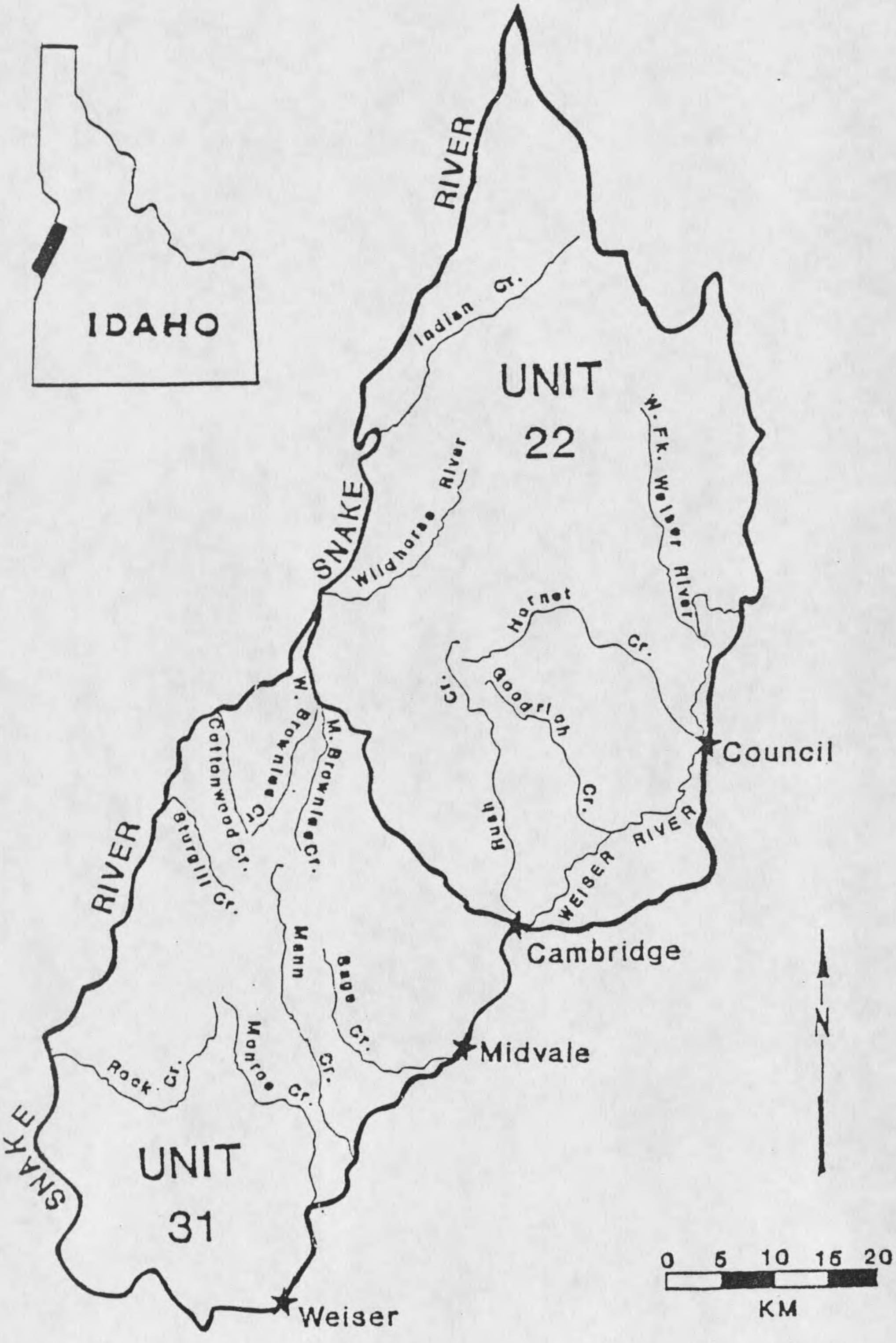


Figure 1. Location of the double-survey study area composed of Game Management Units 22 and 31 in west-central Idaho.

moderately steep slopes with flat and gently rolling benchlands to deeply dissected canyons. Timber stands occupied 40.2% of the area at the time of study. The remainder consisted of grassland with intermittent sagebrush (Artemisia spp.) and dense shrub habitat covering 42.8% and 17.0%, respectively.

Unit 31 (1,642 km^2) ranges in elevation from 680 m to 2,313 m with 5% of the area at elevations greater than 1,750 m. Mountainous, timbered terrain is located in the northwest of the Unit and comprises 14.8% of the total area. Topography of the lower elevations to the south, east, and along the Snake River is characterized by rough breaks and high hills. Sagebrush/grassland covered 65.0% of the Unit at the time of study with the remaining 20.2% occurring as dense shrub and riparian habitat.

Common forest climax series in the study area included ponderosa pine (Pinus pondersoa), Douglas fir (Pseudotsuga menziesii), and grand fir (Abies grandis). Engelmann spruce (Picea engelmannii), subalpine fir (A. lasiocarpa), and lodgepole pine (P. contorta) occurred in scattered stands on mesic sites. Shrubs associated with forest types included serviceberry (Amelanchier alnifolia), chokecherry (Prunus virginiana), huckleberry (Vaccinium globulare), mountain snowberry (Symphoricarpos oreophilus), currant (Ribes cereum), elderberry (Sambucus cerulea), and honeysuckle (Lonicera utahensis) (Steele et al. 1981). Shrubland types were dominated by bitter-brush (Purshia tridentata), hawthorn (Crataegus douglasii), big sagebrush (A. tridentata), rubber rabbit-brush

(Chrysothamnus nauseosus), and curl-leaf mountain mahogany (Cercocarpus ledifolius). Major grasses included bluebunch wheatgrass (Agropyron spicatum), Idaho fescue (Festuca idahoensis), elk sedge (Carex geyeri), cheat grass (Bromus tectorum), and Sandberg's bluegrass (Poa sandbergii). Balsamroot (Balsamorhiza spp.), lomatium (Lomatium spp.), eriogonum (Eriogonum heracleoides), arnica (Arnica cordifolia), strawberry (Fragaria virginiana), yarrow (Achillea millefollium), and mountain sweet-root (Osmorhiza chilensis) were the principle forbs (Asherin and Claar 1976).

METHODS

Elk Collaring Operation

Elk were captured on winter range in Units 22 and 31 in early February 1988 and mid-March 1989 using a dart-delivered immobilizing drug or a hand-held net gun (Barrett et al. 1982) fired from a Bell 206B III Jet Ranger helicopter. Carfentanil (3-4 milligrams/elk) was utilized as the immobilization agent with an antagonist of Naloxone HCL at a 20 milligrams/milliliter concentration given (1/2 intravenous and 1/2 intramuscular or 100% intramuscular) at doses of 10-15 milliliters/animal. Thirty-one elk were fitted with radio transmitters with time-delay, mortality-sensing devices mounted on 5-cm wide collars made of white butyl rubber (Telonics Inc., Mesa, AZ). Fourteen collars were covered with a 7.5-cm-wide strip of highly visible, yellow plastic, and 10 were covered with highly visible blue plastic. Data recorded for each animal included sex, age as determined from tooth replacement and wear (Quimby and Gaab 1957), and location of capture.

An attempt was made to place collars in proportion to relative densities in the 2 Units (IDFG, unpubl. data) and at a ratio of 2 females:1 male. Twelve transmitters were placed in Unit 22 in 1988 (8 females, 4 males) and 9 in Unit 31 (6 females, 3 males). Ten additional animals were equipped with transmitters in 1989 replacing those elk lost following the 1988 field season in order to maintain an adequate sample. Seven collars were placed in Unit 22 (4 males, 3 females) and 3 in Unit 31 (2 males, 1 female).

An effort was made to disperse radio transmitters widely among elk groups observed during fixed-wing flights in early February 1988 and early March 1989. The goal was to collar only 1 elk per group. However, budget and time constraints resulted in 3 groups containing 2 collared elk each.

Radio Relocation Flights

Thirty-four radio relocation flights were made from February through May 1988-1990 using a Maule MX7-235 fixed-wing aircraft. Flights provided information on movements of radiocollared elk, habitat use, mortality, factors influencing sightability, and whether instrumented animals were present in the study area during double-survey tests. The observer recorded weather, time of day, latitude and longitude (via LORAN-C system), elk group information (group size, activity, movement, and direction), and habitat information (cover, terrain, and aspect).

Elk Ecology

All spring (March-May) locations (latitude and longitude) of collared animals and groups observed during double-survey flights were recorded using the LORAN-C system or transcribed from U.S.G.S. 15-minute topographic maps. Locations were converted into X and Y coordinates of the Universal Transverse Mercator (UTM) grid system. The sizes of activity areas utilized by elk in spring were calculated using the 100% minimum convex polygon estimate of home range size (Hayne 1949, Mohr and Strumpf 1966) computed using the computer program HOME RANGE (Ackerman et al. 1990). Analysis of variance was used to determine differences in the average group size by month and sex.

Habitat preferences in spring were examined by determining differences between proportionate use and availability of 3 cover types: timber, shrub, and grassland. Availability of each type was determined following the nonmapping technique of Marcum and Loftsgaarden (1980). Differences between availability and use were examined using the chi-square test of heterogeneity (Zar 1984) in conjunction with Bonferoni Z tests (Marcum and Loftsgaarden 1980).

Yearlong and cause-specific mortality rates were calculated for males and females using the computer program MICROMORT (Heisey and Fuller 1985). Mortalities from the study area included harvest, illegal harvest, wounding loss, and unknown (elk not located following the 1988 and 1989 field seasons).

Double-Survey Technique Tests

Double-survey flights were initiated when high numbers of elk were observed in open areas during radio relocation flights. Each survey required 2 fixed-wing aircraft. The first aircraft

(Maule M5-180 or Scitaborea) flew at an altitude of 300 meters above ground (mag) and entered the survey area approximately 30 min prior to the second aircraft (Maule MX7-235) which flew at an altitude of 150 mag. The altitude of the first plane was greater than that of the second in order to reduce disturbance to elk groups. Flight speeds for both aircraft averaged 125 km/hour (hr).

Each aircraft began and ended the surveys at the same predetermined locations, but flight patterns were based on individual pilot and observer preferences. Both planes followed a general plan of flying up and down ridges or drainages to aid in navigation and to insure complete coverage of the area. Two observers, one primary (experienced) and one secondary (experienced or inexperienced), and the pilot located elk groups. Counts and classifications were performed only by the observers. Observers recorded the weather, time of day, latitude and longitude (via LORAN-C navigation system), elk group information (group size, activity, movement, and direction), and habitat information (cover, terrain, and aspect) for each group encountered. On each flight, LORAN-C positions were recorded at 5 predetermined locations to analyze accuracy and consistency of readings between aircraft.

Population estimates (P) were calculated by using the formula:

$$P=NG \tag{1}$$

where N is the estimated number of elk groups in the Unit and G is the average group size. The estimated number of groups was determined using a model equivalent to the Petersen estimate incorporating Chapman's (1951) correction:

$$N= \frac{(S1+B+1)(S2+B+1)}{B+1} -1 \qquad (2)$$

where S1 was the number of elk groups seen by aircraft 1 and not aircraft 2; S2 was the number of groups seen by aircraft 2 and not aircraft 1; and B was the number of groups seen by both (Magnusson et al. 1978).

I plotted the location and size of elk groups observed during double-survey tests on separate transparent mylar sheets for each aircraft. For each group located by aircraft 1, the difference in geographic position (bearing and distance) from each group located by aircraft 2 was calculated using a computer program (Ferguson, unpubl. data). In order to determine which groups were seen by both aircraft or by only 1 aircraft, the transparencies and differences in group positions between planes were compared. A group sighted by the first aircraft was presumed to have been seen by the second aircraft if it exhibited a similar location, group size, group composition, and movement direction. No groups differing in position by greater than 0.75 km were considered identical.

The average group size was calculated using the formula:

$$G = \frac{\Sigma G1+\Sigma G2+\Sigma GB}{S1+S2+B} \qquad (3)$$

where $\Sigma G1$ is the sum of the group sizes seen only by the first aircraft, $\Sigma G2$ is the sum of the group sizes seen only by the second plane, and ΣGB is the sum of the high group size counts seen by both replicates.

Group sizes with similar probabilities of being recaptured (i.e. observed) by the second aircraft in the survey were combined to produce 3 subpopulations. Estimates were calculated for each subpopulation and a total population estimate for each Unit was derived by summing all strata.

The variance in numbers of groups was calculated from a translation of Seber's formula (1982):

$$\mathrm{Var}(N) = \frac{S1S2(S1+B+1)(S2+B+1)}{(B+1)^2(B+2)} \qquad (4)$$

Total variance was:

$$\mathrm{Var}(T) = (\bar{X}^2N)(\mathrm{Var}\ G/NT) + (\bar{X}^2G)(\mathrm{Var}\ N) + (\mathrm{Var}\ N)(\mathrm{Var}\ G/NT) \qquad (5)$$

where N was the number of groups, G was the average group size, and NT was the total number of groups seen by both aircraft (S1+S2+B). The finite population correction was used in computing confidence intervals (Zar 1984).

Two complete double-survey tests of Unit 22 and 1 test of Unit 31 were conducted between the end of March and mid-April 1988. Two double-survey tests of both Unit 22 and Unit 31 were performed during mid to late April 1989. One double-survey test of both Unit 22 and Unit 31 was conducted in late March 1991. Unit 31 was divided into east and west components with the former flown in the morning and the latter flown in the evening to accommodate sun angle. Unit 22 was subdivided into 3 parts to compensate for the larger flight area.

The goodness-of-fit method (Seber 1982) was used to test differences between surveys. The consistency of estimates was compared with a helicopter sightability technique (Samuel et al. 1987) regarded as one of the best available aerial techniques for elk (Unsworth et al. 1990). Coefficients of variation ((SE(P)/P) x 100) were calculated to determine how they compared to the 10% level regarded as desirable for wildlife censuses by White et al. (1982). Rates of population increase were determined using linear regression following logarithmic (ln) transformation (McCorquodale et al. 1988) of double-survey estimates and trend counts.

Validity of Assumptions

Closed Population

Violations of this assumption could include: 1) deaths, births, immigration, or emigration in/from the sample area between flights; 2) a subpopulation of animals that were not available to be seen (due to chance, behavior, or environmental conditions) during survey flights; and 3) changes in the numbers, sizes, or locations of groups that would lead to a different set of groups available for counting in each flight of the survey (Munholland 1991).

In order to minimize violations due to changes in the population in the sample area (violation set 1), double-survey flights were conducted during a short, specific time period (early morning or late afternoon/early evening hours) when previous flights indicated elk were most visible (Schlegel, pers. commun.). Movement out of the study area was reduced by the < 1 hr interval between passes by different airplanes. Differences in use of open habitat during morning and evening flights were investigated using the chi-square test of heterogeneity (Zar 1984).

I tested the possibility that closure was violated because some elk groups were "invisible" (violation set 2) by classifying each radio relocation as "seen" (the individual or the group with which it was associated was visible) or "unseen". Frequencies of sighting > 0.0 were assumed to support the possibility of population closure. Frequencies of sighting were analyzed in relation to probability of being sighted rather than to population closure.

The impacts of changes in numbers of groups available to be counted between the first and second flights (violation set 3) could only be evaluated in a general manner. I calculated the percentage of groups that were sufficiently disturbed by the first plane to move. If groups that moved were more likely to break into subgroups that would be seen as independent groups by the second plane than undisturbed groups, this percentage would serve as an index to the potential magnitude of the problem. Disturbance of elk groups and the impacts of changes in group size and location were analyzed in relation to survey flight independence and accuracy of identification of marks, respectively, rather than to population closure.

Loss and Accuracy of Identifying Marks

During this study, a mark consisted of an elk group of a specific size and location sighted on the first survey flight. The loss or incorrect identification of a mark could occur if an elk group size or location changed between the 2 flights.

Differences in counts of groups assumed to have been seen by both aircraft were analyzed by testing the equality of the mean group size between aircraft using the paired-t test (Zar 1984). The percentage of times the first aircraft recorded larger, smaller, and equal group sizes was examined by testing the fit of the frequency to a theoretical ratio of 1:1:1 using the one-way chi-square test (Zar 1984).

Sensitivity of the double-survey technique to miscounts or errors in group identification was examined using 2 methods. The first approach determined the effect of different values for the average group size on population estimates. Estimates computed using average group sizes calculated using equation (3) were compared with estimates computed using an alternate formula:

$$G = \frac{\Sigma G1+\Sigma G2+\Sigma GL}{S1+S2+B} \qquad (6)$$

where ΣGL is the sum of the low group size counts seen by both replicates. The goodness-of-fit method (Seber 1982) was used to test differences between estimation methods.

The second approach determined the probable effect on population estimates of changes in the geographic position of elk groups between flights. In order to minimize the influence of other factors, the only criteria used to determine groups seen by both aircraft or only 1 aircraft was location. All groups located by aircraft 2 within a given distance from group locations recorded by aircraft 1 were presumed seen by both. I made comparisons between estimates computed using 6 different distances (0.25, 0.50, 0.75, 1.00, 2.00 and 5.00 km) between positions. During 9 of 34 radio relocation flights, collared elk were located twice. The 30-60 minute (min) interval between locations simulated conditions in the double-survey technique and provided an estimate of distances elk might travel between the first and second planes in the survey.

Probability of Being Sighted

As noted in the "population closure" section, radio relocations were recorded as "seen" or "unseen" to determine if the probability of a group being seen was greater than zero. Differences in the frequency with which radiocollared animals (and the group with which it was associated) were seen in late winter-spring were tested among individuals, sex, age, unit, and year using the chi-square test of independence (Zar 1984).

Survey Flight Independence

Disturbance of elk groups by the first aircraft could result in changes in position and/or movement into cover types in which elk would not be visible from the air. The influence of the first flight on the succeeding flight was measured by recording the disturbance rate of elk groups seen only by plane 1 or only by plane 2 and the direction of movement. Differential disturbance rates between aircraft were examined by testing the equality of means using the paired-t test (Zar 1984).

Differences in the direction of movement of disturbed groups were analyzed using the chi-square test of independence (Zar 1984).

Factors Influencing Sightability

Degree-days, accumulated departures of mean temperatures on successive days from a reference temperature of 32^{o} Fahrenheit (F), were computed to determine thermal conditions present during estimation flights. Thermal conditions were examined to determine their utility in identification of the "survey window", defined as the set of phenological conditions associated with a small number of elk groups and large group sizes in or adjacent to open areas. The total number of degree-days over the period beginning January 1 until double-survey tests were initiated was computed for estimation flights in both 1988 and 1989. Consistency in the average elk group size and number of groups observed between multiple double-survey flights was analyzed as a further indicator of accurate survey timing.

Univariate statistical procedures were used to determine factors significantly influencing the sightability of elk groups during spring. Information collected during radio relocation flights was used to determine the influence of time of day, weather, vegetative cover, terrain, aspect, sex, age, and Unit on sightability of groups containing collared elk. The number of groups seen or missed was analyzed for each variable using the chi-square test of independence (Zar 1984) to determine which factors had a significant effect on visibility.

Differential sightability of elk groups on double-survey flights due to observer skill was analyzed by testing for equality of the mean number of elk and groups seen by each primary observer using the paired-t test (Zar 1984). The effect of observer fatigue was determined by testing the fit of the frequency of groups observed per one-third segment of flight time to a theoretical ratio of 1:1:1 using the one-way chi-square test (Zar 1984).

Stepwise logistic regression procedures (Dixon et al. 1981) were used to determine factors which contributed to groups being observed by the first and second aircraft in double-survey tests. Groups seen by both aircraft and groups seen by only one aircraft were treated as dichotomous dependent variables. Categorical independent variables included wind, clouds, vegetative cover, topography, and aspect. Continuous independent variables were temperature, time of day, and group size. A variable was regarded as important when its stepwise improvement chi-square computed from the log-likelihood ratio significantly improved predictions ($\underline{P} \leq 0.10$) (Dixon et al. 1981). Significant independent variables were used to develop a model to predict conditions associated with groups seen by both aircraft.

RESULTS

Elk Ecology

Cover Type Use

During the spring of 1988-1990, radiocollared elk utilized areas totaling 2,860.1 km^2 in Unit 22 (Fig. 2) and 859.3 km^2 in Unit 31 (Fig. 3). The size of activity areas increased from 862.6 km^2 in March to 1,412.0 km^2 in May in Unit 22 in 1988.

Areas utilized by elk groups observed on double-survey flights during 1988 occupied 67% (1,489.2 km^2) and 30% (493.6 km^2) of the study area in Unit 22 (Fig. 4) and Unit 31 (Fig. 5), respectively. Elk groups utilized 69% (1,584.8 km^2) of Unit 22 (Fig. 6) and 50% (824.9 km^2) of Unit 31 (Fig. 7) in 1989.

Cover types were not used in proportion to availability by either collared males or females ($\underline{P} < 0.10$) during spring (Table 1). Similarly, elk groups observed on double-survey flights did not use cover types in proportion to availability (Table 2).

Table 1. Habitat type availability and use (%) for 31 collared elk, 1988-1990. A + or - indicates a significant difference ($\underline{P} < 0.10$) from expected.

Habitat type	Availability (N=1000)	Female use (N=146)	Male use (N=71)
Timber	28	43+	45+
Shrub	19	21	23
Grass/sagebrush	54	36-	32-

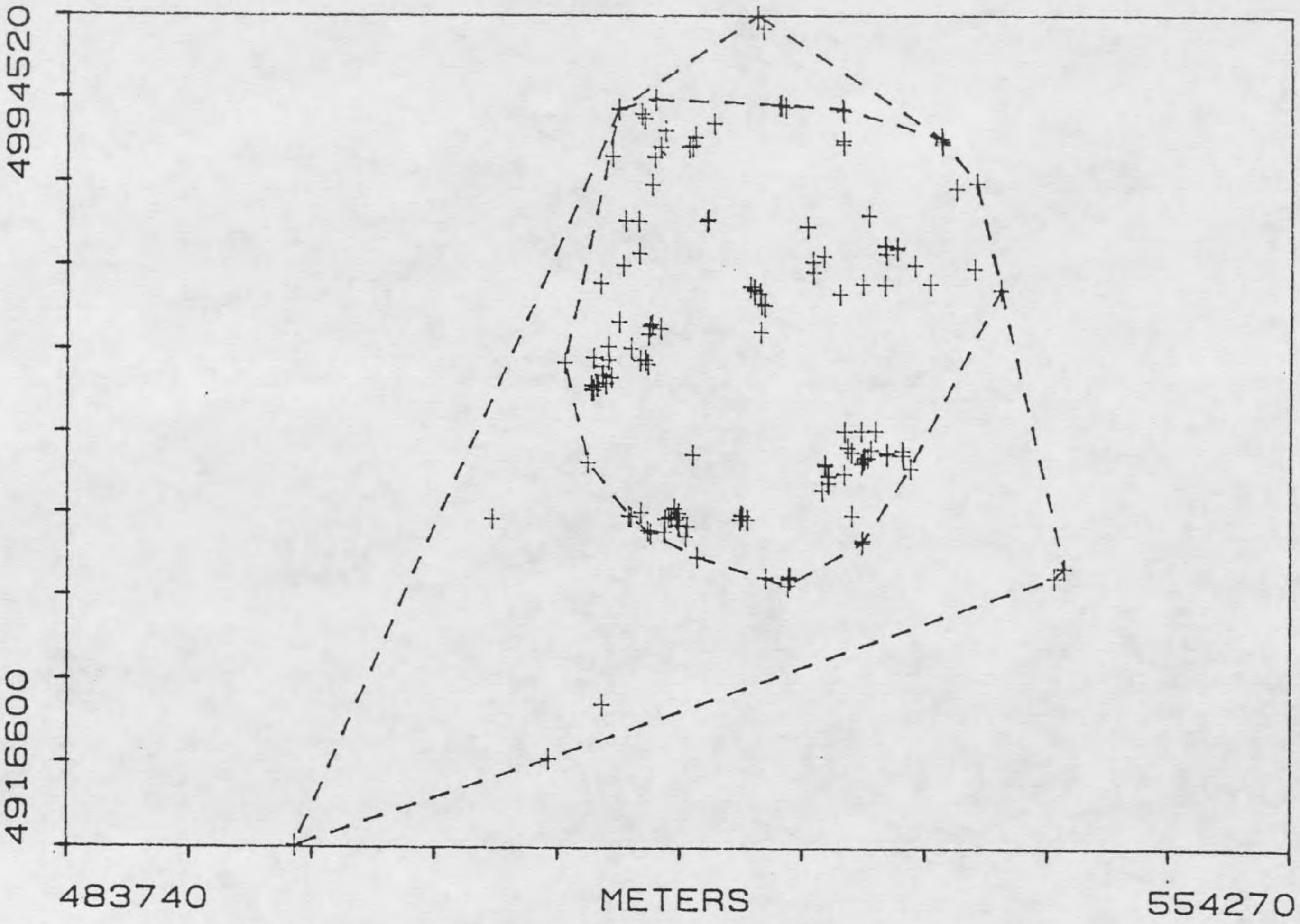


Figure 2. Spring 100% minimum convex polygon (exterior dashed line) and 95% minimum convex polygon (interior dashed line) plotted on a UTM grid for radiocollared elk within Unit 22, 1988-1990. A "+" represents an individual elk location.

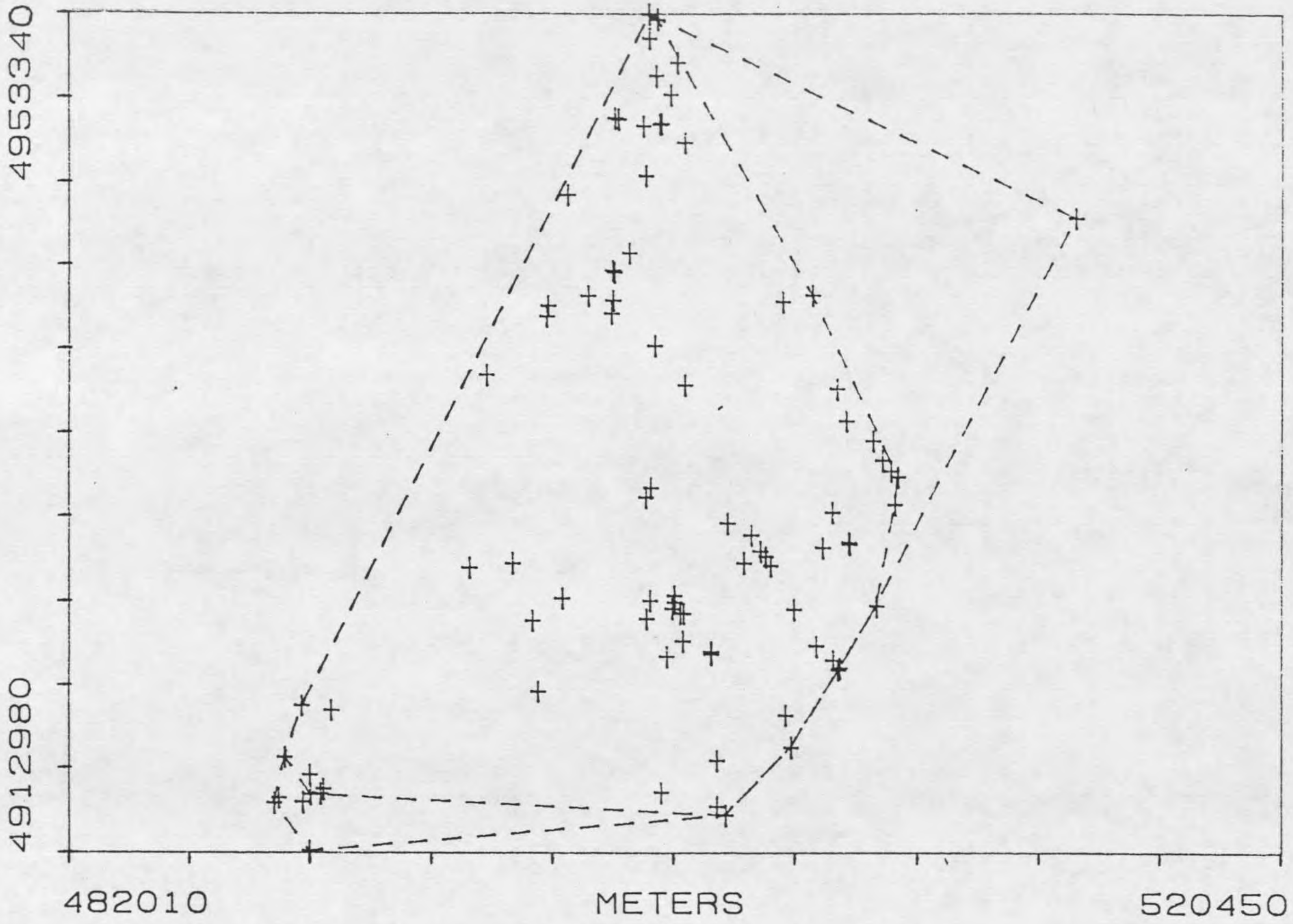


Figure 3. Spring 100% minimum convex polygon (exterior dashed line) and 95% minimum convex polygon (interior dashed line) plotted on a UTM grid for radiocollared elk within Unit 31, 1988-1990. A "+" represents an individual elk location.

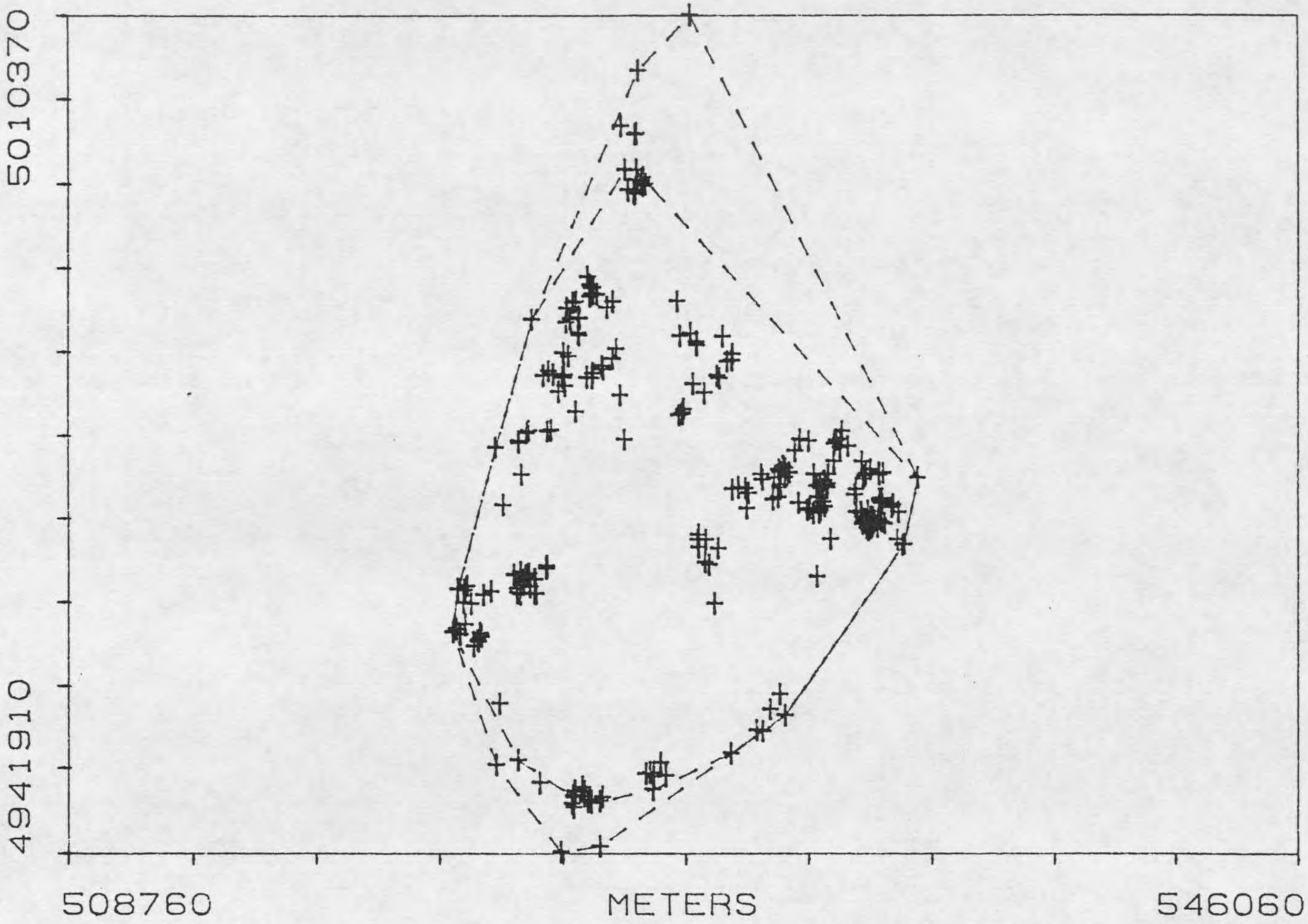


Figure 4. The 100% minimum convex polygon (exterior dashed line) and 95% minimum convex polygon (interior dashed line) plotted on a UTM grid for double-survey flights within Unit 22 in 1988. A "+" represents individual elk group locations.

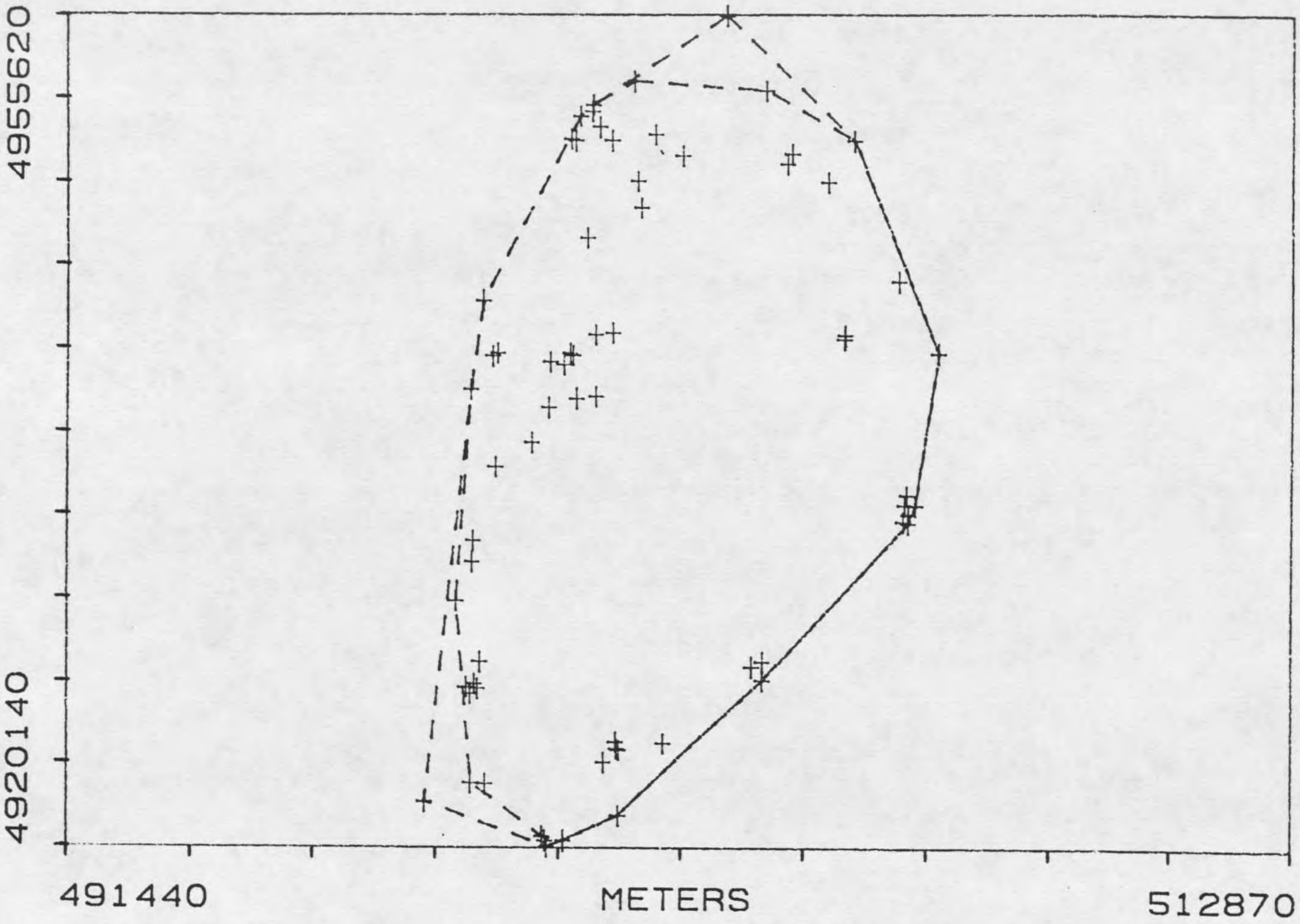


Figure 5. The 100% minimum convex polygon (exterior dashed line) and 95% minimum convex polygon (interior dashed line) plotted on a UTM grid for double-survey flights within Unit 31 in 1988. A "+" represents individual elk group locations.

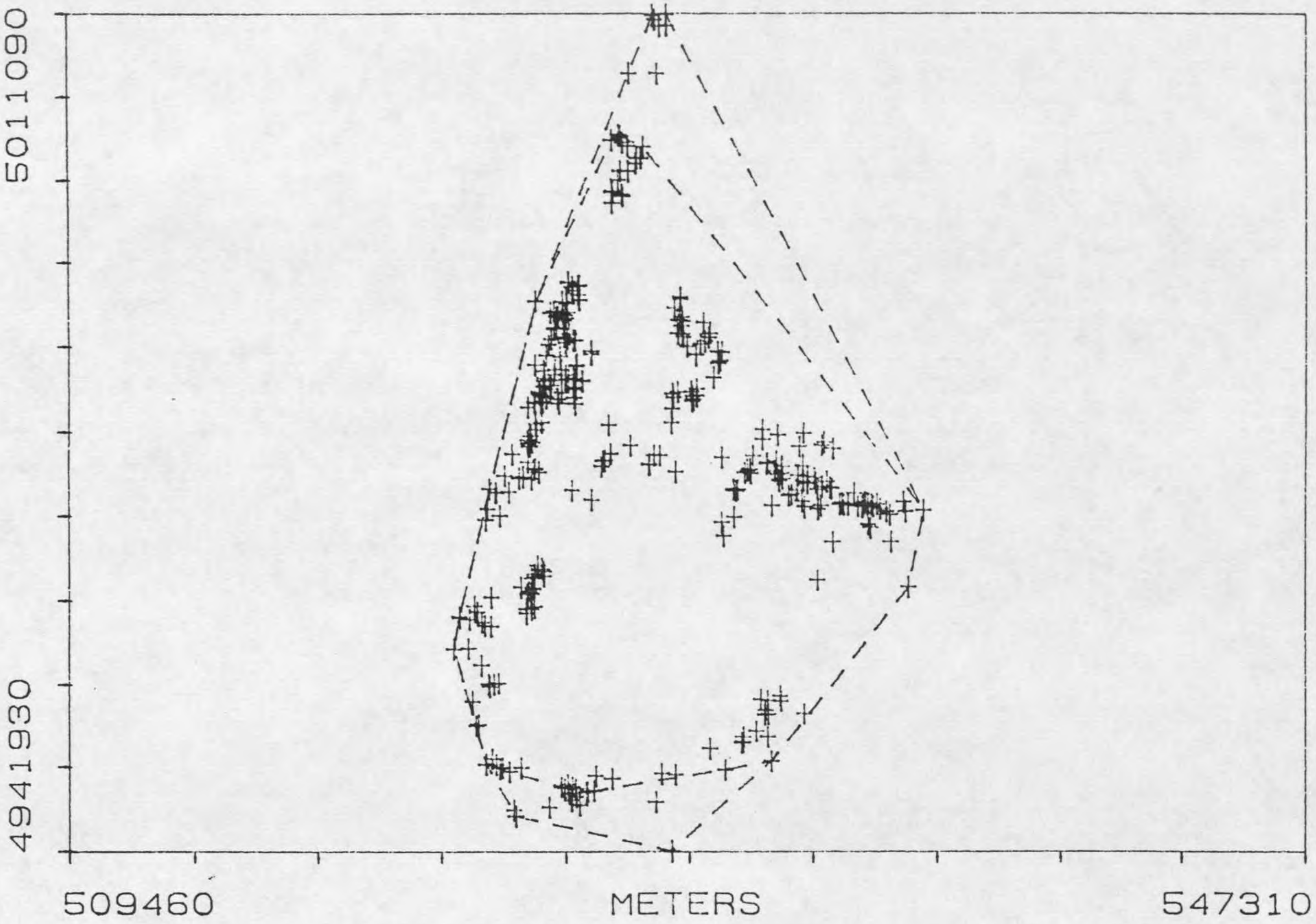


Figure 6. The 100% minimum convex polygon (exterior dashed line) and 95% minimum convex polygon (interior dashed line) plotted on a UTM grid for double-survey flights within Unit 22 in 1989. A "+" represents individual elk group locations.

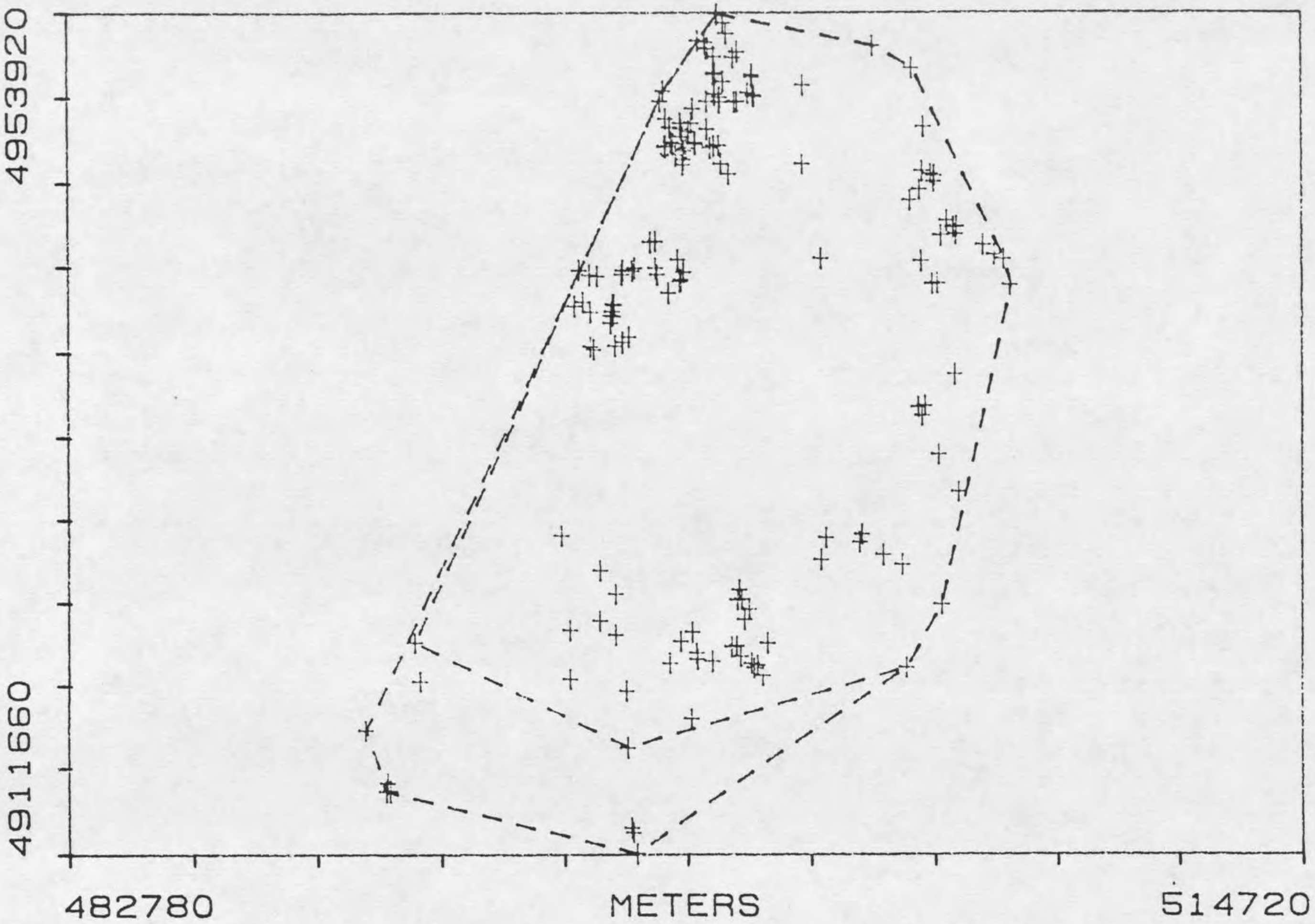


Figure 7. The 100% minimum convex polygon (exterior dashed line) and 95% minimum convex polygon (interior dashed line) plotted on a UTM grid for double-survey flights within Unit 31 in 1989. A "+" represents individual elk group locations.

Table 2. Habitat type availability and use (%) for elk groups observed on double-survey flights, 1988-1990. A + or - indicates a significant difference ($P < 0.10$) from expected.

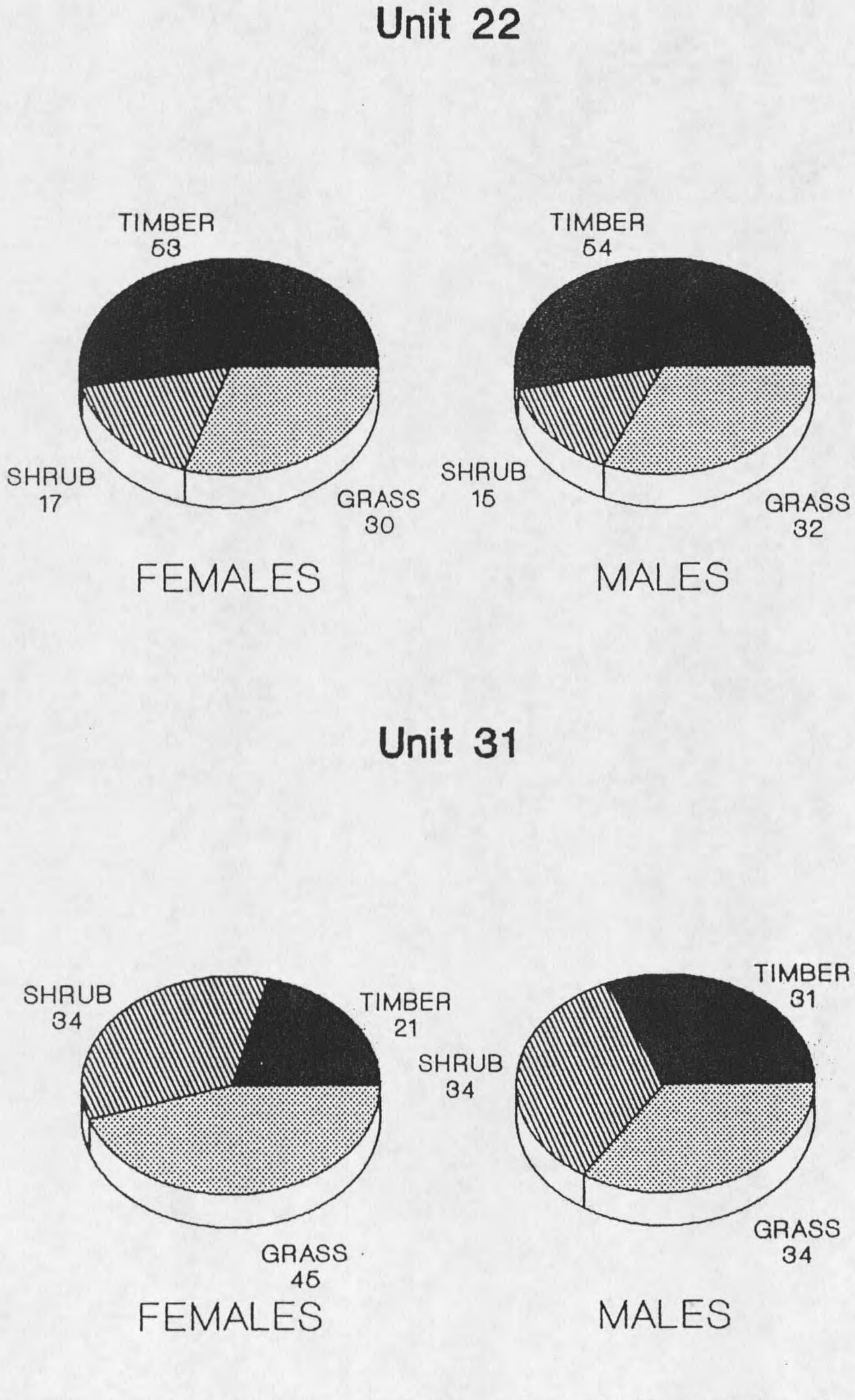
Habitat type	Availability (N=1000)	Group use (N=406)
Timber	28	10-
Shrub	19	6-
Grass/sagebrush	54	84+

Use of cover types did not vary significantly between all collared male and female elk (chi-square = 0.320, df = 2, P = 0.852). Similarly, cover type use did not vary significantly between male and female elk in Unit 22 (chi-square = 0.384, df = 2, P = 0.825) and between male and female elk in Unit 31 (chi-square = 2.086, df = 2, P = 0.353) during spring (Fig. 8).

Group Characteristics

Mean size of elk groups containing radiocollared animals declined during spring (Fig. 9). The average size of groups with instrumented females decreased significantly from 24.4 elk in March to 12.6 elk in April (P = 0.048). A reduction to 7.7 elk per group in May was not significantly different from the mean group size in April (P = 0.192). The average size of groups with collared male elk significantly declined from 44.0 elk in March to 9.7 elk in April (P = 0.024) and from 9.7 to 4.8 elk (P = 0.082) in April and May, respectively.

The mean sizes of groups containing collared female elk were not significantly different from groups with instrumented males in March (P = 0.187), April (P = 0.467), and May (P = 0.307). The most common group size for both sexes in each month was 1-5



Unit 22

Unit 31

Figure 8. Cover type use (%) by collared elk in Units 22 and 31 during spring, 1988-1990.

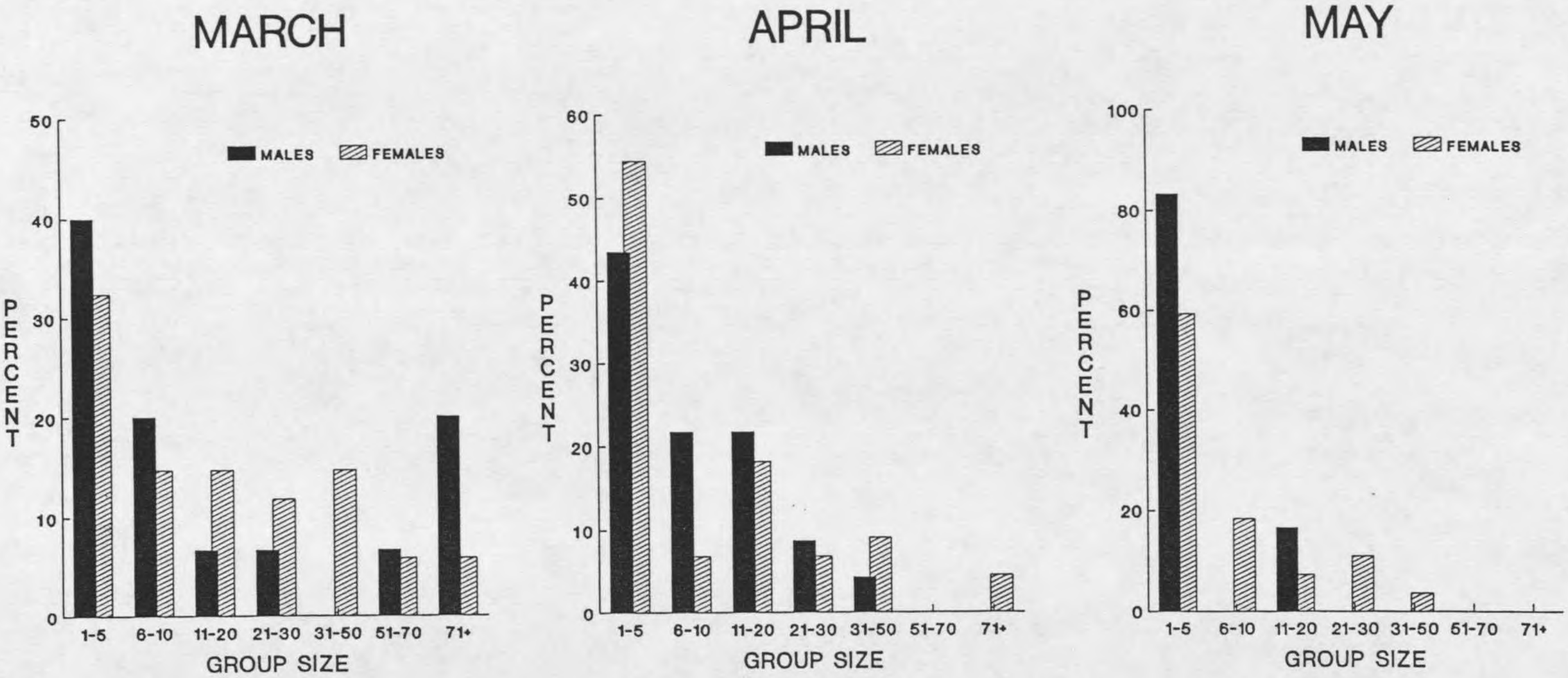


Figure 9. Percentage of occurrence of various size groups containing collared elk during spring (March-May), 1988-1990.

members. Group sizes of 1-20 individuals composed 84% of all male elk group sightings and 75% of all female groups.

Mortality

Elk hunting opportunity in Unit 22 was provided by a 28-day either-sex general archery hunt in September, a 12-day general hunt for antlered elk held in early October, and a 12-day controlled (permit) hunt for antlerless elk in November. The number of controlled hunt permits increased from 25 in 1983 to 500 in 1991. Harvest data generated from telephone surveys for general and controlled hunts are presented in Table 3.

Table 3. Elk harvest estimated from telephone surveys in general and permit hunts in Unit 22.[a]

Year	General harvest	Controlled harvest	Total harvest
1982	125	0	125
1983	185	10	195
1984	123	82	205
1985	84	100	184
1986	298	116	414
1987	231	121	352
1988	305	124	429
1989	264	221	485
1990[b]	310	241	551

[a] Kuck et al. 1989

[b] From IDFG, unpublished data.

Hunting season structure in Unit 31 included a 28-day general either-sex archery hunt in September, 12-day antlerless and antlered controlled hunts in October, and a 53-day either-sex controlled muzzleloader hunt in November and December. Controlled permits increased from 85 in 1982 to 700 in 1991. Estimated harvests for 1982-1990 are listed in Table 4.

Table 4. Elk harvest estimated from telephone surveys in general and permit hunts in Unit 31.[a]

Year	General harvest	Controlled harvest	Total harvest
1982	0	41	41
1983	0	70	70
1984	0	85	85
1985	0	141	141
1986	5	115	120
1987	0	123	123
1988	0	95	95
1989	0	178	178
1990[b]	0	305	305

[a] Kuck et al. 1989

[b] From IDFG, unpublished data.

Elk radio relocations (N=401) recorded during 1988-1991 resulted in a total of 16,031 radio days of data for annual mortality rate calculations. Twenty mortalities occurred during the monitoring period: 11 harvest, 1 illegal harvest, 3 rifle wounding losses, and 5 unknown. Harvest and related activities (illegal harvest and wounding loss) accounted for all known mortalities (75%). In addition, 4 males (all 3 years old) dispersed from Unit 22 following population estimation tests.

The annual survival rate for females in the study area was 0.70 (95% CI, 0.56-0.86). Male elk had an annual survival rate of 0.51 (95% CI, 0.33-0.79). Estimates of survivorship were conservative because of the assumption that all animals missing had died. Cause-specific mortality rates are presented in Table 5. Mortality and survival rates for Unit 22 and Unit 31 are listed in Tables 6 and 7, respectively.

Table 5. Cause-specific mortality rates for all collared elk, 1988-1991. Confidence intervals (95%) are in parenthesis.

Method	Mortality rates (95% CI) Females (N=18)	Males (N=13)
Harvest	0.17 (0.04-0.29)	0.27 (0.07-0.47)
Poaching	0.03 (0.00-0.08)	0.00 (0.00-0.00)
Wounding loss	0.06 (0.00-0.13)	0.05 (0.00-0.16)
Unknown	0.06 (0.00-0.13)	0.16 (0.00-0.33)

Table 6. Cause of death, annual survival rates, and cause-specific mortality rates for collared elk in Unit 22, 1988-1991. Confidence intervals (95%) are in parenthesis.

	Females (N=12)	Males (N=8)
Cause of death		
Harvest	4	3
Illegal harvest	1	0
Wounding loss	1	0
Unknown	2	1
Survival rate (95% CI)	0.65 (0.49-0.88)	0.61 (0.38-0.99)
Mortality rate (95% CI)		
Harvest	0.17 (0.02-0.33)	0.29 (0.01-0.56)
Illegal harvest	0.04 (0.00-0.13)	0.00 (0.00-0.00)
Wounding loss	0.04 (0.00-0.13)	0.00 (0.00-0.00)
Unknown	0.09 (0.00-0.20)	0.10 (0.00-0.28)

Double-Survey Technique Tests

Logistical Costs

Logistical costs for double-survey flights conducted in 1988, 1989, and 1991 are presented in Table 8. The rate per hour for fixed-wing aircraft varied from $85 for the Maule MX7-235 and $65 for the Maule M5-180 in 1988 to $100 and $90, respectively, in 1989. Total costs include post-survey radio relocation flights. In 1991, a Scitaborea ($60/hr) was used in place of the Maule M5-180 and no post-survey radio relocation flights were performed.

Table 7. Cause of death, annual survival rates, and cause-specific mortality rates for collared elk in Unit 31, 1988-1991. Confidence intervals (95%) are in parenthesis.

	Females (N=6)	Males (N=5)
Cause of death		
Harvest	2	2
Illegal harvest	0	0
Wounding loss	1	1
Unknown	0	2
Survival rate (95% CI)	0.77 (0.58-1.00)	0.39 (0.17-0.89)
Mortality rate (95% CI)		
Harvest	0.15 (0.00-0.35)	0.25 (0.00-0.54)
Illegal harvest	0.00 (0.00-0.00)	0.00 (0.00-0.00)
Wounding loss	0.08 (0.00-0.22)	0.12 (0.00-0.35)
Unknown	0.00 (0.00-0.00)	0.25 (0.00-0.54)

Table 8. Logistical costs of double-survey flights performed in Units 22 and 31 in 1988-1991.

Unit	Date(s)	Flight hours	Flight cost[a]
22	4/2-4/5/88	15.5	1171.50
22	4/11-4/12/88	17.3	1300.50
22	4/10-4/11/89	17.8	1691.00
22	4/16-4/17/89	14.5	1381.00
22	3/28-3/29/91	16.2	1264.00
31	3/31/88	12.3	927.50
31	4/12/89	11.3	1081.00
31	4/13/89	11.7	1113.00
31	3/27/91	13.9	1094.00

[a] In dollars.

Population Estimates

The probability of recapture for 7 group-size intervals was determined for groups located during double-survey flights in 1988, 1989, and 1991 (Table 9). Group-size intervals with similar recapture probabilities were combined to produce 3 strata (group-size intervals 1-10, 11-30, 31+) for determination of population size. Data used to calculate population estimates for Units 22 and 31 are given in Tables 10 and 11, respectively.

Table 9. The recapture probabilities by group-size intervals for all double-survey flights, 1988-1991. S1 was the number of elk groups seen by aircraft 1 and not aircraft 2; S2 was the number of groups seen by aircraft 2 and not aircraft 1; and B was the number of groups seen by both.

Group size interval	S1	S2	B	% recapture (B/S2+B)
1-5	124	110	57	34
6-10	62	65	45	41
11-20	43	42	64	60
21-30	12	13	26	67
31-50	13	9	36	80
51-70	5	1	12	92
71+	1	2	18	90

Population estimates for Unit 22 (Table 12) in 1988 were 1,336 and 1,444. These values were not significantly different ($\underline{z} = -0.915$, $\underline{P} = 0.360$). Estimates of 1,951 and 1,953 in 1989 were not significantly different ($\underline{z} = -0.152$, $\underline{P} = 0.879$). The single estimate of 2,207 in 1991 was significantly different from an estimate of 1,773 obtained from a helicopter survey using the sightability technique of Samuel et al. (1987) performed in February 1991 ($\underline{z} = 3.251$, $\underline{P} = 0.001$). Coefficients of variation for total population estimates were all $\leq 7\%$. Each estimate in 1988 was significantly different ($\underline{P} \leq 0.001$) from each estimate in 1989. Each estimate in 1989 was significantly different ($\underline{P} \leq$

0.100) from each estimate in 1991.

Table 10. Data by date used in 5 estimations of population size by the double-sample technique in Unit 22, 1988-1991. S1 was the number of elk groups seen by aircraft 1 and not aircraft 2; S2 was the number of groups seen by aircraft 2 and not aircraft 1; and B was the number of groups seen by both.

Group size intervals	S1	S2	B	Estimated No. of groups	Average group size
4/2-4/5/88					
1-10	28	3	8	48.3	5.4
11-30	9	2	11	23.5	17.3
31+	2	2	6	10.6	63.2
4/11-4/12/88					
1-10	47	26	19	153.1	4.0
11-30	6	6	12	26.8	16.0
31+	2	0	7	9.0	45.7
4/10-4/11/89					
1-10	24	29	12	118.5	5.1
11-30	12	6	15	37.5	16.8
31+	3	2	11	16.5	43.3
4/16-4/17/89					
1-10	25	40	18	135.6	4.6
11-30	5	11	11	31.6	17.6
31+	0	2	13	15.0	51.6
3/28-3/29/91					
1-10	16	19	11	71.3	5.2
11-30	5	3	16	24.9	19.4
31+	3	3	13	19.6	68.8

The single double-survey population estimate for Unit 31 in 1988 of 851 elk was not statistically different from an estimate of 1,223 elk obtained from a helicopter survey using the sightability technique of Samuel et al. (1987) performed in April 1988 ($\underline{z} = -1.536$, $\underline{P} = 0.125$). Estimates in 1989, 1,220 and 959, were significantly different ($\underline{z} = 1.950$, $\underline{P} = 0.051$). The population estimate for 1988 was significantly different ($\underline{z}$ = -

2.462, $P = 0.014$) from the first estimate in 1989 and not significantly different ($z = -1.002$, $P = 0.316$) from the second estimate. The single estimate for 1991 of 1,321 elk was not significantly different from the first estimate in 1989 ($z = 0.683$, $P = 0.495$) but was significantly different ($z = 3.447$, $P = 0.006$) from the second estimate. Coefficients of variation (CV) for total estimates were all ≤ 11% (Table 13).

Table 11. Data by date used in 4 estimations of population size by the double-sample technique in Unit 31, 1988-1991. S1 was the number of elk groups seen by aircraft 1 and not aircraft 2; S2 was the number of groups seen by aircraft 2 and not aircraft 1; and B was the number of groups seen by both.

Group size intervals	S1	S2	B	Estimated No. of groups	Average group size
3/31/88					
1-10	11	9	9	38.9	5.5
11-30	3	10	5	23.0	16.6
31+	1	2	2	5.7	45.4
4/12/89					
1-10	6	22	6	52.9	5.3
11-30	2	10	6	20.9	16.8
31+	4	1	3	9.0	65.6
4/13/89					
1-10	14	18	14	62.8	4.0
11-30	3	3	2	11.0	16.5
31+	3	0	3	6.0	87.7
3/27/91					
1-10	15	9	5	51.5	5.7
11-30	10	4	12	29.1	17.5
31+	1	0	8	9.0	57.6

Double-survey estimates indicated population increases in Unit 22 of 40% between 1988 and 1989 and 13% between 1989 and 1991. Population estimates yielded an intrinsic rate of increase, r, of 0.34 for 1988-1989 and 0.12 for 1989-1991.

Table 12. Population estimates for Unit 22 by subunit and date conducted during 1988-1991 using high counts for groups seen by both aircraft.

Subunit	Total seen	Estimate[a]	90% CI	CV(%)
East				
4/2/88	576	585	27	3
4/11-4/12/88	437	609	153	13
4/10-4/11/89	457	588	154	12
4/16-4/17/89	557	695	154	10
3/28-3/29/91	818	934	185	4
West				
4/5/88	648	804	300	16
4/11-4/12/88	721	827	111	6
4/10-4/11/89	1123	1330	234	7
4/16-4/17/89	1074	1225	146	5
3/28-3/29/91	1196	1263	110	8
Total				
4/2-4/5/88	1224	1336C	203	6
4/11-4/12/88	1158	1444C	199	6
4/10-4/11/89	1580	1951D	327	7
4/16-4/17/89	1631	1953D	242	5
2/20-2/27/91[b]	1590	1773E	159	5
3/28-3/29/91	2014	2207F	244	4

[a] Total estimates within years followed by different letters are different (z-test; $P < 0.10$).

[b] Estimate obtained from a helicopter survey using the sightability technique (Samuel et al. 1987).

Trend data developed from raw counts from a single fixed-wing aircraft gave similar estimates of population growth. The 1989 count represented a 36% increase over the 1988 count and the 1991 count represented a 20% increase over the 1989 count (Table 14). The overall regression estimate of r calculated from trend counts for 1983-1991 was 0.11 (Fig. 10). Maximum and minimum year-to-year values of r were 0.41 (1983-84) and 0.04 (1985-86), respectively.

Table 13. Population estimates for Unit 31 by subunit and date conducted during 1988-1991 using high counts for groups seen by both aircraft.

Subunit	Total seen	Estimate[a]	90% CI	CV(%)
East				
3/31/88	256	318	142	18
4/12/89	279	356	110	14
4/13/89	261	372	155	18
3/27/91	547	704	233	18
West				
3/31/88	429	522	136	12
4/12/89	729	781	136	8
4/13/89	582	602	24	3
3/27/91	592	669	111	7
Total				
3/31/88	685	851C	246	11
4/03/88[b]	771	1223C	371	18
4/12/89	1008	1220D	330	10
4/13/89	843	959E	135	6
3/27/91	1139	1321	195	7

[a] Total estimates within years followed by different letters are different (z-test; $P < 0.10$).

[b] Estimate obtained from a helicopter survey using the sightability technique (Samuel et al. 1987).

Table 14. Unit 22 elk population trend data, fixed-wing survey, 1983-1991.[a]

Year	East Side	West side	Total
1983			575
1984			870
1985	484	318	802
1986	352	482	834
1987	403	474	877
1988	540	463	1003
1989	474	886	1360
1991[b]	579	1053	1632

[a] From Kuck et al. 1989.

[b] From IDFG, unpublished data.

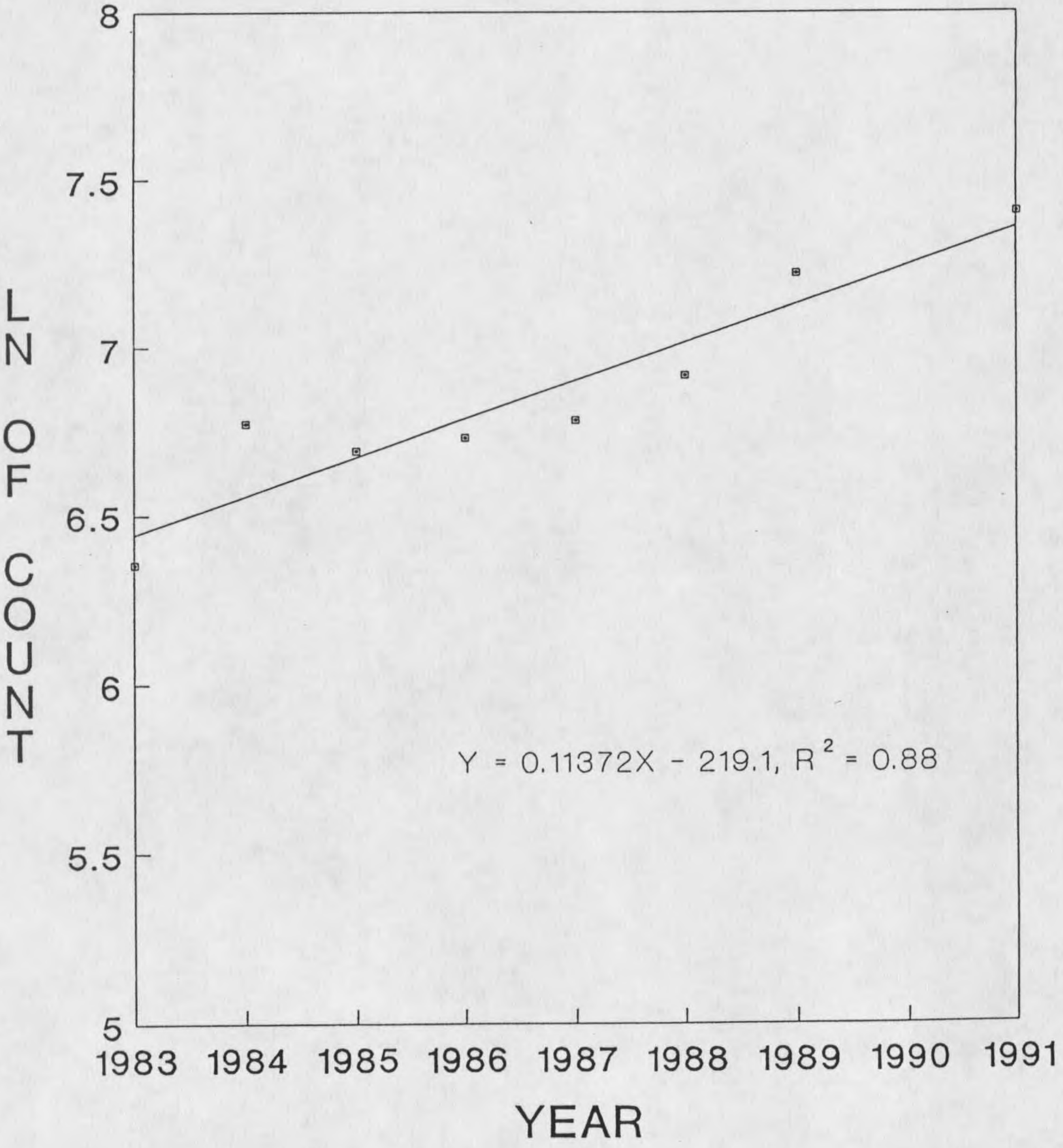


Figure 10. Increase of elk trend counts in Unit 22, 1983-1991, using a single fixed-wing aircraft.

Validity of Assumptions

Closed Population

Radio relocation flights indicated no emigration or mortality of instrumented elk during population estimation flights or in the < 1 hr interval between the passage of the first and second aircraft. One female moved from Unit 31 to Unit 22 prior to the onset of survey flights and remained there throughout the test period. A second female moved southeast from Unit 31 to Unit 32 prior to the onset of the surveys but returned before double-count tests commenced. Another female moved from Unit 22 to Unit 31 and back between replicates in 1989.

A plot of visibility vs. time of day based on radiocollared elk (Fig. 11) indicated that the decision to limit double-survey flights to early morning and late afternoon/early evening hours was justified. This timing allowed population estimation to occur prior to systematic movements of elk into habitat types in which groups had the lowest probability of being visible from the air. The percentage of radio relocations of collared animals in open habitats ranged from 89% (2000-2100 hr) to 4% (1100-1200 hr). The sample size for flight data between 1200-1500 hr was small and results were not conclusive. Elk groups were significantly more visible (chi-square = 5.846, 1 df, $\underline{P} = 0.015$) during evening (1600-2100 hr) than during morning (0700-1000 hr) flights with 62% versus 41% sightability, respectively. Elk sightability in open habitat decreased 50% after 1000 hr. At temperatures of 15 C or higher, sightability greatly decreased

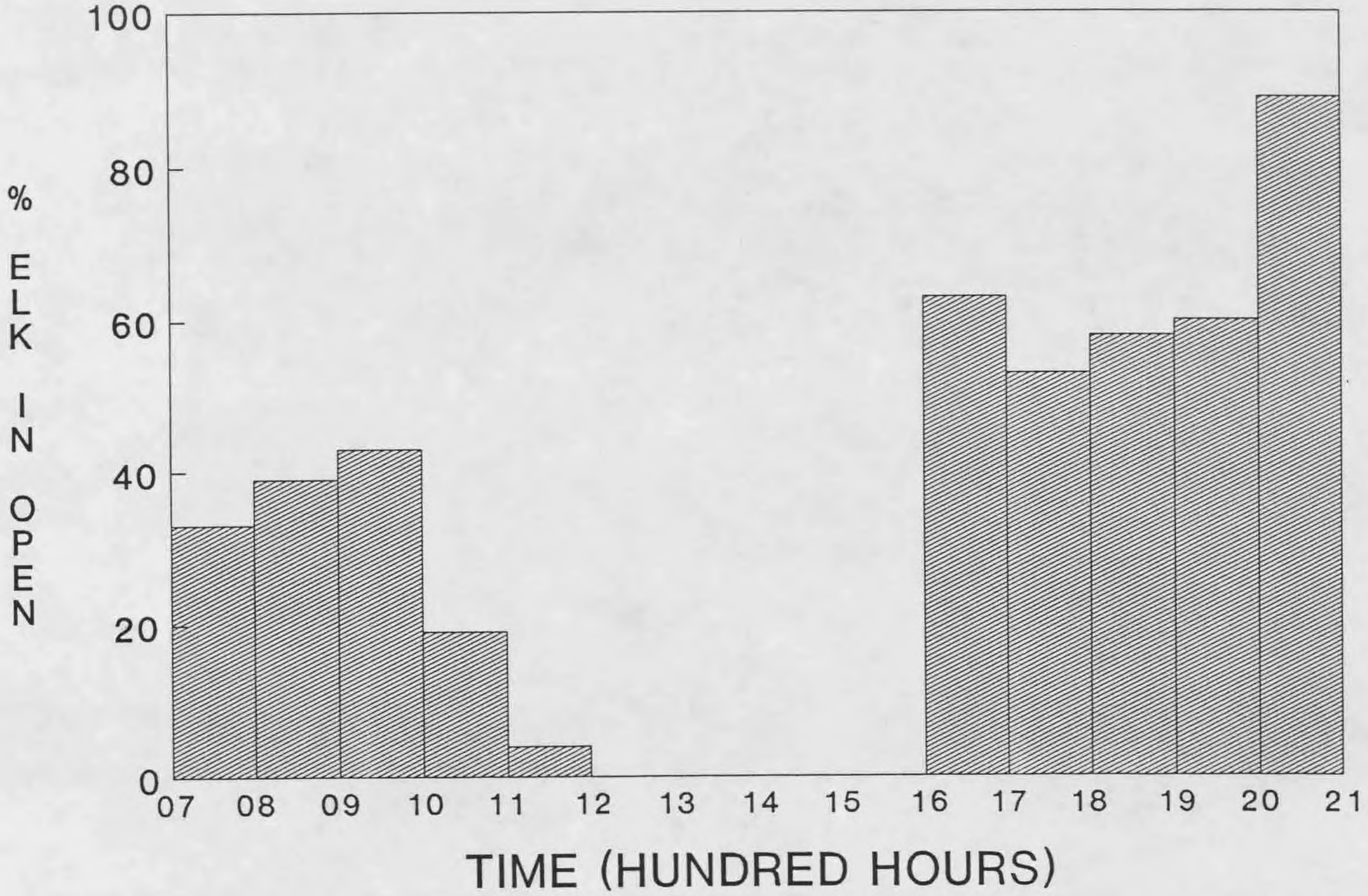


Figure 11. Open habitat use versus time of day of collared elk on the study area, 1988-1989.

after 0900-0930 hr.

All radiocollared animals were sighted on 1 or more relocation flights, and no time or environmental factors sampled had sighting frequencies of 0. Although sightability varied, all segments of the population were potentially available for counts.

I was unable to accurately assess the impact that creation of new groups due to the breakup of groups between the first and second survey flight had on population closure. The brief interval between flights and the relatively low disturbance rate for elk groups noted by the first aircraft during double-survey tests (mean = 23%, range = 15-31%) suggests that the potential for this effect was low to moderate.

Loss and Accuracy of Identifying Marks

The average difference between counts for 258 groups assumed to be identical and seen by both planes in the double-survey tests was 4 elk. There was no significant difference in the size of groups observed by both aircraft ($\underline{t} = 0.424$, df = 257, $\underline{P} = 0.671$).

The percentage of times the first aircraft recorded larger, smaller, and equal group sizes was not significantly different (chi-square = 0.853, df = 2, $\underline{P} = 0.652$) from that of the second plane. The size of groups seen by both planes coincided 32% of the time. The first aircraft recorded larger group sizes 36% of the time while 32% of the groups recorded by the second aircraft were larger.

Population estimates computed for both Unit 22 (Fig. 12) and

31 (Fig. 13) using low group size counts for groups observed by both aircraft differed by 3.5-12.5% from estimates calculated using high group size counts. Of 9 comparisons, only the second survey of Unit 22 in 1989 indicated significant differences ($\underline{Z}$ = 1.648, $\underline{P}$ = 0.099) between estimation methods.

Misidentification of groups due to changes in the location of groups between flights could be influenced by three variables: 1) LORAN-C error; 2) the magnitude of movement of groups between flights; and 3) the mean distance between adjacent groups. If LORAN-C error and movement of groups between flights in double-survey tests proved to be greater than the distance between adjacent groups, accuracy in identification of marks would be greatly reduced. Thirty comparisons of LORAN-C coordinates between aircraft on fixed locations resulted in an error of 0.25 ± 0.13 (SD) km. The average distance moved by collared elk between sequential relocations at 30-60 min intervals (N = 53) was 0.77 ± 0.66 (SD) km. Distance moved estimates likely overrepresented actual movement during survey flights. The average time between sequential relocations of identical elk groups during aerial tracking flights (52 min) was greater than between relocations during double-survey tests (37 min). Mean distances between adjacent elk groups on double-survey flights during 1988-1991 are presented in Table 15.

LORAN-C error plus average distance moved was 1.02 km (95% CI, 0.831-1.189) and was not significantly different from each of 5 estimates of the average distance between groups in Unit 22

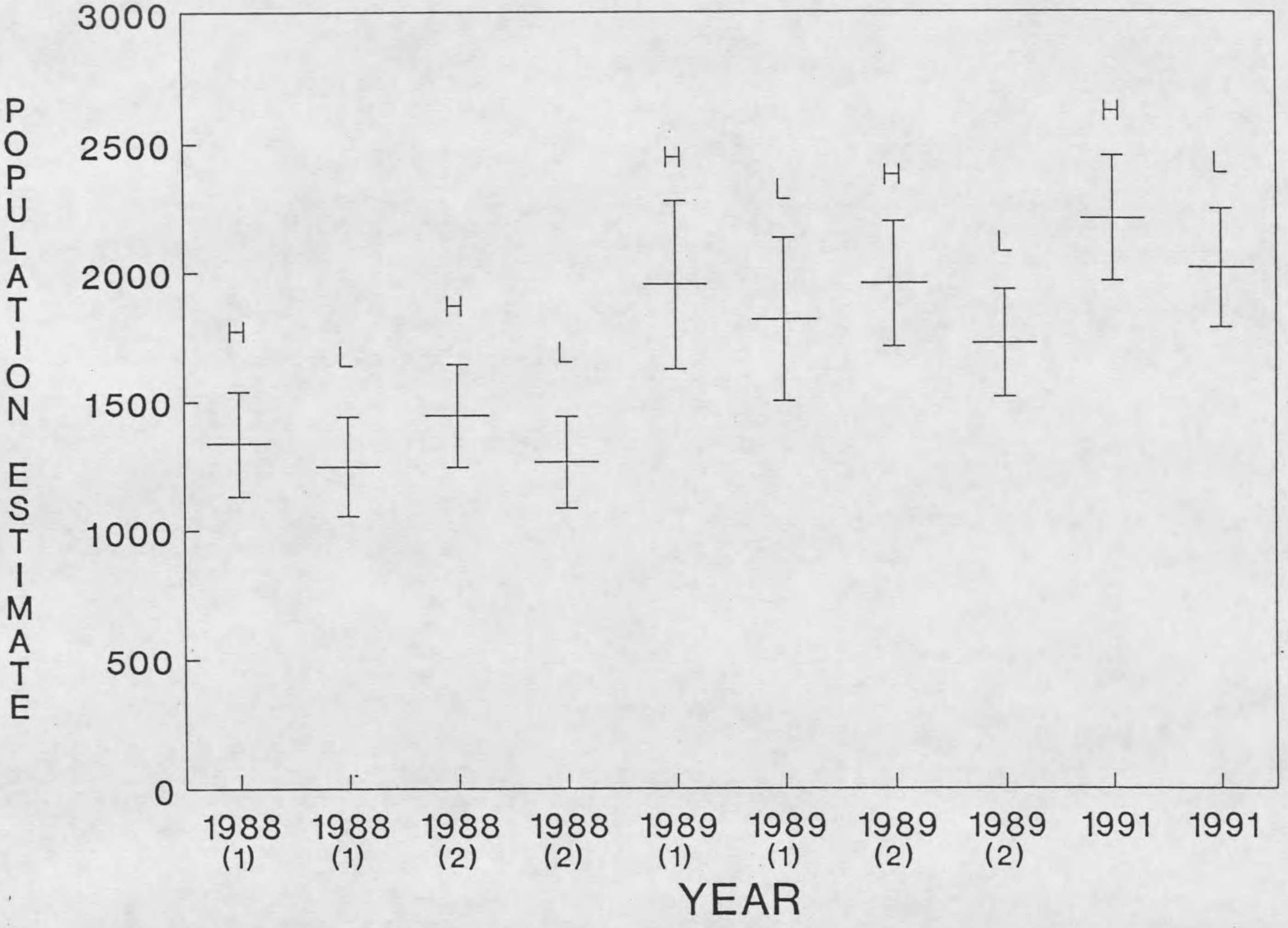


Figure 12. Comparison of population estimates and 90% CI in Unit 22 during 1988-1991 calculated using high counts (H) and low counts (L) for groups seen by both aircraft. Numbers in parenthesis indicate the first and second tests within years.

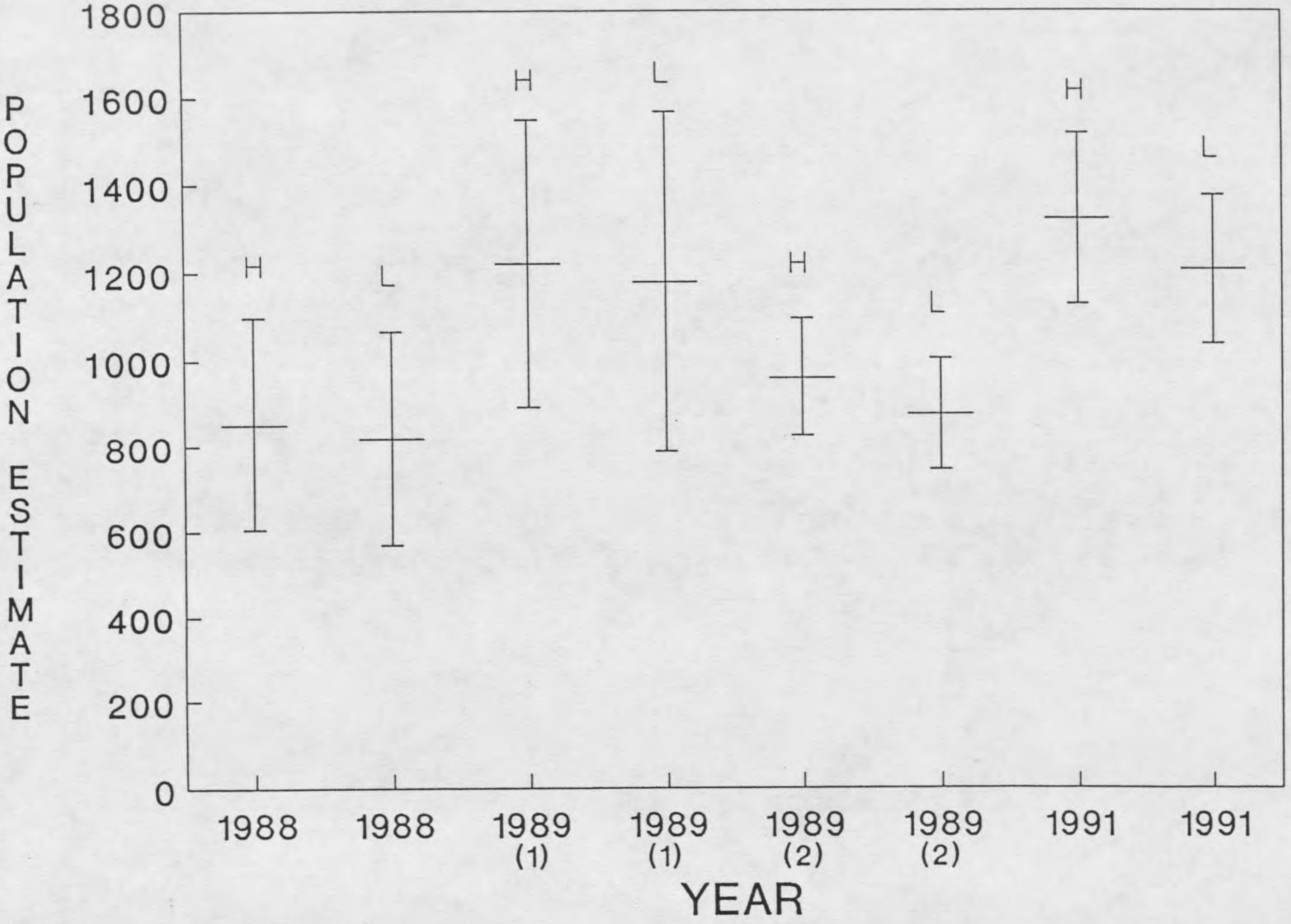


Figure 13. Comparison of population estimates and 90% CI in Unit 31 during 1988-1991 calculated using high counts (H) and low counts (L) for groups seen by both aircraft. Numbers in parenthesis indicate the first and second tests within years.

(0.729 $\leq$ P $\leq$ 0.936) and 4 estimates in Unit 31 (0.646 $\leq$ P $\leq$ 0.751).

Table 15. Mean distance between adjacent elk groups on double-survey flights, 1988-1991.

Unit	Locations	Mean distance (km)	SD
22			
1988-1	96	1.5	2.8
1988-2	163	1.1	1.2
1989-1	155	1.2	1.3
1989-2	170	1.3	1.2
1991	138	1.6	1.7
31			
1988	68	1.8	1.6
1989-1	77	1.6	1.2
1989-2	80	2.0	2.8
1991	98	1.7	1.9

Population estimates calculated using geographic location as the only criterion determining elk groups seen by both aircraft most closely approached population estimates calculated using all criteria (i.e., position, group size, group composition, habitat information, and movement direction) when groups separated by $\leq$ 1 km were considered the same (Tables 16 and 17). Estimates calculated using a distance between positions of 0.25 km as the cutoff for considering groups the same were greater than estimates using all criteria in Unit 22 and Unit 31 by 166-262% and 180-425%, respectively. Estimates calculated using a difference in position of 5.00 km were lower than estimates calculated using all criteria in Unit 22 and Unit 31 by 19-33% and 22-37%, respectively.

Table 16. Double-survey population estimates and 90% confidence limits in Unit 22 calculated with the only criterion determining groups seen by both aircraft being the difference in position (km) on the earth's surface.

Distance criterion (km)	Estimates 1988-1	1988-2	1989-1	1989-2
0.25	2230 ± 914	3527 ± 1737	5121 ± 2684	4735 ± 2187
0.50	1497 ± 312	1783 ± 432	2286 ± 580	2496 ± 598
0.75	1327 ± 183	1353 ± 177	1982 ± 417	2149 ± 403
1.00	1276 ± 269	1328 ± 184	1856 ± 370	2017 ± 336
2.00	1197 ± 199	954 ± 75	1852 ± 633	1644 ± 225
5.00	1087 ± 71	972 ± 0	1319 ± 27	1384 ± 0

Table 17. Double-survey population estimates and 90% confidence limits in Unit 31 calculated with the only criterion determining groups seen by both aircraft being the difference in position (km) on the earth's surface.

Distance criterion (km)	Estimates 1988	1989-1	1989-2
0.25	3622 ± 3579	2493 ± 1455	1734 ± 893
0.50	1385 ± 816	1797 ± 793	976 ± 128
0.75	997 ± 362	1183 ± 295	938 ± 111
1.00	831 ± 209	1145 ± 284	895 ± 99
2.00	891 ± 338	962 ± 157	830 ± 109
5.00	565 ± 0	774 ± 0	751 ± 44

Probability of Being Sighted

A total of 266 radio relocations were obtained for 31 elk (18 females, 13 males) during late winter-spring (February-May), 1988-1990. The percentage of relocations in which groups containing collared animals were seen was calculated for both Unit 22 (Table 18) and Unit 31 (Table 19). All groups were seen in at least 1 flight. The mean probability of sighting a collared elk group for both Units was 66%. The mean probabilities for groups containing collared females (67%) and collared males (63%) were not significantly different (chi-square = 0.408, df = 1, P = 0.523). Sightability was not significantly different for groups with collared young males (≤ 2 years of age) seen 72% of the time and older males (2+ years) with a sightability of 56% (chi-square = 1.920, df = 1, P = 0.166). Groups containing female #4 (4-5 years) and groups containing male #30 (2 years) were each sighted 100% of the time. The lowest probability of sighting (25%) was associated with groups containing female #1 (9+ years) and female #28 (9 years). The lowest sightability for males was associated with groups containing #17 (3 years) and #27 (4 years) with 33%.

Table 18. Sex, age, number of radio locations, and sightability of groups containing collared elk in Unit 22, 1988-1990.

Elk #	Sex	Age[a]	Locations	Sightability(%)[b]
9	F	9	13	69
10	F	7	6	67
11	F	4	7	43
12	F	5	13	62
13	F	3	7	29
14	F	7	8	75
16	F	4	13	62
18	F	6	10	90
21	F	2	10	80
25	F	4	5	80
28	F	8	4	25
29	F	3	4	50
15	M	2	6	83
17	M	3	6	33
19	M	2	7	71
20	M	2	6	67
26	M	4	4	75
27	M	3	3	33
30	M	1	4	100
31	M	1	5	60

[a] Age in 1988.

[b] Percentage of times group containing collared elk was seen.

Table 19. Sex, age, number of radio locations, and sightability of groups containing collared elk in Unit 31, 1988-1990.

Elk #	Sex	Age[a]	Locations	Sightability(%)[b]
1	F	8	12	25
2	F	3	13	92
4	F	4	10	100
5	F	4	7	71
6	F	3	7	86
22	F	6	4	75
3	M	3	11	46
7	M	3	9	67
8	M	3	5	80
23	M	2	3	67
24	M	1	4	50

[a] Age in 1988.

[b] Percentage of times group containing collared elk was seen.

Sightability between Unit 22 and Unit 31 did not vary significantly for groups with collared female elk (chi-square = 1.447, df = 1, P = 0.229) or for groups with collared male elk (chi-square = 0.324, df = 1, P = 0.570). Sightability varied significantly between groups with older males (46%) and younger males (75%) in Unit 22 (chi-square = 3.285, df = 1, P = 0.070). The mean probabilities of sighting a group containing a collared elk in 1988 and 1989 were 68% and 62%, respectively, and were not significantly different (chi-square = 0.959, df = 1, P =0.328).

Survey Flight Independence

The influence of aircraft 1 on the second plane was reduced by conducting flights at different altitudes, allowing pilots to choose routes within predetermined search areas, and minimizing radio contact between planes. In individual survey flights, 8-33% of elk groups were disturbed. Disturbance rates of elk groups (Table 20) were not statistically different for each aircraft ($t = -0.342$, df = 8, $P = 0.741$), but movement directions following disturbance (Table 21) were not random (chi-square = 18.32, df = 3, $P < 0.001$). Elk disturbed by planes generally moved toward forested areas where they would be less visible.

Table 20. Disturbance rate of elk groups seen only by plane 1 or only by plane 2 on double-survey flights, 1988-1991.

	% of groups distubed	
Survey area (Year)	High plane	Low plane
Unit 22 (1988)	24 (N=63)	23 (N=39)
Unit 22 (1989)	26 (N=80)	26 (N=90)
Unit 22 (1991)	21 (N=24)	16 (N=25)
Unit 31 (1988)	31 (N=16)	33 (N=21)
Unit 31 (1989)	21 (N=34)	19 (N=54)
Unit 31 (1991)	15 (N=26)	8 (N=13)
Total	23 (N=243)	22 (N=242)

Table 21. Percentage of elk moving by direction on double-survey flights in 1988-1991.

	Movement direction of disturbed elk(%)			
Survey area	N-E	E-S	S-W	W-N
Unit 31-East	34	11	8	47
Unit 31-West	29	21	14	36
Unit 22-East	45	12	12	32
Unit 22-West	28	31	21	21
TOTAL	38	16	13	33

Factors Influencing Sightability

Environmental Factors

Sightability was not affected consistently by degree-days. The number of degree-days in Unit 22 in 1988 ranged from 358-401 between April 2 and 5 (first test) and 491-516 between April 11-

12 (second test). Average group size decreased 46% and the number of groups increased 76% between double-survey tests. The first (April 10-11) and second survey (April 16-17) in 1989 were conducted at degree-days of 366-384 and 512-532, respectively. A 6% decrease in group size and a 10% increase in the number of groups were recorded.

The single survey flight (March 31) in Unit 31 in 1988 was conducted at 327 degree-days. Total degree-days ranged from 405 to 427 for the first (April 12) and second (April 13) survey of Unit 31 in 1989, respectively. Group size decreased 16% while the number of groups did not change.

The influence of weather, vegetative cover, terrain, and aspect on the sightability of 226 groups of elk containing collared animals is presented in Table 22. Time of day, covered in the section on validity of assumptions, also influenced visibility (Fig. 11), primarily through the negative relation between elk use of open habitats and daylight intensity.

Sightability was significantly influenced by weather (chi-square = 9.173, df = 3, $\underline{P} = 0.027$). Elk groups were most visible under mostly cloudy weather conditions (83%). Sightability when overcast conditions prevailed ranked second (63%), followed closely by partly cloudy (61%) and clear (59%) conditions.

Cover type played a prominent role in sightability (chi-square = 61.30, df = 3, $\underline{P} < 0.001$). Elk groups in open grasslands had the highest sightability (99%). Sightability dropped to less than 45% when animals were in timber.

Table 22. Influence of variables on sightability of groups containing radiocollared elk in Units 22 and 31 in 1988-1991.

Variable	Radiocollared animals located	seen	%
Weather			
Clear	76	45	59
Partly Cloudy	46	28	61
Mostly Cloudy	53	44	83
Overcast	51	32	63
Cover			
Grass	78	77	99
Timber	96	41	43
Shrub	52	31	60
Terrain			
Ridgetop	53	45	85
Sidehill	102	67	66
Bottom	42	17	40
Flat	29	20	69
Aspect			
N-E	28	12	43
E-S	11	11	100
S-W	22	16	73
W-N	18	6	33

Sightability differed significantly with terrain type (chi-square = 20.73, df = 3, $P < 0.001$). Animal groups were most visible on ridgetops (85%) and less likely to be seen on flat terrain (69%) or hillsides (66%). Elk were seen least often in bottoms or draws (40%).

On flights in which aspect was recorded, aspect significantly influenced sightability (chi-square = 16.91, df = 3, $P < 0.001$). Elk located on E-S aspects had the greatest sightability (100%) while elk groups found on W-N aspects were least visible (33%).

Observer Factors

The 3 primary observers did not differ in ability to locate elk groups during double-survey flights. Primary observer MWS located an average of 400 elk in 24 groups per flight, and primary observer TCF located an average of 386 elk in 22 groups on flights with both observers participating (N=14). The average number of elk ($\underline{t}$ = 0.493, df = 13, $\underline{P}$ = 0.630) and the average number of elk groups ($\underline{t}$ = 0.823, df = 13, $\underline{P}$ = 0.426) did not differ statistically between observers. The distribution of sightings reported by different observers among group-size intervals (Fig. 14) also was not significantly different (chi-square = 5.572, df = 6, $\underline{P}$ = 0.472).

The average number of elk ($\underline{t}$ = -0.620, df = 6, $\underline{P}$ = 0.558) and the average number of groups ($\underline{t}$ = -1.448, df = 6, $\underline{P}$ = 0.198) located by observers TCF and WLB on flights with both observers (N=7) were not statistically different. TCF located an average of 370 elk and 25 groups and WLB an average of 345 elk and 21 groups. The distribution of sightings among group-size intervals (Fig. 15) also was not significantly different (chi-square = 1.284, df = 6, $\underline{P}$ = 0.972).

Elk sightability did not differ between the first and second aircraft. Observers in plane 1 located an average of 385 elk and 24 groups per flight, and observers in plane 2 observed 369 elk and 23 groups. The average number of elk ($\underline{t}$ = 0.753, df = 21, $\underline{P}$ = 0.460) and the number of groups ($\underline{t}$ = 0.415, df = 21, $\underline{P}$ = 0.683) located by each aircraft were not statistically different. The distribution of sightings among group-size classes (Fig. 16) was not significant (chi-square = 1.987, df = 6, $\underline{P} = 0.921$).

Observer fatigue, analyzed by determining the percentage of groups seen per one-third segments of double-survey flight time, did not significantly influence sightability (chi-square = 1.743, df = 2, $\underline{P} = 0.417$) on evening flights. In the first one-third of flight time, 31% of all groups were sighted. A total of 35% of groups were seen on the second and 34% on the final third of double-survey flights. There was a significant difference (chi-square = 16.07, df = 2, $\underline{P} < 0.001$) among the percentage of groups seen per flight segment on morning surveys. A total of 42%, 29%, and 29% of groups were sighted on the first, second, and final one-third of flight time, respectively.

Multiple Factor Influence

Logistic regression analysis indicated that group size ($\underline{P} < 0.001$), temperature ($\underline{P} = 0.014$), and topography ($\underline{P} = 0.029$) were significantly related to sightability of groups seen by both aircraft. Wind, clouds, time, vegetative cover, and aspect variables were not significant. The model developed to predict sightability (u) is:

$$\begin{aligned} u = {} & -1.3565 + 0.0338(\text{group size}) + 0.0135(\text{temperature}) \\ & + 0.1750(\text{ridge}) - 0.5590(\text{sidehill}) - 0.2036(\text{bottom}) \\ & + 0.0885(\text{flat}). \end{aligned}$$

Model coefficients indicated that the probability of sighting an elk group on both replicates increased with larger values for group size and temperature, and with locations on ridge and flat topography. Sightability decreased with elk groups observed on sidehill and bottom terrain.

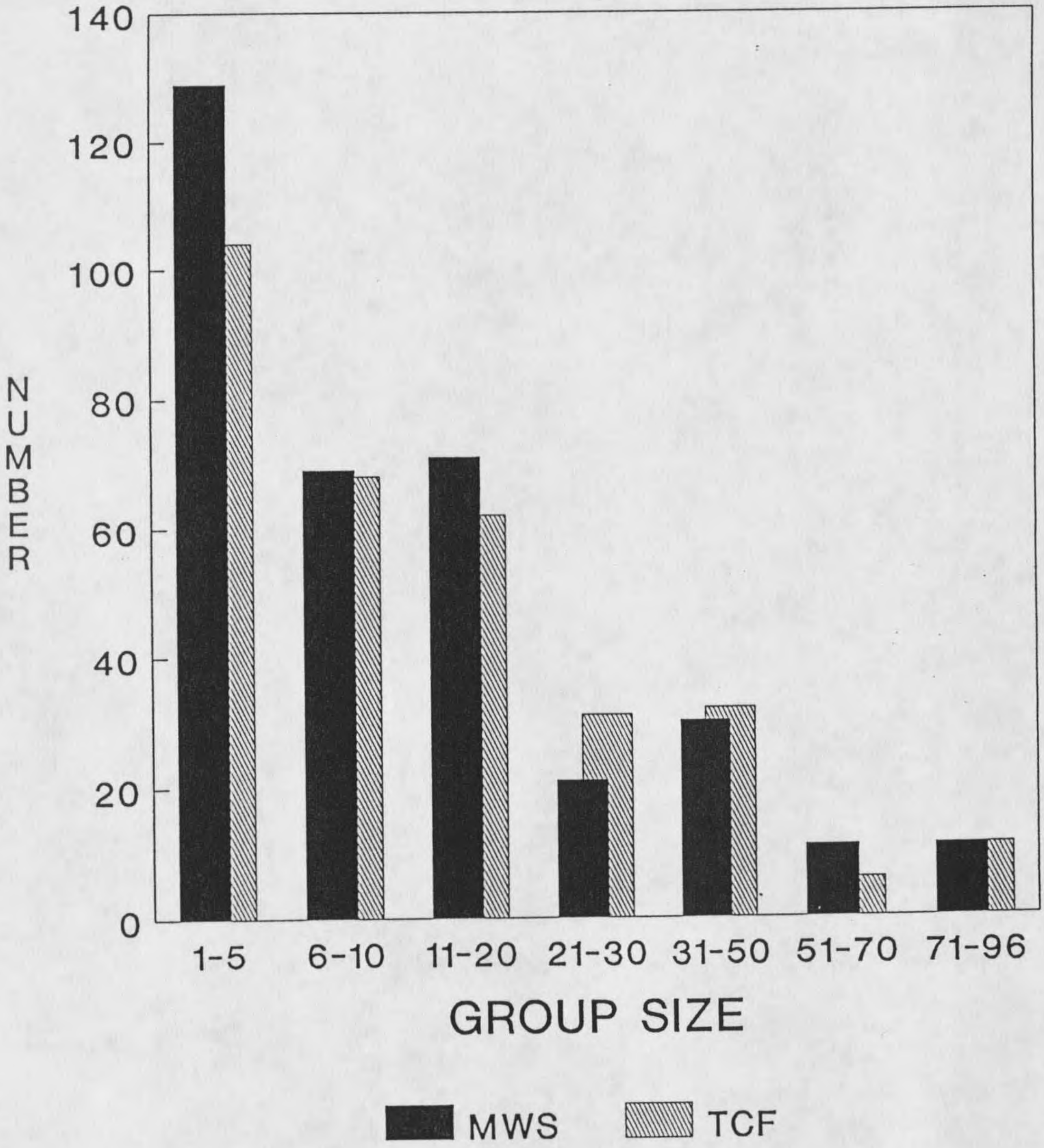


Figure 14. Number of elk groups seen by group-size interval by primary observers (MWS and TCF).

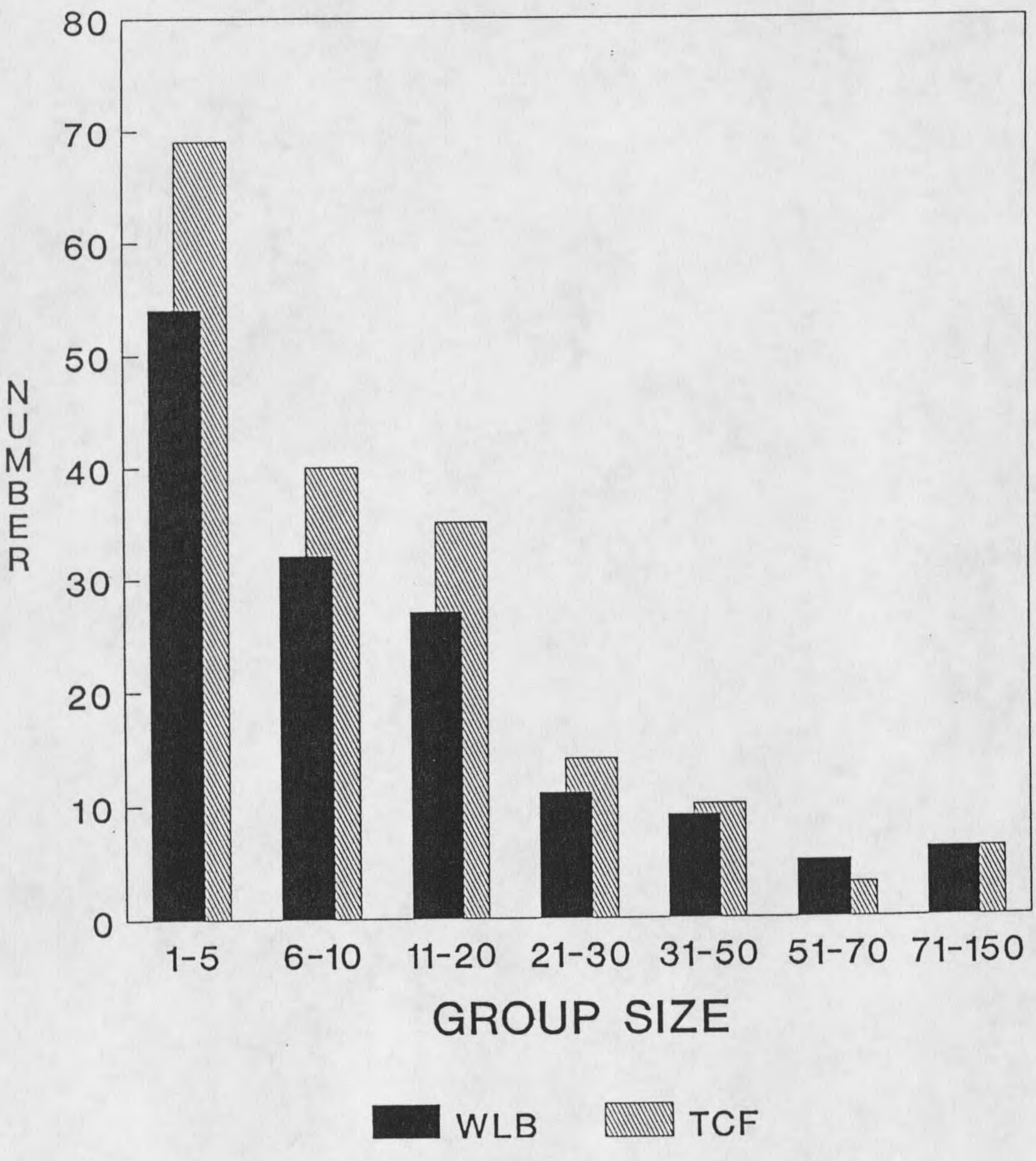


Figure 15. Number of elk groups seen by group-size interval by primary observers (WLB and TCF).

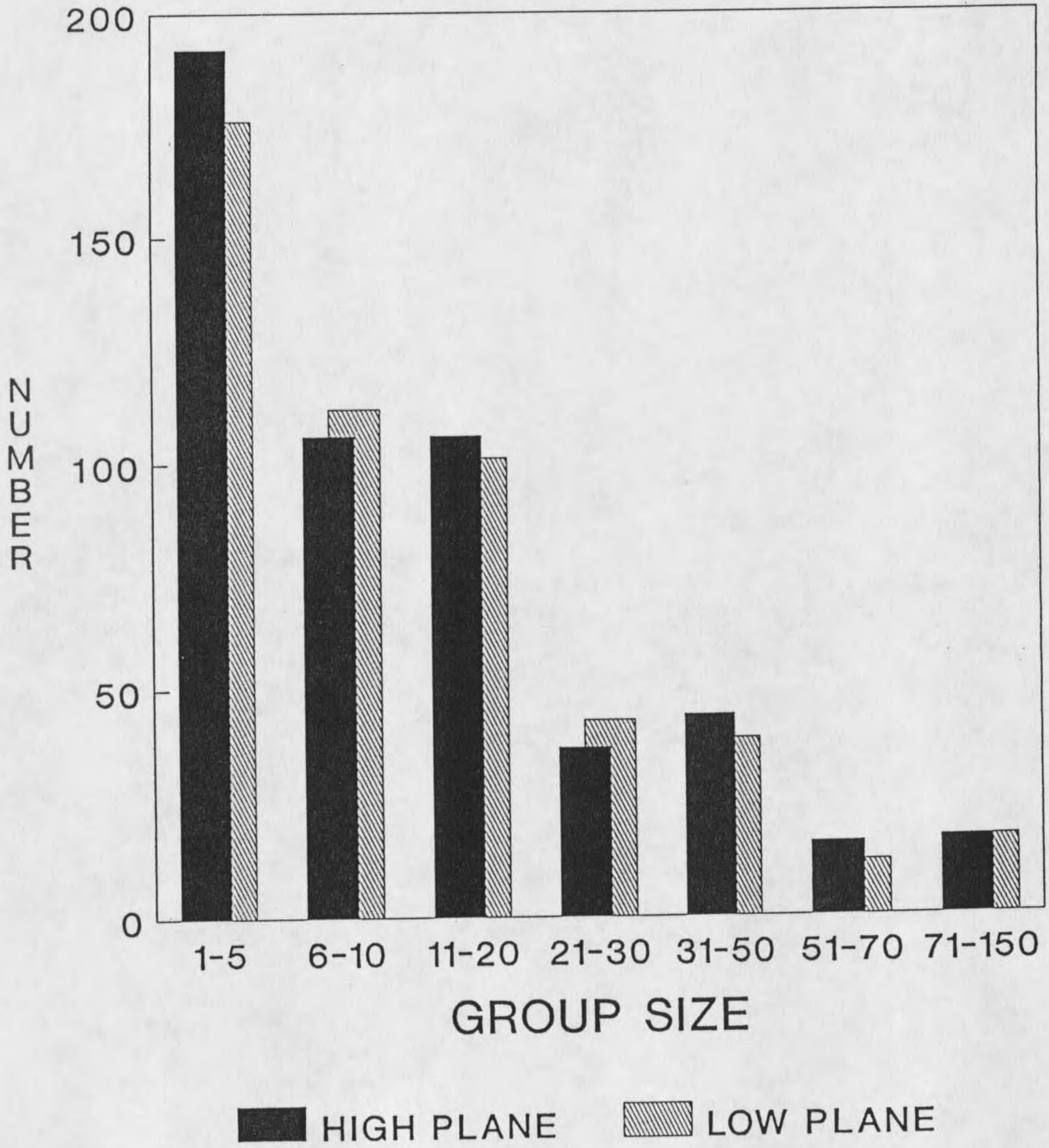


Figure 16. Number of elk groups seen by group-size interval by primary observers in the high (first) and low (second) aircraft during double-survey flights, 1988-1991.

DISCUSSION

Elk Ecology

In northern temperate environments, elk migrate between summer and winter ranges in order to avoid the hardships of snow accumulation. As habitat available for exploitation expands in spring, populations disperse across available range. Travel routes used during spring migration are typically referred to as transition range (Adams 1982). Sampling during this study occurred in spring and, as expected, elk were distributed throughout much of the study area. Highest densities on transition range were observed on both the west and east portions of Unit 22 and the northwest of Unit 31. Little expansion in areas utilized in spring occurred between years in Unit 22. However, observed densities on the west side of the Unit increased each year of the study. Some expansion of areas utilized in Unit 31 occurred with greater use of the east side in both 1989 and 1991. Transition range was used by some elk during all seasons.

The primary stimulus influencing the timing and rate of spring migration from lower to higher elevations is the availability of succulent forage during greenup (Adams 1982). During this study, many elk utilized new plant growth on winter range prior to migration. Peak numbers of elk on transition range were observed during April and May. The extent to which elk used spring range varied among years. Transition range received the least use when severe weather delayed elk from leaving winter ranges in 1989. Similar elk migratory patterns were documented by Knight (1970) and Craighead et al. (1972).

Radiocollared elk exhibited a preference for timber and an avoidance of grassland/sagebrush cover types during March-May. Open cover types were important feeding sites but were used primarily during early morning and early evening hours. Other studies have documented a spring preference for habitats that supply early succulent forage (Knight 1970, Irwin and Peek 1983, Unsworth 1990). Skovlin (1982) indicated a heavy preference for timber was related to human activity associated with high road densities and logging activity, protection from the elements, and the availability of succulent forbs. The selection of timber in this study was likely related to the need for security rather than thermal cover.

With the progression of greenup and spring migration, elk become more mobile with group sizes decreasing and the number of groups increasing. The mean size of groups containing collared elk declined during spring with the greatest decrease occurring between March and April. Other studies have identified calving activity, migration, and a shift in forage use from grass to forbs as reasons for the breakup of large groups and the increase in use of forested types (Knight 1970, Skovlin 1982).

Knight (1970) observed the largest mean group size for the Sun River elk herd in January followed by slight declines in February and March. A sharp decrease in mean group size occurred during April-June.

Male survival rates were similar to those found by Unsworth and Ferguson (1990) in north-central Idaho in the roaded portion of the Lochsa study area (lx = 0.45). Female survivorship was lower than that measured in north-central Idaho (lx = 0.93). Unlike this study, a large portion of the Lochsa study area was closed to the harvest of antlerless elk.

Double-Survey Technique Tests

The double-survey technique proved to be much less expensive than other commonly used census techniques for elk. The sightability technique of Samuel et al. (1987) had an average cost of $16,993 for helicopter rental per elk survey of Unit 12 (3100 km^2) in north-central Idaho during 1985-1988 (Unsworth and Kuck 1988). The survey area in north-central Idaho was 20% smaller than the double-sample study area. Mark-resighting techniques (assuming a sample of 200 marked animals at a cost of $144 per elk) would require an investment of approximately $28,800 for trapping, helicopter rental and equipment to census Units 22 and 31. Intensive labor required for restraint and handling of animals could increase the cost to census the study area to $70,000 (assuming a sample of 200 marked animals at $350 per elk) (Bear et al. 1989). The double-survey technique had an average cost for aircraft rental of $2430.75 per survey (both Unit 22 and 31 combined) during 1988-1991. These costs included post-survey aerial relocations of collared elk which could be eliminated for management purposes, saving an additional 10-20%.

Savings on census methods are useless unless the technique can be demonstrated to provide valid population estimates. The accuracy of surveys can be evaluated by comparison against a population of known size, replicabilty, precision, comparison against a method with proven accuracy, and biological feasibilty. Enclosed populations of free-ranging animals of known size are rare, but I was able to compare double-survey estimates against a sightability model (Samuel et al. 1987) and trend counts to assess consistency in replicate tests. Consistency and precision (coefficients of variation) of estimates have been used as indicators of accuracy in other studies. However, Roff (1973) and McCullough and Hirth (1988) cautioned against dependence on precision in validating techniques due to the positive correlation between population size and standard error.

In Unit 22, estimates were consistent with no significant differences detected between replicates within a given year. Estimates from multiple surveys in 1988 and 1989 were within 8% and 1% of one another, respectively. Unit 31 was sampled twice only in 1989. The second replicate was 16% lower than the first. Maximum dissimilarities occurred on the west portion of the Unit with estimates on the first survey 30% greater than in the second survey. The gently rolling, featureless sagebrush/grassland terrain in the western part of Unit 31 likely resulted in missed area by one or both planes in the second survey thereby biasing results. The larger estimate of 1,224 elk obtained in the first survey appeared to be the most accurate. Coefficients of variation were low (4-11%) for all surveys in both units.

The helicopter sightability estimate for Unit 31 in 1988 was not significantly different from the double-survey estimate. In 1991, estimates for Unit 22 obtained from the 2 techniques were significantly different. The double-survey estimate for 1991 was likely to be more valid than the helicopter sightability estimate since the number of elk seen during the double-survey was 241 elk greater than the population estimate for the sightability model. Coefficients of variation for the double-survey technique were slightly lower than those calculated using the sightability technique in both comparisons.

Changes in population size within Units between years indicated by double-survey estimates were biologically feasible, but not all were reasonable. The increases in the population suggested by estimates in Unit 22 (35-46%) in 1988 and 1989 and that suggested by comparing the high 1989 estimate for Unit 31 with the 1988 estimate (43%) were unlikely. The population increases were not a result of greater visibility of elk groups. Sightability of groups containing collared elk in 1988 was not significantly different than in 1989. The calculated value for rate of growth per individual ($\underline{r} = 0.34$) between 1988 and 1989 in

Unit 22 was comparable to values determined for elk populations exhibiting rapid increase following introduction into unoccupied areas, 0.29-0.37 (Murphy 1963, Caughley 1970, Burris and McKnight 1973, Gogan and Barret 1987, McCorquodale et al. 1988). High rates of increase should only be achieved when plant biomass is available in quantity and quality in excess of maintenance needs and with substantial reproduction by 2-year-old and yearling females (Eberhardt 1985). Female:calf:male ratios and recruitment rates were not available, but the study area supported an established elk population, relatively stable land use pattern, and harvest and estimated survival rates suggest a low likelihood of dramatic increases in population size.

The apparent 40% increase represented by mean estimates may be unrealistic, but an increase within confidence intervals for both years is feasible. A 90% confidence interval implies the actual population estimate will be included in the confidence interval 90% of the time. A significant population increase may have been detected, but actual growth may be smaller than that indicated by mean estimates. Differences in upper values of confidence intervals calculated in 1988 and lower values of intervals computed in 1989 varied by 4-11%.

Trend counts for Unit 22 exhibited similar growth patterns to double-survey estimates. The overall intrinsic rate of growth ($\underline{r} = 0.11$) calculated for 1983-1991 represented a moderate increase in population size. Trend counts were not available for Unit 31 prior to 1988.

Validity of Assumptions

Empirical tests of a census technique may indicate it has utility, but validity of the assumptions inherent in the model from which the technique was derived should be demonstrated before the technique is accepted as a management tool. I found that all of the assumptions associated with the double-survey technique were not met or only partially met.

Closed Population

The assumption of population closure was not met. The short interval (30 min) between replicates and restrictions on survey timing to periods when elk were most likely to be observed in open habitat (i.e. flights conducted during early stages of greenup during early morning and evening hours) reduced the possibility of losses or gains of individual animals to the visible population to low levels. These restrictions could eliminate a significant portion of the problems associated with population closure but do not address the failure of closure due to changes in size, number, and location of groups between the first and second survey flight. I was unable to accurately assess the extent to which these factors influenced population closure, but a small (group size and number) to moderate (group location) change did occur between flights.

Loss and Accuracy of Identifying Marks

The assumption of no loss of marks and absolute accuracy in identifying marks was also not met. Misidentification of marked groups (groups sighted on the first flight of the survey) due to changes in group size was a minor problem. The double-survey technique was not sensitive to the use of high versus low counts in groups seen by both aircraft. Estimates in all but 1 of 9 cases were not significantly affected by differences in counts of group size. The larger group count was judged more accurate due to the tendency to undercount animals in clumped groups, particularly in timbered habitats (Graham and Bell 1989).

Identification of marked groups was sensitive to group size and distribution. A large number of small groups positioned closely together increased the likelihood of misclassifying marked elk groups as unmarked and tended to inflate estimates. This situation was analogous to double-sample simulations conducted by Eberhardt and Simmons (1987) which consistently biased estimates upward. Other mark-recapture techniques also tend to overestimate true population size when marked animals are incorrectly identified (White et al. 1982, McCullough and Hirth 1988, Bear et al. 1989).

Group movement between the first and second survey flights produced a major source of error. The LORAN-C system used to record the locations of elk groups was reasonably accurate, but when the average LORAN-C error (0.25 km) was combined with the average movement of groups (0.77 km) it closely approximated the average distance between groups during some surveys (1.1-2.0 km) making accurate identification of marked groups impossible. A refinement of techniques to insure each aircraft follows identical procedures when taking LORAN-C readings of elk group positions may further reduce some of this source of error. The LORAN system has been used effectively in locating position in biological research along coastal landscapes (Patric et al. 1988) and as a navigational aid in aerial surveys (Boer et al. 1989). However, accuracy is reported to decrease as distance from radio transmitters increase. Results from this study offer promise for the future applications of the LORAN-C system in biological research.

Probability of Being Sighted

The assumption of probabilities of sighting elk groups greater than 0 was met. Sighting probabilities for instrumented elk (and the group with which it was associated) ranged from 25-100%. The mean probability of sighting an instrumented animal (66%) via fixed-wing aircraft was similar to helicopter surveys of white-tailed deer (DeYoung 1985), mule deer (Bartmann et al. 1987), and elk (Bear et al. 1989).

However, the validity of this assumption is questionable. One critical assumption underlying many mark-recapture models is that the probability of sighting an animal is constant. Magnusson et al. (1978) indicated that if the probability of seeing an object approximated a beta distribution, heterogeneous sightability would not bias estimates if the 2 surveys were independent of each other. Using this approach, the assumption of equal catchability can be replaced by the assumption that each elk must have a finite chance of being seen during surveys.

Burnham (1972) demonstrated problems inherent in this model as a result of estimating parameters from a probability distribution. If particular entities are difficult to see by both observers, negative bias will occur (Pollock and Kendall 1987). Simulations performed by Caughley and Grice (1982) determining the effect of correlation between simultaneous tandem observers indicated estimates were often biased low by ≥ 10%.

If the assumption of finite probabilities of sighting is invalid, the assumption of equal catchability would apply. Constant sightability is unlikely in wild populations. Otis et al. (1982) demonstrated that heterogeneity of capture probabilities results in an overestimation of the actual proportion of marked animals causing considerable negative bias to estimates. Munholland (1991) indicated that variable sightability in this study could result in an underestimation of the number of groups and an overestimation of the average group sizes. Bartmann et al. (1987) and Bear et al. (1989) found heterogeneous sighting probabilities in mark-recapture studies did not bias estimates but did produced an underestimate of variance.

Sightability during this study was not constant. Sightability on radio relocation flights was dependent on time of day, weather, vegetative cover, terrain, and aspect. Few consistent differences were detected among sexes, age classes, and Management Units. LeResche and Rausch (1974) found sightability to be influenced by observer experience and currentness, number of observers, snow conditions, habitat and terrain, and time of day.

Group size, temperature, and topography were major factors influencing the probability of sighting an elk group on both replicates during double-survey tests. Large groups, moderate temperatures, and ridgetop topography favored sightings. Observer experience did not consistently affect sightability. Statistical differences detected as a result of observer fatigue on morning flights were the result of a decreased use of open habitat by elk groups during latter portions of flight time. Estes and Jameson (1988) found activity and group size affected sightability of sea otters by both survey teams during simultaneous double-survey shore-based counts. Group size and flying height influenced visibility of feral horses and donkeys during simultaneous aerial double-counts by tandem observers (Graham and Bell 1989). Samuel et al. (1987) cautioned against the use of univariate analysis to determine sightability due to the tendency to inflate the number of factors affecting visibility. They determined that sightability of elk was significantly influenced by group size and vegetative cover but not significantly affected by snow cover, search rate, animal behavior, and different observers.

I adjusted the model to reduce the effects of variable sightability bias by stratifying data on the basis of group sizes with similar probabilities of being recaptured by the second aircraft in the survey. A more suitable model could involve stratification with more criteria than just group size (Munholland 1991). Additional adjustments to the model and/or more stringent restrictions on survey timing could minimize the effects of weather and habitat variables.

Survey Flight Independence

The assumption of survey flight independence was violated but was probably a minor source of error compared to misidentification of groups. Although independence was maximized by allowing pilots to independently select flight patterns within the study area and minimizing radio contact between aircraft, the disturbance rate of 15-31% of the groups sighted by the first plane resulted in changes in group size and/or location in some groups. Munholland (1991) indicated that this violation could influence the correct identification of marks by the second plane and/or contribute to the loss of marks. Misidentification of marks results in a biased estimate of N. This violation would be analogous to a trap response in which the capture probability changes after the first capture (White et al. 1982). Bias from this source could be reduced by developing a model allowing capture probabilities to differ between the first and second survey flights (Seber 1982).

Other Factors Influencing Sightability

The optimum period for double-survey flights varied from year to year. Based on 3 years data, an acceptable "survey window" appears to exist in north-central Idaho when 300-500 degree-days have accumulated. Optimum conditions occurred in the range of 300-400 degree-days in 1988 and 1989. Degree-day data indicated an earlier initiation of greenup in 1988 but a faster rate of progression in 1989. Unit 31 exhibited signs of greenup prior to Unit 22 due to lower elevations.

The "survey window" was associated with the relationship between degree-days, greenup, and elk response to greenup. Elk congregate in large groups on open areas during spring in response to temperature and snowmelt conditions affecting the emergence of new vegetation (Skovlin 1982). With the progression of greenup, elk become more mobile, group sizes decrease and the number of groups increase. Calving activity and a shift in forage use from grass to forbs possibly precipitates the breakup of large groups and the increase in use of forested cover types (Knight 1970, Skovlin 1982).

Group size, use of topography, and temperatures under which flights are conducted can be partially controlled by timing surveys with specific environmental conditions. Flights performed within the "survey window" will maximize the accuracy and precision of estimates by increasing the probability of groups being observed by both aircraft. Large groups were recaptured at much greater frequencies than small groups by the second aircraft during double survey flights. A minimum of model correction for groups seen by only 1 plane would occur if the majority of groups were observed by both planes.

Double-sample population surveys in 1988 were performed 7-10 days following the optimum "survey window". A large decrease in mean group size and increase in the number of groups between the first and second survey of Unit 22 indicated that the breakup of large groups began in March.

Greenup conditions present during double-survey population estimation tests in 1989 were near ideal. Changes in the number of groups and the average group size detected between multiple surveys of both Units were minor.

MANAGEMENT IMPLICATIONS

Empirically, the double-survey technique yielded relatively consistent and biologically feasible population estimates over the period of this study. The results compared favorably with those obtained from the helicopter sightability model, at 1/7 the cost. However, the validity of all 5 assumptions outlined by Magnusson et al. (1978) is questionable. Deviations from assumptions related to closed population, probability of sighting, and independence could be minimized by revisions in techniques or in analysis, but the ability to correctly identify which elk groups were seen by both aircraft in the survey is doubtful.

If the empirical results I saw indicate an underlying consistency associated with the technique that exists independent of the original model, further testing may be justified. If additional testing is done, I recommend validation of the revised model against a controlled population of known size. Removal of a specific number of animals from the known population would provide a more accurate measure of the ability of the technique to statistically detect changes in the population.

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