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Aerial survey estimates of fallow deer abundance

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Reliable estimates of the distribution and abundance of an ungulate species is essential prior to establishing and implementing a management program. We used ground surveys to determine distribution and ground and aerial surveys and individually marked deer to estimate the abundance of fallow deer (*Dama dama*) in north-coastal California. Fallow deer had a limited distribution at heterogeneous densities. Estimated post-rut densities across 4 annual surveys ranged from a low of 1.4 (SE = 0.2) deer/km^2 to a high of 3.3 (SE = 0.5) deer/km^2 in a low density stratum and from 49.0 (SE = 8.3) deer/km^2 to 111.6 (SE = 18.7) deer/km^2 in a high density stratum. Sightability was positively influenced by the presence of white color-phase deer in a group and group size, and varied between aerial and ground-based observers and by density strata. Our findings underscore the utility of double-observer surveys and aerial surveys with individually marked deer, both incorporating covariates to model sightability, to estimate deer abundance.

Key words: abundance, aerial surveys, California, *Dama dama*, density estimation, fallow deer, Point Reyes National Seashore

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Fallow deer (*Dama dama*) are a widely distributed cervid species as the result of introductions throughout the world (Chapman and Chapman 1980). Four color variants of the species, including white, were introduced to the Point Reyes Peninsula, California, in the 1940s (Wehausen and Elliott 1982). Culling by agency personnel replaced sport hunting as a means of population control in the early 1970s when the National Park Service asserted management authority over deer within the newly created Point Reyes National Seashore (PRNS) (Gogan et al. 2001). The population numbered an estimated 500 to 600 animals of four color variants by the late 1970s (Wehausen and Elliott 1982) and early 1980s (Gogan et al. 1986). However, culling ceased in the mid-1990s (Gogan et al. 2001) and only one or two per year have been removed since that time (N. Gates, unpublished data). Deer numbers and distribution were thought to have increased in the absence of culling. With lead management authority for fallow deer at PRNS, the National Park Service opted to assess adaptive management alternatives for the population, including culling. Successful adaptive management of fallow deer at Point Reyes requires accurate and precise estimates of population abundance and distribution. We employed a multiple-phase sampling strategy to assess the abundance of fallow deer at Point Reyes between June 2000 and January 2004. We used preliminary ground surveys to determine the distribution of fallow deer and delineate count units and strata. We then obtained a mark-resight dataset by conducting simultaneous ground and aerial surveys in 2000 and 2001. In 2003 and 2004 we captured and radio-marked deer and recorded mark-resight observations via aerial surveys in each year utilizing the radio-marked deer. We then developed a combined mark-resight model with sightability correction covariates for individual deer groups to analyze the data from these multiple surveys and sources and produce corrected statistical population and precision estimates.

Study Area

The 218 square kilometer (km^2) Point Reyes Peninsula (38°42’48” N, 122°52’30” W) is located in Marin County, approximately 60 km north of San Francisco, California and extended about 40 km northwest along the California coastline (Figure 1). Inverness Ridge, at a maximum height of 428 m, forms the backbone of the Point Reyes Peninsula with elevations descending to sea level. The Mediterranean climate of the area was characterized by cool

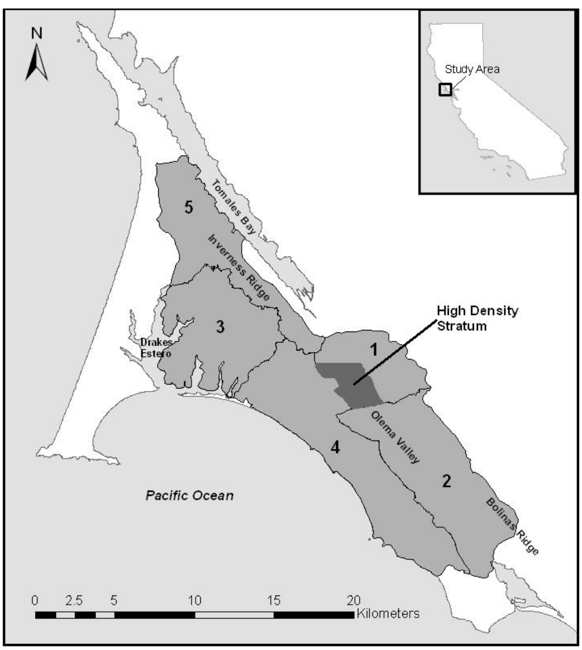

Figure 1.—Fallow deer distribution determined by ground surveys between June 2000 and September 2002 and aerial survey units at Point Reyes, Marin County, California.

wet winters and warm, drier summers (Weber 1981) with annual ambient temperatures rarely below 4.5° C or above 32.5° C. However, summer temperatures were strongly influenced by low-lying fog and strong north-westerly winds (20–35 kph) in coastal areas (Barbour et al. 1973). Most precipitation was in the form of rainfall and the Inverness Ridge exhibited an orographic effect that resulted in precipitation levels double that along the shoreline (Brown et al. 1999).The area supported a mosaic of low growing coastal scrub and prairie (Heady et al. 1977, Kuchler 1977) converted to open grassland at lower elevations (Elliott and Wehausen 1974, Shuford and Timossi 1989) intergrading to a 1.5–2.5-m tall scrub type (Shuford and Timossi 1989) at mid-elevations. Higher elevations supported a closed canopy conifer forest interspersed with grassland openings (Shuford and Timossi 1989). Native black-tailed deer (*Odocoileus hemionus*) were widespread throughout the area and non-native axis deer (*Axis axis*) were sympatric with fallow deer northwest of Inverness Ridge. Domestic cattle utilized areas to the north and northwest of Inverness Ridge and throughout the Olema Valley.

Materials and Methods

Distribution and density strata.—We determined the fallow deer distribution at Point Reyes by recording the locations of all deer groups sighted from a network of trails between June and December 2000 and set the boundaries of distribution at the point where observers estimated that densities were $<1/km^2$. We confirmed the overall fallow deer distribution during a survey of the area by helicopter in December 2000. We classified the distribution into one high density and 5 moderate density survey units using readily detectable features such as ridgelines and roads to delineate survey unit boundaries (Figure 1).

Double sampling with aerial and ground surveys.—We conducted simultaneous ground and aerial surveys in January 2001 and January 2002 and utilized mark-recapture double survey (Caughley and Grice 1982, Graham and Bell 1989, Pollock et al. 2006) analyses to estimate fallow deer abundance. Composition of the aerial survey crews differed between years. The double survey method treats animal groups counted by one method as "marked" and those counted by both methods as "marked and recaptured." Ground and aerial observers identified all detected fallow deer groups spatially (using Global Positioning System [GPS] units), temporally (time of observation), by group size and composition (number of unsexed fawns, spike males, adult males, and yearling and adult females), and color variants (white or non-white) present. We then utilized this information to classify groups as either detected from the ground only, air only or from both the air and ground.

Aerial surveys with radio-marked deer.—We captured fallow deer with modified Clover traps (McCullough 1975) or by net-gunning from a helicopter (Barrett et al. 1982, Krausman et al. 1985, Potvin and Breton 1988) and fitted them with very high frequency (VHF) radio collars (Telonics, Tucson, AZ) in November and December 2002. We used helicopter net-gunning to capture and fit with VHF radio collars additional fallow deer during December 2003. We conducted aerial surveys from a helicopter and utilized radio-marked deer to estimate detectability in January 2003 and January 2004. Aerial survey crew composition differed between years. We counted all deer in all groups detected from a helicopter within each survey unit and recorded information on all deer groups seen as described for the double sampling counts along with the number of radio-marked deer in each group. We also recorded the vegetative cover type in which the group was located as herbaceous, shrub, or forest.

Subsequent to the aerial search for fallow deer within each survey unit, we used radio-telemetry from the helicopter to locate all instrumented deer within that count unit and made a determination of whether groups containing radio-marked deer were seen during our initial aerial survey based upon its location, group size, age and sex composition, and number of white and non-white deer present. We simultaneously located all radio-collared deer from the ground to confirm that the VHF transmitters were functioning and that radio collars remained attached to deer, and to assess the characteristics of each deer group detected from the ground as described above. This permitted us to characterize groups containing radio-marked deer not detected from the air. In instances where radio-collared deer could be located but not be seen from the helicopter, we used the information from our ground observations to characterize the group as to size, the number of white and non-white deer, and the number of radio-marked deer present.

Analytical methods.—We considered the following covariates as candidates for predicting sighting probability from the ground or air during the aerial surveys for each observed group, *i*:

W_i = 1 if >0 white deer were present in a group *i*; 0 otherwise
N_i = Number of deer in group *i*
$\mathrm{Ln}(N_i)$ = Natural logarithm of N_i
H_i = 1 if vegetative cover was herbaceous; 0 otherwise
S_i = 1 if vegetative cover was shrubs; 0 otherwise
T_i = 1 if vegetative cover was trees; 0 otherwise
G_i = 1 if predicting ground observer sighting probability; 0 if aerial
D_i = 1 if high-density stratum; 0 otherwise
$Y_i(1)$ = 1 if survey year was 2001; 0 otherwise
$Y_i(2)$ = 1 if survey year was 2002; 0 otherwise
$Y_i(1,2)$ = 1 if survey year was either 2001 or 2002; 0 otherwise.

The covariate for ground observer (G_i) is only applicable to the 2001 and 2002 surveys. The three vegetation cover covariates (H_i, S_i, and T_i) were only recorded in 2003 and 2004 and those effects apply only to models for those years. We did not consider separate year effects for surveys in 2003 and 2004 because in 2003 only 16 of the detected groups contained radio collared deer (and only 4 of these were in the high density stratum). We considered this to be too few to reliably estimate unique effects for that year. Therefore, we considered only models in which 2003 and 2004 had the same covariates for survey effect. Only five combinations of the survey year effect were considered: No effect; $Y_i(1)$; $Y_i(2)$; $Y_i(1)$ and $Y_i(2)$; and, $Y_i(1, 2)$.

We used the Huggins closed capture model in Program MARK (White and Burnham 1999) to fit a series of candidate models. We began by fitting a single parameter ($K = 1$) constant probability model. We then added each of the above covariates one at a time and evaluated the evidence supporting each. We chose just the most strongly supported of the three possible vegetation covariates and the most strongly supported of the two population size covariates for further analysis. We included a given covariate in every model considered if support for it was overwhelming (Akaike Information Criteria corrected for small sample size [AIC_c] evidence ratio >100) and constructed models with all possible combinations of the remaining parameters.

Program MARK produces estimates of the number of groups seen, not the number of individual deer. Therefore, we chose the top models identified by AIC_c in MARK (all those with AIC_c model weight >5%) and computed the group-specific sighting probabilities using each of these in an Excel spreadsheet for both aerial (p_{ai}) and ground (p_{gi}) observers. The probability that a given group, i, was seen was calculated as

$$p_i = 1 - (1-p_{ai})(1-p_{gi})(1-p_{ri})$$

where

p_{ri} = 1 if a radio collar is present; 0 otherwise. We computed the estimated number of groups, θ_i, in the true population like the observed group, i:

$$\widehat{\theta_\iota} = \frac{1}{p_i}$$

and the number of deer in each of these projected groups, $\widehat{N_\iota}$,

$$\widehat{N_\iota} = \hat{\theta} N_i$$

where

N_i = the number of deer in observed group i. The total population estimate is then $\widehat{N} = \sum_{i=1}^{n} \widehat{N_\iota}$, where n is the number of groups observed. These calculations were repeated for each of the top models and the final estimate was computed as the weighted average of the individual estimates using AIC_c model weights (Burnham and Anderson 2002).

The estimation error for the above estimate must include multiple components: (1) model selection error (in the form of differing model weights); (2) sighting probability estimation error (the error in estimating the parameters of a given model); and, (3) binomial sampling error for sighting given a probability. To accurately estimate reliable errors incorporating all of these sources of error, we applied a bootstrap simulation analysis. For each actual observed group we generated a number of groups equal to the integer portion of the estimated true number of groups, plus possibly one additional group with a probability equal to the fractional portion of the estimated true number of groups. This was done for all observed groups to produce an empirically simulated population from which to resample. Each empirically simulated group retained the same sighting characteristics, group size, and presence of radio collars as the original observed group. To illustrate this process, a sighting probability of 40% for p_i yields an estimate of 2.5 groups in the empirically simulated population for the single group actually observed. The empirical population from which we would resample would contain two groups and possibly a third group, with 50% probability, each with identical covariates and other values as the original observed group. Re-sampling the sighting of these groups with 40% probability would produce one observed group, on average.

We sampled the empirically simulated population with replacement using the estimated sighting probabilities from the original data to produce a replicate set of survey data. We then analyzed these data exactly as the original data had been by refitting the parameters of top models from the original analysis and calculating the estimated population size in the same way using multiple refitted models and weighted population estimates. We repeated this process and estimated standard errors for the original population estimates using the standard deviation of the simulated estimates, including the original. We also estimated 95% confidence intervals as the 2.5%–97.5% percentiles of the simulated estimates. We ran simulations until the change in the standard error was <1% for each annual estimate when the number of simulated surveys was increased by 10%.

To estimate the growth rate of the population over the four-year period of the study, we fit an exponential model to the four estimated population sizes. We used weighted least squares fitting with the inverse of the variances of the individual estimates as weights (Gerrodette 1991), which places more emphasis on the more precisely estimated values and addresses potential bias in the regression parameter estimates and their standard errors.

Results

Distribution and density strata.—Fallow deer were limited to the Point Reyes Peninsula and immediately adjacent lands. We identified five survey units over the fallow deer distribution at Point Reyes based upon landscape features and distribution of observed deer groups. We classified four survey units totaling 211.3 square kilometers (km^2) as a low density stratum, and classified a fifth survey unit of 6.9 km^2 as a high density stratum (Figure 1).

Aerial surveys with double sampling.—We classified 542 fallow deer in 54 groups in January 2001 and 657 fallow deer in 63 groups in January 2002 (Table 1) as detected from the ground only, air only, or both ground and air within each stratum utilizing records of the location, number of deer, age and sex composition and color variants of deer present for each group detected. Air and ground observers jointly detected 10 (18.5%) of the 54 groups in 2001 and 8 (12.6%) of the 63 groups in 2002.

Some two-thirds of detected deer were in the high density stratum in 2001 and approximately half of all deer were detected in each stratum in 2002 (Table 1). The numbers of deer detected in the high density stratum were very similar in both years and estimated numbers are similar. In contrast, markedly fewer deer were detected in the low density stratum in 2001 than 2002 with the observed percentage of deer sighted rising from 31% in this stratum in 2001 to 43% in the same stratum in 2002 (Table 1).

Table 1.—Results of two double-survey method estimates of fallow deer numbers at Point Reyes, Marin County, California, 2001 and 2002.

		Groups Seen							
Date	Strata	Ground Only	Air Only	Both	Number Seen	Estimated Number	SE	95% CI	Percent Seen
Jan. 2001	Low	7	10	8	167	338	57	265–486	57.7
	High	8	19	2	375	650	104	533–933	49.4
	Pooled	15	29	10	542	989	160	796–1,419	54.8
Jan. 2002	Low	16	22	6	285	770	129	573–1,093	37.0
	High	14	3	2	372	694	99	564–952	53.6
	Pooled	30	25	8	657	1464	226	1,138–2,054	44.9

Aerial surveys with radio-marked deer.—We captured and fitted with radio collars 29 white and non-white fallow deer of both sexes in both strata during December 2002. In January 2003, we counted 492 fallow deer in 44 groups including 24 instrumented deer in 13 groups (range 1–9 instrumented deer/group) during the initial aerial survey (Table 2). We located 4 of the remaining 5 instrumented deer in 3 groups containing 41 animals using radio-telemetry. One instrumented deer was not located. We captured and radio-marked an

Table 2.—Results of two aerial surveys with radio-marked deer estimates of fallow deer numbers at Point Reyes, Marin County, California, 2003 and 2004.

Date	Strata	Marked Deer Available	Marked Deer Seen	Unmarked Deer Seen	Total Number Seen	Estimated Number	SE	95% CI	Percent Seen
Jan. 2003	Low	16	14	284	298	528	62	475–715	56.5
	High	13	10	184	194	298	33	272–400	65.2
	Pooled	29	24	468	492	825	94	749–1,108	59.6
Jan. 2004	Low	20	7	340	347	538	53	494–701	64.5
	High	19	12	475	480	691	70	638–911	69.5
	Pooled	39[1]	19	815	827	1229	120	1,135–1,595	67.3

[1]Two deer were not detected by radio telemetry during the aerial surveys.

additional 17 white and non-white deer of both sexes during December 2003. Forty-one radio-marked deer were available for detection during the January 2004 aerial survey as four radio-marked deer died and we lost contact with a fifth instrumented deer prior to January 2004. Two radio-marked deer were not located by radio-telemetry during the January 2004 survey and were considered unavailable. We detected 827 deer in 67 groups ranging in size from 1–74, including 19 radio-collared deer in 12 groups (range 1–6 instrumented deer/group) during the initial aerial survey (Table 2). We used radio-telemetry to locate the remaining 20 instrumented deer in 20 groups containing 199 deer.

Over the 4 surveys, marked deer group sizes ranged from 1 to 134 deer. Of these, 145 (64%) groups contained at least 1 white fallow deer and 80 (36%) groups were in the high density stratum. During the surveys when vegetation cover was recorded (2003 and 2004), 62% of detected groups were in herbaceous cover, 24% in shrubs, and 14% in trees.

Analytical methods.—We initially tested each candidate model covariate individually (plus an intercept, K=2) against a simple model with a constant sighting probability (intercept only, K=1) for evidence of support and found that model weight when the presence of white deer in a group was included had 12,547 times greater support than the intercept only model. Including ln(N) received 968 times the level of support as the intercept only. We concluded that further model testing should include these variables in all cases.

The remaining candidate covariates received substantially less support (<24 times intercept only). These initial tests also indicated that of the 3 vegetation cover types, the indicator for herbaceous cover was a superior predictor to those for shrub or tree cover (evidence ratios herb/shrub=2.4; herb/tree=14.6). Evidence for ln(N) was strongly superior to N (evidence ratio: 194.1). Based on these results, we constructed models that included the W_i and ln(N_i) covariates plus all possible combinations of the H_i, G_i, D_i, the 5 combinations of survey year effect described in the methods section for a total of $2 \times 2 \times 2 \times 5 = 40$ models.

The sum of model weights containing the covariates tested provided the strongest evidence for the inclusion of strata (97.1%), followed by ground observer (84.2%). The weight of evidence for inclusion of at least one covariate for survey year was similarly strong (85.7%), but this was split among the several alternatives, with a single effect for 2001 and 2002 the most strongly supported (45%). Finally, the effect of herbaceous cover received modest support (34.1%). The most strongly supported model contained the covariates for strata, ground observer, and the single effect for 2001 and 2002, but did not include an effect for herbaceous cover.

The best model for sighting probability, p_i, of group i, was: $p_i = \frac{1}{1+e^{-x_i}}$, where $x_i = -\ 2.202 + 2.015W_i + 0.5184\ \ln(N_i) + 0.5368 * G_i - 1.0396\ Y_i(1,2) - 0.8509\ D_i$. This illustrates that the presence of white deer had a strongly positive effect; larger groups were more visible; sighting probability was higher for ground-based observers; and that sighting probability was lower in 2001 and 2002 and in the high density stratum (Figure 2). The worst predicted sighting probability possible (no white deer, group size =1, aerial observers, 2001 or 2002, and high density stratum) had an estimated sighting probability of only 1.6%.

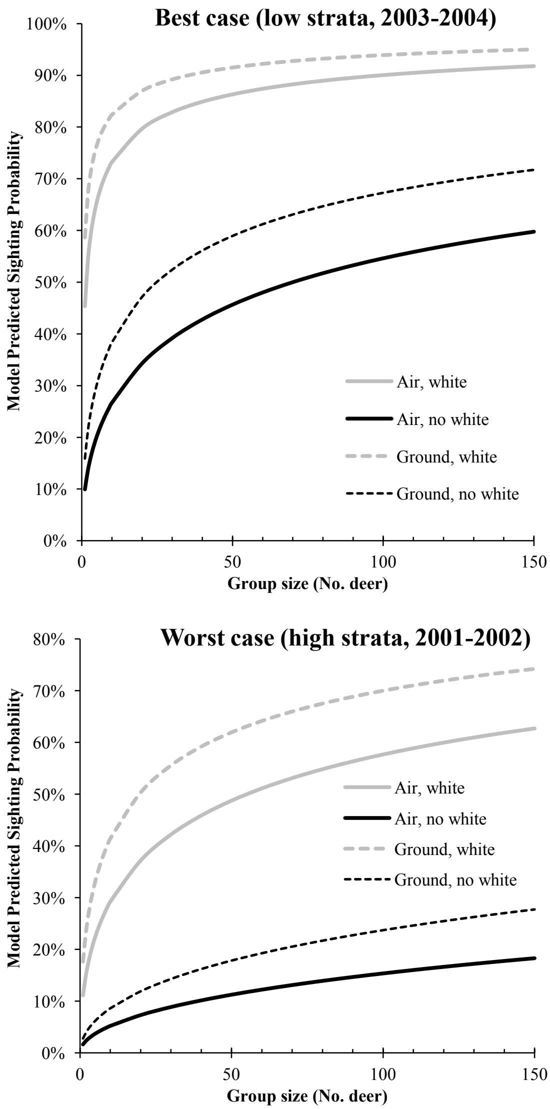

FIGURE 2.—Model-predicted sighting probability of fallow deer as a function of conditions at Point Reyes, Marin County, California. Upper panel is for best case conditions: low density stratum during 2003 and 2004 surveys. Lower panel is for worst case conditions: high density stratum during 2001 and 2002. Curves show predicted sighting probabilities for air and ground observers and for groups with and without white fallow deer present.

A single group with these characteristics was seen during the study. The highest estimated sighting probability for an actual observation was 84.2% for a group of 36 deer containing white deer in the low density stratum observed from the air in 2004. Sighting probabilities were distributed widely in an almost random pattern with somewhat more low than high probability groups for aerial observers but were more clustered around moderate sighting probabilities for ground observers (Figure 3).

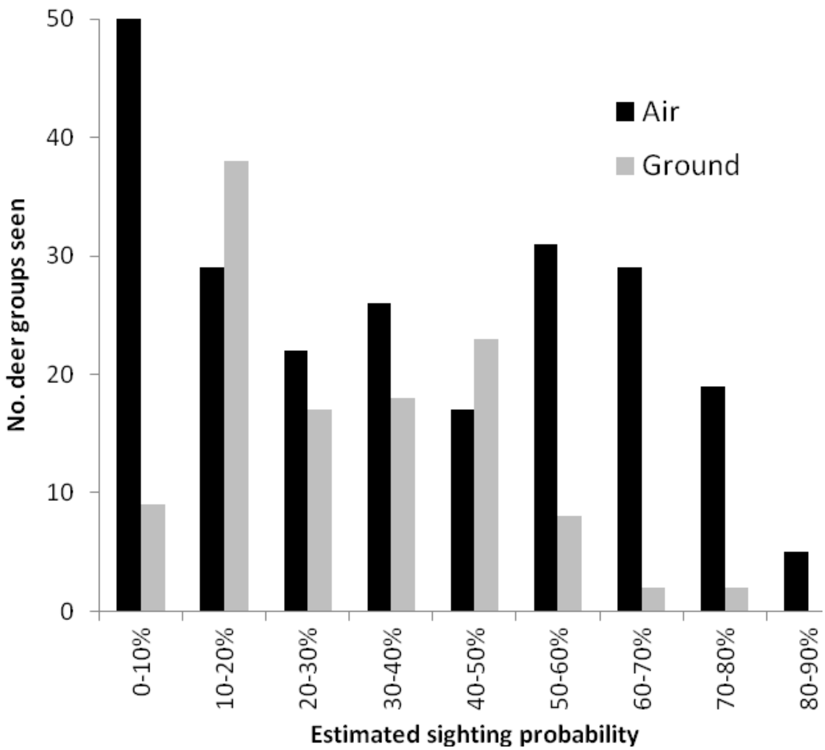

FIGURE 3.—Histogram showing the number of fallow deer groups actually observed during surveys (y-axis) with estimated sighting probabilities (x-axis) for aerial and ground-based observers for all surveys combined at Point Reyes, Marin County, California.

Six models received AIC_c weight of >5% and together accounted for 69% of the total model weight. All of these included the strata and ground observer covariates, but various combinations of the herbaceous cover and survey year effect covariates. We selected these 6 models for refitting in the bootstrap analysis to represent the range of model selection uncertainty while avoiding the excessively time consuming process of refitting all 40 models. We calculated population estimates based on the weighted average estimates of these top 6 models (Table 1 and Table 2) for both high and low density strata. We found that that confidence interval estimates (Table 1 and Table 2) were stable after 500 bootstrap simulations (adding 10% more simulations resulted in <1% changes in each of the individual annual error estimates).

Finally, we fit both log-linear and constant regression models to the 4 annual population estimates using weighted least squares by weighting each observation by the estimated inverse variance. The AIC_c evidence was 340 times higher for the constant model than for the 2-parameter model with a constant growth rate indicating a complete absence of evidence for either growth or decline in this population. Consequently, the best estimate of this population is the weighted mean across the 4 surveys and its standard error. These were 416 ± 27.7 (95% CI = 370 – 461) deer for the high density stratum and 487 ± 31.8 (435 – 539) for the low density stratum. Pooling these estimates provides a total population estimate of 903 ± 42.1 (834 – 972) deer. The density estimates for the 4 surveys ranged from 1.4 ± 0.2 to 3.3 ± 0.5 deer/km^2 in the low density stratum over 4 surveys and between 49.0 ±8.3 and 111.6 ± 18.7 deer/km^2 in the high density stratum.

Discussion

Our aerial surveys provided relatively complete spatial coverage of the fallow deer distribution, with few deer occurring beyond the limits of our survey area. All detected radio-marked deer were within the boundaries of our count units during the January 2003 and January 2004 surveys. The presence of fallow deer color variants in combination with age and sex composition provided an opportunity to identify deer groups without radio-marked deer more confidently than would have been possible using age and sex composition information alone. This permitted reliable assessments of which groups of deer were detected during the ground and aerial surveys. We considered the combination of group composition in terms of age and sex classes and color variants and location as unambiguous ‘marks’ (Barker 2008).

Confidence intervals on the population estimates are wide for these aerial surveys due to the relatively low sighting probabilities and relatively small sample sizes due to the modest number of deer groups. The use of different observers in each year undoubtedly introduced variability in the sighting probabilities that could not be estimated and corrected due to insufficient sample sizes for individual observers. Consequently, this source of variability added uncertainty to the estimates. The absence of evidence for a change in this population over the 4-year study period may be the result of low precision of the estimates and consequent inability to detect any change that may have occurred.

Furthermore, for the double observer method to be valid, the sighting probabilities conditional on the covariates must be independent (uncorrelated). In other words, if the covariates fail to account for all (or at least most) of the variability in sighting probability among groups, the corrections will be biased. Such heterogeneity in sighting probabilities is known to produce low estimates of the population, on average (Barker 2008). The presence of sighting heterogeneity cannot be tested with these data; however, the problem is likely to be exacerbated by overall low sighting probabilities, as in this case.

A potential additional source of bias comes from undercounting the deer in each group. Our method adjusts for missed groups, but assumes that once a group is spotted, that all deer within that group are seen and accurately counted. Cogan and Diefenbach (1998) and Walsh et al. (2009) cast doubt on this assumption. Future surveys could benefit from using multiple aerial photographs of each group to help observers locate and count deer that might be missed during their initial airborne count, or modified data collection to enable application of the statistical correction method of Walsh et al. (2009).

Our estimated low sightability of solitary non-white color variant deer is consistent with low detectability rates for smaller groups of elk (*Cervus elaphus*) in areas where overstory vegetative cover is common (Samuel et al. 1987, Anderson et al. 1998, Cogan and Diefenbach 1998, Eberhardt et al. 1998, Gilbert and Moeller 2008). Deer (*Odocoileus hemionus*) density also affects the proportion of deer seen (Bartmann et al. 1986). The importance of white color variant fallow deer in group detectability suggests that aerial surveys may be most appropriate for fallow deer populations in which the white color-variant is common.

Our surveys reveal post-rut densities of up to111.6 ± 18.7 deer/km^2 in the northern Olema Valley (Figure 1) contrasting with densities of ≤ 3.3 ± 0.5 deer/km^2 throughout the remainder of this population's range. Annual density estimates averaged across the population's distribution (both high and low density strata) ranged between 3.8 ± 0.4 and 6.7 ± 1.0 deer/km^2. Fallow deer densities of >100 deer/km^2 have been reported elsewhere along the west coast of North America (Moody et al. 1994), as have densities of <1/km^2 (Jurek 1977). Reported densities for other populations range from 7.5/km^2 (Nugent 1988, Thirgood 1995) to 31/km^2 (Feldhamer et al. 1988, Feldhamer and Armstrong 1993). These populations were subjected to varying control measures. Fallow deer at Point Reyes have not been subjected to population control since 1996 (Gogan et al. 2001).

Our sightability estimates indicate that a large portion of this population would be missed by a simplistic raw count or "census" survey without statistical corrections. Furthermore, the wide range of sighting probabilities among deer groups emphasizes the importance of correcting for this sighting heterogeneity using appropriate covariates, rather than relying on simpler mark-resight models. The differences detected among survey years also indicate that a static sightability model calibrated once and extrapolated to future surveys would be less reliable than models updated with double-observer data from each new survey. Although the number of (uncorrected) deer observed in the pooled strata over the 4 surveys (mean = 630, range 492-827) bracket agency personnel estimates of 600 deer present in the area made prior to our study, the substantial differences between these raw counts and our final estimate of 903 ± 42.1 (834 – 972) underscores the value of statistical adjustments for detectability in raw counts. These more accurate and meaningful survey results are a prerequisite to assessing adaptive management alternatives that include population control.

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Literature Cited

Anderson, C. R., D. S. Moody, B. L. Smith, F. G. Lindzey, and R. P. Lanka. 1998. Development and evaluation of sightability models for summer elk surveys. Journal of Wildlife Management 62:1055-1066.

Barbour, M. G., R. B. Craid, F. R. Drysdale, and M. T Ghiseline. 1973. Coastal ecology: Bodega Head. University of California Press, Berkeley, USA.

Barker, R. 2008. Theory and application of mark-recapture and related techniques to aerial surveys of wildlife. Wildlife Research 35:268-274.

Barrett, M. W., J. W. Nolan, and L. D Roy. 1982. Evaluation of a hand-held net gun to capture large mammals. Wildlife Society Bulletin 10:108-114.

Bartmann, R. M., L. H. Carpenter, R. A. Garrott, and D. C. Bowden. 1986. Accuracy of helicopter counts of mule deer in pinyon-juniper woodland. Wildlife Society Bulletin 14:356-363.

Brown, P. M., M. W. Kaye, and D. Buckley. 1999. Fire history in Douglas-fir and coast redwood forests at Point Reyes National Seashore, California. Northwest Science 73:205-216.

Burnham, K. P., and D. R. Anderson. 2002. Model selection and multi-model inference. Springer-Verlag, New York, USA.

Caughley, G., and D. Grice. 1982. A correction factor for counting emus from the air and its application to counts in Western Australia. Australian Wildlife Research 9:253-259.

Chapman, N. G., and D. I. Chapman. 1980. The distribution of fallow deer: a worldwide review. Mammal Review 10:61-138.

Cogan, R. D., and D. R. Diefenbach. 1998. Effects of undercounting and model selection on a sightability-adjustment estimator for elk. Journal of Wildlife Management 62:269-279.

Eberhardt, L. L., R. A. Garrott, P. J. White, and P. J. Gogan. 1998. Alternative approaches to aerial censusing of elk. Journal of Wildlife Management 62:1046-1055.

Elliott, H. W. III, and J. D. Wehausen. 1974. Vegetation succession on coastal rangeland of Point Reyes Peninsula. Madrono 22:231-238.

Feldhamer, G. A., K. C. Farris-Renner, and C. M. Barker. 1988. Dama dama. Mammalian Species 317:1-8.

Feldhamer, G. A., and W. E. Armstrong. 1993. Interspecific competition between four exotic native artiodactyls in the United States. Transactions of the North American Wildlife and Natural Resources Conference 58:468-477.

Gerrodette, T. 1991. Models for power of detecting trends—a reply to Link and Hatfield. Ecology 72:1889-1892.

Gilbert, B. A., and B. J. Moeller. 2008. Modeling elk sightability bias of aerial surveys during winter in the central Cascades. Northwest Science 82:222-228.

Gogan, P. J. P., S. C. Thompson, W. Pierce, and R. H. Barrett. 1986. Line-transect censuses of fallow and black-tailed deer on the Point Reyes Peninsula. California Fish and Game 72:47-61.

Gogan, P. J. P., R. H. Barrett, W. W. Shook, and T. E. Kucera. 2001. Control of ungulate numbers in a protected area. Wildlife Society Bulletin 29:1075-1088.

Graham, A., and R. Bell. 1989. Investigating observer bias in aerial survey by simultaneous double-counts. Journal of Wildlife Management 53:1009-1016.

Heady, H. F., T. C. Foin, M. K. Hektner, D. W. Taylor, M. G. Barbour, and W. J. Barry. 1977. Coastal prairie and northern coastal scrub. Pages 733-757 *in* M. G. Barbour and J. Major, editors. Terrestrial vegetation of California. John Wiley and Sons, New York, USA.

Jurek, R. M. 1977. Status, ecology and behavior of a wild population of fallow deer in Mendocino County, California 1968–1970. M.S. Thesis, Humboldt State University, Arcata, California, USA.

Krausman, P. R., J. J. Hervert, and L. L. Ordway. 1985. Capturing deer and mountain sheep with a net-gun. Wildlife Society Bulletin 13:71-73.

Kuchler, A. W. 1977. The map of the natural vegetation of California. Pages 909-938 *in* M. G. Barbour and J. Major, editors. Terrestrial vegetation of California. John Wiley and Sons, New York, USA.

McCullough, D. R. 1975. Modification of the Clover deer trap. California Fish and Game 61:242-244.

Moody, A., B. Burtin, and R. Moody. 1994. An investigation into the ecology of fallow deer of Sidney Spit Provincial Park. British Columbia Parks Occasional Paper No. 1. Ministry of Environment, Lands and Parks. Victoria, British Columbia, Canada.

Nugent, G. 1988. Successful control of fallow deer by recreational hunters in the Blue Mountains, Otago. New Zealand Journal of Forestry Science 18:239-252.

Pollock, K. H., H. D. Marsh, I. R. Lawler and M. W. Alldredge. 2006. Estimating animal abundance in heterogeneous environments—an application to aerial surveys for dugongs. Journal of Wildlife Management 70:255-262.

Potvin, F., and L. Breton. 1988. Use of a net gun for capturing white-tailed deer, *Odocoileus virginianus*, on Anticosti Island, Quebec. Canadian Field Naturalist 102:697-700.

Samuel, M. D., E. O. Garton, M. W. Schlegel, and R. G. Carson. 1987. Visibility bias during aerial surveys of elk in northcentral Idaho. Journal of Wildlife Management 51:622-630.

Shuford, W. D., and I. C. Timossi. 1989. Plant communities of Marin County. Special Publication Number 10. California Native Plant Society, Sacramento, USA.

Thirgood, S. J. 1995. The effects of sex, season, and habitat availability on patterns of habitat use by fallow deer (*Dama dama*). Journal of Zoology 235:645-659.

Walsh D. P., C. F Page, H. Campa, S. R Winterstein. and D. E Beyer. 2009. Incorporating estimates of group size in sightability models for wildlife. Journal of Wildlife Management 73:136-143.

Weber, G. E. 1981. Physical environment. Pages 61-121 *in* B. J. LeBoeuf and S. Kaza, editors. The natural history of Ano Nuevo. Boxwood Press, Pacific Grove, California, USA.

Wehausen, J. D., and H. W. Elliott III. 1982. Range relationships and demography of fallow and axis deer on Point Reyes National Seashore. California Fish and Game 68:132-145.

White, G. C., and K. P. Burnham. 1999. Program MARK—survival estimation from a population of marked animals: Bird Study 46(supplement):S120-S138.

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