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# Double-observer evaluation of pronghorn aerial line-transect surveys

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**Abstract**

***Context.*** Distance sampling is used to estimate abundance for several taxa, including pronghorn (*Antilocapra americana*). Comparisons between population estimates derived from quadrat sampling and distance sampling suggest that distance sampling underestimates pronghorn density, likely owing to violations of the critical assumption of distance sampling that all pronghorn within the innermost distance band (A band; nearest to the aircraft) are detected.

***Aims.*** We sought to rigorously test the assumption that all pronghorn clusters are detected within the innermost distance band by applying a double-observer approach to an established pronghorn aerial-survey protocol. Additionally, we evaluated potential effects of cluster size, landscape composition and seat position (front seat versus rear) on the probability of detection.

***Methods.*** We conducted aerial line-transect distance-sampling surveys using independent, paired observers and modelled the probability of detection with mark–recapture distance-sampling (MRDS) analysis techniques that explicitly estimate the probability of detection for pronghorn clusters in the innermost distance band. We compared density estimates produced by the MRDS analysis with those produced by multiple-covariate distance sampling (MCDS), a method that assumes complete detection for clusters on the transect line.

***Key results.*** We identified violations of the assumption that all clusters within the innermost distance band were detected, which would contribute to proportional biases in density estimates for analysis techniques that assume complete detection. The frequency of missed clusters was modest from the front-seat position, with 45 of the 47 (96%) clusters in the A band detected. In contrast, the frequency of missed clusters was more substantial for the rear position, from which 37 of 47 (79%) clusters in the A band were detected. Further, our analysis showed that cluster size and landscape composition were important factors for pronghorn sightability.

***Conclusions.*** When implementing standard survey methodologies, pronghorn aerial-line transect surveys underestimated population densities. A double-observer survey configuration allowed us to quantify and correct for the bias caused by the failure of observers to detect all pronghorn clusters within the innermost distance band.

***Implications.*** Population monitoring programs should incorporate double-observer validation trials to quantify the extent of bias owing to undetected clusters within the innermost distance band realised under typical survey conditions. Wildlife managers can improve the precision of pronghorn aerial line-transect surveys by incorporating cluster size and measures of landscape composition and complexity into detection models without incurring additional survey costs.

**Additional keywords:** *Antilocapra americana*, detection bias, distance sampling, mark–recapture, population estimation.

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## Introduction

Effective wildlife management requires precise and unbiased estimates of density and rates of population change (Rabe *et al.* 2002; Pojar 2004; Jacques *et al.* 2014). Accordingly, aerial surveys are frequently used to monitor populations of large mammals including pronghorn (*Antilocapra americana*). Pronghorn are assumed to be ideally suited for aerial surveys, given that the species largely occupies open habitats and availability bias (animals present but not available for detection because of complete visual obstruction) is likely to be minimal (Marsh and Sinclair 1989; Buckland *et al*. 2004). However, even in open habitats, perception bias (disproportionate detection of groups because of intrinsic (e.g. group size, animal activity) and extrinsic factors (e.g. lighting conditions, flight speeds, vegetation composition and structure)) is likely to contribute to the failure to detect all groups within surveyed areas (Caughley *et al*. 1976; Marsh and Sinclair 1989; Jacques *et al*. 2014).

Managers have developed various survey and analysis methods to minimise or quantify and correct for perception bias to produce unbiased estimates of pronghorn abundance. However, alternative survey methods offer unique advantages and disadvantages for management applications. Pojar *et al*. (1995) introduced a quadrat-sampling method in which pronghorn individuals were censused from low-flying (15–30 m) helicopters within 2.59-$km^2$ quadrats. The low altitude and slow flight speeds (60–70 $km\,h^{-1}$) minimised perception bias, and the tendency for pronghorn to flee in response to the approaching aircraft further increased pronghorn visibility. Evaluation of Pojar *et al*.'s (1995) quadrat surveys with a second helicopter flying in tandem demonstrated that this method produced unbiased estimates of abundance. However, helicopter operation is more expensive than the use of fixed-wing aircraft, and there can be extensive ferry time between quadrats when applying this method across broad spatial scales.

Jacques *et al*. (2014) developed sightability models using mark–resight techniques to correct for visibility bias in fixed-wing strip-transect surveys. Methodologically, sightability models are established by radio-collaring a subset of individuals within a population and using radio-telemetry to independently evaluate whether marked individuals were detected or missed during model-development surveys. Evaluating detection rates as a function of intrinsic (number of animals in a group and animal activity) and extrinsic (cover type, percent vegetation, and topography) attributes, Jacques *et al*. (2014) identified correction factors that could be applied in subsequent strip-transect surveys to produce unbiased estimates of abundance. The limitation of sightability models is that they produce unbiased estimates only if subsequent surveys are conducted under conditions similar to those in which the model was developed, and they require the capture and marking of a subset of individuals for initial quantification of visibility bias and formulation of correction factors.

Fixed-wing line-transect distance-sampling methods developed by Guenzel (1986) and Johnson *et al*. (1991) correct for perception bias in pronghorn surveys, while not requiring the capture and marking of individuals. In distance sampling, the probability of detection is modelled as a function of the perpendicular distance of an object from the transect line (Buckland *et al*. 2001). Distance sampling should produce unbiased population estimates if the following three key assumptions can be met: (1) clusters ($\geq$1 object) directly on the line are always detected, (2) clusters are detected at their initial location, before moving in response to the observer, and (3) distances to clusters are measured accurately (Buckland *et al*. 2001). For extension of the well-developed theory of distance sampling to fixed-wing pronghorn surveys, observers use calibrated markings on the window and wing strut to place detected pronghorn clusters into distance bands that translate to known distances off the line, given the above-ground level of the aircraft (Guenzel 1997). Despite the simplification of distance measurement, observers must still detect all clusters on the transect line to produce unbiased estimates (Guenzel 1997). Comparisons of pronghorn population estimates from quadrat sampling to those from line-transect distance sampling suggest that distance sampling substantially underestimates pronghorn density (negatively biased by 27%; Pojar and Guenzel 1999), which is likely to occur because of undetected clusters on the transect line.

Recent developments in distance sampling have sought to relax the assumption that all clusters on the line must be detected by using independent, paired observers (double-observers) in a mark–recapture distance-sampling (MRDS) context (Graham and Bell 1989; Quang and Becker 1996; Borchers *et al*. 1998; Potvin *et al*. 2004). This method uses encounter histories generated by detections between two observers (Observer 1: detect, Observer 2: miss (1, 0); Observer 1: miss, Observer 2: detect (0, 1); or Observer 1: detect, Observer 2: detect (1, 1)) to estimate the proportion of clusters on the line that are detected. Given the observed bias in population estimates derived from pronghorn fixed-wing line-transect surveys, we sought to apply a double-observer approach to this established survey protocol to rigorously test the assumption that all clusters within the A band are detected. Further, we sought to quantify bias associated with missed pronghorn clusters on the transect line by comparing density estimates derived from a MRDS approach, which explicitly estimates the probability of detection on the transect line, to estimates derived from traditional distance sampling, which rather assumes complete detection.

## Materials and methods

### Study sites

We conducted pronghorn aerial surveys in two study areas (Fig. 1). The Kemmerer study site (41.855°N, 110.165°W) spanned portions of Lincoln and Sweetwater counties in south-western Wyoming, USA. The Kemmerer landscape was typical of pronghorn winter-range habitat that retains small populations of pronghorn throughout the growing season. Vegetation communities were dominated by Wyoming big sagebrush (*Artemisia tridentata wyomingensis*), with lesser amounts of desert-scrub communities and small pockets of aspen (*Populus tremuloides*), mountain big sagebrush (*A. t. vaseyana*), greasewood flats (*Sarcobatus vermiculatus*) and riparian zones (Wyoming GAP Analysis 1996). The Pinedale study site (43.043°N, 110.137°W) spanned portions of Sublette County in west-central Wyoming. Habitats encountered in Pinedale were typical of pronghorn summer range, seasonally supporting high population densities. Pinedale was dominated by mountain big sagebrush communities with forest stands and irrigated agriculture interspersed throughout the landscape (Wyoming GAP Analysis 1996).

### Survey methods

We implemented standard line-transect methods for pronghorn aerial surveys described previously by Guenzel (1997), with


**Fig. 1.** Spatial extent of pronghorn (*Antilocapra americana*) double-observer line-transect aerial surveys conducted in westcentral (Pinedale) and south-western (Kemmerer) Wyoming, USA, with transects represented as lines through the shaded regions in the enlargement.

modification described below. Briefly, the standard line-transect configuration includes two observers seated on opposite sides of the aircraft (i.e. front right and rear left), dowels attached to the struts to delineate a blind-area offset (0–65 m) and four perpendicular distance bands (A–D) that correspond to known widths when the aircraft is flown at the specified above-ground level (AGL) of 91.4 m, and calibrated window markings for alignment with distance-band delineations on the strut (Guenzel 1997). During surveys, observers align window markings with the dowels on the strut; this ensures a fixed eye position for the observer and consistency when classifying detected clusters into respective distance bands. We conducted surveys in a Maule 5 aircraft that had window and door modifications to increase visibility, a global positioning system (GPS) to guide transect navigation, and a radar altimeter to aid in the maintenance of the specified AGL. In accord with standard survey protocols, we recorded the number of individuals and distance band (i.e. A (65–90 m), B (90–115 m), C (115–165 m), D (165–265 m)) for each pronghorn cluster detected.

We modified aerial line-transect survey protocols by positioning both observers on the right side of the aircraft in a double-observer arrangement. To maintain independence, we hung an opaque curtain between observers to prevent transfer of visual cues that may signal the presence of a pronghorn cluster. We delayed indication of cluster detection until the pronghorn had passed beyond the aircraft and out of view for both observers. At that point, an observer announced that a cluster had been detected; the opposing observer then indicated whether the cluster had been detected from the front, rear or both positions, with all data being recorded by the pilot.

We conducted surveys on 16–17 June 2004, within the seasonal timeframe of maximal dispersion and highest uniformity in pronghorn cluster size (Guenzel 1997). We restricted surveys to the time between sunrise and 1030 hours to minimise the proportion of individuals bedded. We oriented survey lines both east-west and north-south to capture the breadth of lighting conditions encountered during typical surveys. We spaced transect lines at intervals of $\geq$1-min latitude or longitude to provide adequate coverage of the survey areas, while minimising the potential of detecting the same cluster on adjacent transects. All observers (G. Frost (front, Kemmerer), R. King (front, Pinedale), and T. J. S. (rear, Kemmerer and Pinedale)) that participated in this experiment had extensive experience with pronghorn aerial line-transect surveys and were knowledgeable of the assumptions and requirements of distance sampling.

### Statistical analysis

Analysis of double-observer surveys in an MRDS context allowed us to explicitly model the probability of detection for pronghorn clusters within the A band. Mark–recapture distance sampling integrates unconditional and conditional detection functions. Unconditional detection functions describe the probability of detection, given the distance of a cluster from the transect line with the assumption that clusters are uniformly distributed with respect to the transect line (Laake and Borchers 2004; Buckland *et al*. 2010; Burt *et al*. 2014). In contrast, conditional detection functions use the conceptual mark–recapture encounter histories to model the probability of detection. Deviations between the unconditional and conditional detection functions (delta($x$)) then reflect dependence between observers in the detection of clusters (Laake and Borchers 2004). Assuming point independence (detections between double observers are independent for clusters on the transect line; delta(0) = 1), conditional detection functions can be used to estimate the probability of detection on the transect line (Laake and Borchers 2004; Buckland *et al*. 2010; Burt *et al*. 2014). We evaluated models using an independent-observer configuration, given that observers in the front and rear positions independently searched for pronghorn and the detection of clusters from each position reciprocally created trials for the opposing position (Burt *et al*. 2014). We followed the sequential-analysis recommendations of Laake and Borchers (2004), in which we first identified the best unconditional detection function, while holding the conditional detection function constant (mark–recapture model ~distance; Table 1) and then carried forward the highest-ranked unconditional detection model to evaluate a series of competing conditional detection functions. Specifically, we used Akaike information criterion corrected for finite sample sizes ($AIC_c$) to evaluate the following three unconditional detection functions with a half-normal key function without series expansions: (1) a constant scale, (2) cluster size (size) introduced as a covariate in the scale parameter of the detection function, and (3) study site (site) introduced as a scale-parameter covariate, reflecting variation in pronghorn sightability associated with differences between

**Table 1. Mark–recapture distance sampling (MRDS) models evaluated for double-observer pronghorn aerial line-transect surveys conducted in south-western (Kemmerer) and westcentral (Pinedale) Wyoming, USA, in 2004**

Unconditional model, unconditional detection function implementing a half-normal key function without series expansions in which the probability of detection is based on the distance of clusters from the transect line. Conditional model, conditional detection function describing deviations in independence of detection between observers as a function of specified covariates, used to estimate the proportion of clusters detected within the A (nearest to the aircraft) distance band. $K$, number of parameters. $\Delta AIC_c$, difference in Akaike's information criterion corrected for finite sample sizes relative to minimum $AIC_c$. $w_i$, Akaike weight. $D$, estimated density of pronghorn $km^{-2}$. s.e., standard error of estimated pronghorn density. Size, covariate representing the cluster size (number of individuals in a group) of pronghorn. Dist, covariate representing distance from transect line. Site, covariate representing different study areas. Seat, covariate representing different seat positions within the aircraft (front versus rear)

| Model | Unconditional model | Conditional model | $K$ | $\Delta AIC_c$ | $w_i$ | Kemmerer | | Pinedale | |
|---|---|---|---|---|---|---|---|---|---|
| | | | | | | $D$ | s.e. | $D$ | s.e. |
| 1 | ~size | ~dist | 4 | 0.00 | | | | | |
| 2 | ~1[A] | ~dist | 3 | 5.44 | | | | | |
| 3 | ~site | ~dist | 4 | 7.35 | | | | | |
| 4 | ~size | ~dist + size + site | 6 | 0.00 | 0.24 | 1.04 | 0.30 | 6.04 | 1.14 |
| 5 | ~size | ~dist + site | 5 | 0.42 | 0.20 | 1.04 | 0.30 | 6.05 | 1.14 |
| 6 | ~size | ~dist + size + site +seat | 7 | 0.83 | 0.16 | 1.04 | 0.30 | 6.04 | 1.14 |
| 7 | ~size | ~dist + site + seat | 6 | 1.23 | 0.13 | 1.04 | 0.30 | 6.05 | 1.14 |
| 8 | ~size | ~dist + size + site + seat + dist × seat | 8 | 1.25 | 0.13 | 1.03 | 0.30 | 6.04 | 1.14 |
| 9 | ~size | ~dist + size + site + seat + dist × size | 8 | 2.62 | 0.07 | 1.03 | 0.30 | 6.04 | 1.14 |
| 10 | ~size | ~dist + size + site + seat + dist × site | 8 | 2.87 | 0.06 | 1.04 | 0.30 | 6.04 | 1.14 |
| 11 | ~size | ~dist + size | 5 | 7.73 | 0.01 | 1.01 | 0.29 | 6.06 | 1.14 |
| 12 | ~size | ~dist + size + seat | 6 | 8.54 | 0.00 | 1.01 | 0.29 | 6.06 | 1.14 |
| 13 | ~size | ~dist | 4 | 8.69 | 0.00 | 1.01 | 0.29 | 6.07 | 1.14 |
| 14 | ~size | ~dist + seat | 5 | 9.48 | 0.00 | 1.01 | 0.29 | 6.07 | 1.14 |
| | | Model-averaged estimates[B] | | | | 1.04 | 0.30 | 6.04 | 1.14 |

[A]Constant scale for the unconditional detection function.

[B]Model-averaged are estimates based on Akaike weight ($w_i$) values for the competing models.

the study sites in vegetation communities and landscape complexity (Table 1; Burnham and Anderson 2002). With the identification of the $AIC_c$ best unconditional detection function, we then evaluated competing conditional detection functions that incorporated distance, in combination with other covariates that included size, site, and observer position (position (front versus rear seat position)). We evaluated all possible main-effect models in addition to full main-effect models that included the interaction between distance and, independently, each of the other covariates (Table 1). We ranked all competing models with $AIC_c$ and calculated corresponding Akaike weights ($w_i$). Given that the covariates size, site, and position were balanced among the conditional detection function models evaluated, we used $w_i$ to rank the relative importance of these variables (Burnham and Anderson 2002). With each of the models evaluated, we estimated a single detection function for the two study sites and derived site-specific density estimates based on differences in encounter rate and cluster size. Finally, we used $w_i$ to calculate model-averaged density estimates for each of the study sites, while accounting for model-selection uncertainty (Burnham and Anderson 2002).

In accord with standard analysis protocols, we also produced parallel density estimates using distance-sampling analyses that assume complete detection for pronghorn clusters within the A band (Guenzel 1997). In a multiple-covariate distance-sampling (MCDS) framework, in which covariates are introduced to scale the detection function, we evaluated the following three detection function models with a half-normal key function without series expansions: (1) a constant scale, (2) size as a scale parameter and (3) site as a scale parameter. Again, we estimated a single detection function for the two study sites, derived site-specific density estimates based on differences in encounter rate and cluster size, ranked competing models with $AIC_c$, and used $w_i$ to generate model-averaged density estimates. Within our trials, the front and rear position had different perspectives of the survey area and, concomitantly, differed in their ability to satisfy the assumption that all clusters within the nearest distance band were detected. Accordingly, we evaluated this suite of MCDS models independently for detections recorded from the front and rear positions, which allowed us to examine limitations and biases in estimates associated with observer position. Comparisons of density estimates between those generated with standard analysis protocols and MRDS methods allowed us to characterise the extent of bias associated with failing to account for pronghorn clusters missed within the A band. We used Program Distance (version 6.2 Release 1; Thomas *et al*. 2010), implementing the MRDS engine (mrds package in R; R Core Team 2015; Laake *et al*. 2013), to evaluate all MRDS and MCDS models.

## Results

We identified 266 clusters (51 in Kemmerer and 215 in Pinedale), comprising 439 individual pronghorn (84 in Kemmer and 355 in Pinedale) across a total of 168.48 $km^2$ surveyed (97.71 $km^2$ in Kemmerer and 70.77 $km^2$ in Pinedale). Group sizes ranged from 1 to 13 individuals (Kemmerer = 1.42, s.e. = 0.15; Pinedale = 1.65, s.e. = 0.10). Of the clusters identified from either position, 47 were detected in the A band, 38 in the B band, 73 in the C band and 103 in the D band. We identified violations of the assumption that all clusters within the A band were detected. Of the 47 clusters detected in the A band from either position, 45 (95.7%) were detected from the front position, whereas 37 (78.7%) were detected from the rear position (Table 2).

Among competing MRDS models, the $AIC_c$ best unconditional detection function incorporated size as a scalar covariate. Among mark–recapture conditional detection functions, the $AIC_c$ best model included distance, size and site; however, other models were competitive ($\Delta AIC_c < 2$; Table 1). Substantial deviations between the unconditional and conditional detection functions derived from the best model demonstrated dependence in cluster detection between observers (Fig. 2). Among the conditional detection functions evaluated, site was the most influential covariate (relative variable importance weight ($w_{site}$) = 0.99) followed by size ($w_{size}$ = 0.67) and position ($w_{position}$ = 0.55; Table 1). Estimates of the probability of detection for pronghorn clusters in the A band derived from the full main-effects model with the addition of distance × position interaction term (Model 8; Table 1) were 0.94 (s.e. = 0.02) from the front position and 0.87 (s.e. = 0.04) from the rear position, whereas the probability of detection for either observer was 0.99 (s.e. = 0.01). The MRDS model-averaged density estimates were 1.04 (s.e. = 0.30) and 6.04 (s.e. = 1.14) pronghorn $km^{-2}$ for Kemmerer and Pinedale respectively (Table 1).

Among MCDS models that assume complete detection for clusters in the A band, models that included size were superior to alternative models ($\Delta AIC_c > 4$) for both the front and rear position (Table 3). Model-averaged density estimates for the front position were 0.85 (s.e. = 0.27) and 5.70 (s.e. = 1.40) pronghorn $km^{-2}$ for Kemmerer and Pinedale respectively. These estimates were 18% and 6% below MRDS estimates for Kemmerer and Pinedale respectively (Tables 1, 3). Model-averaged density estimates for the rear position were 0.71 (s.e. = 0.23) and 5.56 (s.e. = 1.10) pronghorn individuals $km^{-2}$ for Kemmerer and Pinedale respectively (Table 3). Again, MCDS estimates were 32% and 8% below MRDS estimates for Kemmerer and Pinedale respectively (Table 3).

## Discussion

Our double-observer evaluation of pronghorn line-transect surveys revealed a failure from the front and rear positions to satisfy the assumption that all pronghorn clusters within the A band are detected. This critical assumption of distance

**Table 2. Number of pronghorn clusters detected during double-observer aerial line-transect surveys conducted in western Wyoming, USA, in 2004, by observers seated in the front of the aircraft, rear of the aircraft, and duplicate detections, presented by distance band (A = 0–25 m, B = 25–50 m, C = 50–100 m and D = 100–200 m)**

| Detection type | Distance band | | | |
|---|---|---|---|---|
| | A | B | C | D |
| Detected by front observer only | 10 | 6 | 4 | 24 |
| Detected by rear observer only | 2 | 1 | 12 | 19 |
| Detected by both observers | 35 | 31 | 57 | 60 |

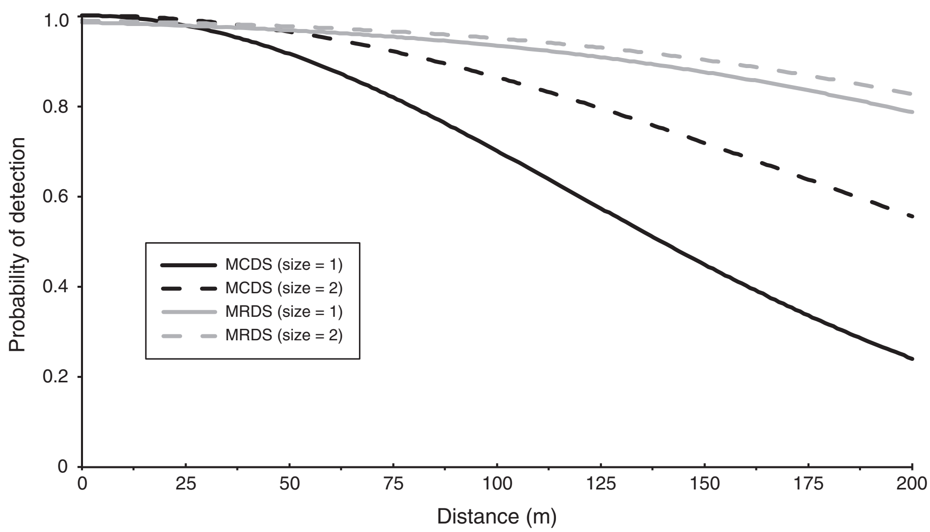


**Fig. 2.** Unconditional (multi-covariate distance sampling (MCDS); black) and conditional (mark–recapture distance-sampling (MRDS); grey) detection functions representing the probability of detection as a function of distance (m) off the transect line for pronghorn (*Antilocapra americana*) groups (clusters) of one (solid) and two (dashed) individuals derived from double-observer MRDS aerial line-transect surveys conducted in westcentral (Pinedale) and south-western (Kemmerer) Wyoming, USA.

**Table 3. Multiple-covariate distance-sampling models with a half-normal key function and no expansion series evaluated for double-observer pronghorn aerial line-transect surveys conducted in south-western (Kemmerer) and westcentral (Pinedale) Wyoming, USA, in 2004**

Position of the observer was either in the front or rear seat of the aircraft. *K*, number of parameters. $\Delta AIC_c$, difference in Akaike's information criterion corrected for finite sample sizes relative to minimum $AIC_c$. $w_i$, Akaike weight. *D*, estimated density of pronghorn $km^{-2}$. s.e., standard error of estimated pronghorn density. Size, covariate representing the cluster size (number of individuals in a group) of pronghorn. Site, covariate representing different study areas

| Observer position | Model | *K* | $\Delta AIC_c$ | $w_i$ | Kemmerer | | Pinedale | |
|---|---|---|---|---|---|---|---|---|
| | | | | | *D* | s.e. | *D* | s.e. |
| Front | ~size | 2 | 0.00 | 0.83 | 0.83 | 0.23 | 5.64 | 1.05 |
| | ~1[A] | 1 | 4.20 | 0.10 | 0.85 | 0.25 | 6.10 | 1.25 |
| | ~site | 2 | 5.07 | 0.07 | 1.00 | 0.33 | 5.89 | 1.23 |
| | Model-averaged estimates[B] | | | | 0.85 | 0.27 | 5.70 | 1.40 |
| Rear | ~size | 2 | 0.00 | 0.98 | 0.71 | 0.23 | 5.55 | 1.07 |
| | ~1[A] | 1 | 8.47 | 0.01 | 0.71 | 0.24 | 6.00 | 1.33 |
| | ~site | 2 | 10.47 | 0.01 | 0.73 | 0.28 | 5.97 | 1.33 |
| | Model-averaged estimates[B] | | | | 0.71 | 0.23 | 5.56 | 1.10 |

[A]Detection function with a constant scale, equivalent to conventional distance sampling.
[B]Model-averaged estimates are based on Akaike weight ($w_i$) values for the competing models.

sampling was nearly satisfied from the front position, with observers detecting 45 of the 47 clusters (96%) within the A band. High detection rates from the front position affirmed the suitability of aerial line-transect distance sampling for pronghorn population monitoring. When detections are restricted to those from the front position, only a modest correction (~4%) to account for imperfect detection within the A band would be required to produce unbiased estimates.

Conversely, we documented substantial violations of the critical assumption of distance sampling from the rear position, detecting only 37 of 47 (79%) pronghorn clusters within the A band. Low detection rates realised from the rear position may have been attributable, in part, to the wing configuration of the Maule 5. Maule 5 wings are supported with a V-shaped strut that generally limits the viewing frame from the rear position to the space delineated between the two struts; this viewing frame is narrowest for the A band and broadens with successive bands. Thus, the brief period in which pronghorn are present within the viewing frame of the A band challenges the ability of observers seated in the rear position to detect all clusters. Additional assessments are needed to determine whether the high rate of undetected clusters within the A band from the rear position is an artefact of small sample size, attributable to individual-observer variation, or represents a systematic bias associated with a visual obstruction for the rear-seat position. Under typical survey protocols, where observations from the front observer (on the right of the aircraft) and rear observer (on the left of the aircraft) are pooled to produce a single detection function and density estimate, the modest bias from the front position (−4% observed) and substantial bias from the rear position (−21% observed) would lead to a negative bias in density estimates of ~13%. Thus, missed detections on the transect line could account for the negative bias of fixed-wing line-transect estimates documented by Pojar and Guenzel (1999). For aircraft, such as the Maule 5, in which the view from the rear position is partially obstructed, management agencies must evaluate whether the benefits of reducing bias by limiting detection to the front position outweigh the costs of reduced precision conceded by forfeiting additional detections from the rear position.

As pronghorn aerial line-transect distance-sampling methods are extended from the Maule 5, in which they were developed, to include other aircraft platforms (e.g. Piper Super Cub or Cessna 152; Guenzel 2007), our results demonstrated the importance of conducting these types of validation trials to quantify potential bias in density estimates. Alternative aircraft types will possess unique attributes for observer visibility and suitability for survey applications. As survey protocols are established for new aircraft platforms, validation trials are essential to assure survey assumption can be met or adapted to produce unbiased estimates. Established protocols (Guenzel 1997) are easily modified to accommodate a double-observer configuration. However, if other aircraft do not permit such an arrangement, video-cameras could be configured to monitor detection rates within the A band.

Our results also demonstrated that both intrinsic and extrinsic factors, beyond distance, influence the probability of pronghorn detection. Among MCDS models, those that included a cluster-size covariate as a scale parameter were superior to alternative models ($\Delta AIC_c > 4$; Table 3). Similarly, among MRDS models, size was included in both the $AIC_c$ best unconditional and conditional detection functions. The importance of cluster size in the present study corroborated the findings of Jacques *et al*. (2014), which suggests managers should account for cluster size in detection functions. Similarly, site was an important covariate among MRDS conditional detection functions, which demonstrated the potential for detection probabilities to vary among landscapes. During survey efforts, we perceived strong differences in pronghorn detectability between the two study areas because of differences in habitat conditions. Pinedale was characterised by lush green vegetation that strongly contrasted with the pelage of pronghorn. In contrast, Kemmerer, the more xeric study site, was visually complex with abundant bare ground and exposed rock, with a general colour signature similar to pronghorn pelage. We introduced the site covariate to capture differences in landscape complexity and greenness at a course level. Future assessments of pronghorn aerial line-transect surveys should evaluate the influence of ordinal measures of percent vegetation and cover type as implemented by Jacques *et al*. (2014), or develop other measures of landscape complexity.

## Implications

Our double-observer assessment of pronghorn aerial line-transect surveys corroborated the conclusions of quadrat-sampling and distance-sampling comparisons (Pojar and Guenzel 1999), namely that distance sampling underestimates pronghorn density because of undetected clusters within the nearest distance band. The substantial bias identified from the rear observer suggests that careful consideration should be given to developing survey protocols that reflect aircraft limitations. Independent, paired observers or analogous methods that use video imagery as a second observer can be used in similar validation trials to determine whether survey assumptions can be adequately met and to develop alternative sampling methods or correction factors as needed. The failure from both observer positions to detect all clusters within the nearest distance band suggests that continued double-observer trials are appropriate for the development of survey- and landscape-specific correction factors. Application of a correction factor in subsequent MCDS analyses will produce unbiased estimates of abundance without increasing survey costs.

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