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Original Article

Aerial Surveys Adjusted by Ground Surveys to Estimate Area Occupied by Black-Tailed Prairie Dog Colonies

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ABSTRACT Aerial surveys using line-intercept methods are one approach to estimate the extent of prairie dog colonies in a large geographic area. Although black-tailed prairie dogs (*Cynomys ludovicianus*) construct conspicuous mounds at burrow openings, aerial observers have difficulty discriminating between areas with burrows occupied by prairie dogs (colonies) versus areas of uninhabited burrows (uninhabited colony sites). Consequently, aerial line-intercept surveys may overestimate prairie dog colony extent unless adjusted by an on-the-ground inspection of a sample of intercepts. We compared aerial line-intercept surveys conducted over 2 National Grasslands in Colorado, USA, with independent ground-mapping of known black-tailed prairie dog colonies. Aerial line-intercepts adjusted by ground surveys using a single activity category adjustment overestimated colonies by ≥94% on the Comanche National Grassland and ≥58% on the Pawnee National Grassland. We present a ground-survey technique that involves 1) visiting on the ground a subset of aerial intercepts classified as occupied colonies plus a subset of intercepts classified as uninhabited colony sites, and 2) based on these ground observations, recording the proportion of each aerial intercept that intersects a colony and the proportion that intersects an uninhabited colony site. Where line-intercept techniques are applied to aerial surveys or remotely sensed imagery, this method can provide more accurate estimates of black-tailed prairie dog abundance and trends. Published 2012. This article is a U.S. Government work and is in the public domain in the USA.

KEY WORDS area occupied, *Cynomys ludovicianus*, line-intercept sampling, monitoring, plague.

The black-tailed prairie dog (BTPD; *Cynomys ludovicianus*) is a burrowing, colonial, diurnal mammal of the squirrel family (Sciuridae) that inhabits the Great Plains of western North America (Hoogland 1995). Directly estimating numbers or density of individuals of black-tailed prairie dogs (prairie dogs hereafter) is difficult because an unknown proportion of animals are underground at any time (Biggins et al. 2006). However, prairie dogs excavate burrows with entrances surrounded by conspicuous mounds of soil up to 1 m high and 3 m wide that can be readily identified from the air (Sidle et al. 2001, White et al. 2005). Line intercepts of areas of burrows or direct mapping of such areas are often used to estimate the extent of prairie dog colonies.

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Prairie dog colony sites (including both active and uninhabited burrows, see below) often contain extensive areas devoid of prairie dogs because of natural population dynamics (Koford 1958, Jachowski et al. 2008), plague (*Yersinia pestis*; Augustine et al. 2008, Cully et al. 2010), shooting (Pauli and Buskirk 2007), and poisoning (Forrest and Luchsinger 2006). Plague and poisoning periodically eradicate entire colonies or portions of colonies, followed by varying degrees of recovery over a period of years. However, the vacant burrows remain visible for several years. Because most prairie dogs live on privately owned land where access requires landowner permission, aerial platforms offer practical methods for estimating the extent of prairie dog colonies over large areas, although vacant burrows complicate aerial assessments (Biggins et al. 2006, McDonald et al. 2011).

How survey methods account for areas of vacant burrows substantially influences estimates of prairie dog colony size (Miller et al. 2005) and also inferences concerning the amount of habitat for rare species associated with prairie dogs such as the black-footed ferret (*Mustela nigripes*), burrowing owl (*Athene cunicularia*), and mountain plover (*Charadrius montanus*; see Kotliar et al. 2006). The U.S. Fish and Wildlife Service recognized the importance of accounting for areas of vacant burrows in their 12-month finding on a petition to list the prairie dog as a threatened species under the Endangered Species Act: "A more accurate large-scale estimate of occupied habitat can be derived by applying a correction factor for percent occupancy (the percent of habitat with burrows currently occupied by black-tailed prairie dogs) to an initial estimate . . . via an on-site inspection of a portion of a survey area to confirm the presence of prairie dogs. This is particularly important in colonies that have been impacted by plague or poisoning. In these instances, burrows remain but prairie dogs are absent. This unoccupied habitat should not be included in estimations of occupied habitat" (12-Month Finding on a Petition to List the Black-tailed Prairie Dog as Threatened or Endangered. *Federal Register* 74:231 [Dec 3, 2009] p. 63346). In their review of prairie dog monitoring McDonald et al. (2011:6) also observed: "Unfortunately, in the case of the BTPD, occupied acres are often being measured—despite the absence of a definition—by drawing a subjective boundary around an indefinite collection of prairie dog burrows that may not even be currently occupied by prairie dogs."

METHODS

Definition of Prairie Dog Colony and Prairie Dog Colony Site

In general, a colony is a dense concentration of breeding animals such as prairie dogs. An area of vacant prairie dog burrows or old nests of a colonial-nesting bird do not constitute a colony. We label such vacant areas as colony sites where animals may well occur again through recolonization. Thus, we define the following terms:

1. Prairie dog colony = an area with burrows that exhibit evidence of recent prairie dog activity, delineated using the method described in the section "Ground-based surveys of National Grasslands in Colorado, USA."
2. Uninhabited prairie dog colony site = an area where burrows are present but abandoned and inactive.
3. Prairie dog colony site = an area with burrow mounds visible from an aerial platform that may include prairie dog colony and uninhabited prairie dog colony site.
4. Non-prairie dog colony site = an area without colony sites.

Approaches to Adjusting Aerial Surveys of Prairie Dog Colonies

Aerial transect surveys have employed Global Positioning System (GPS) receivers in aircraft to record proximal and distal points where aerial transects intercepted prairie dog colony sites (hereafter, an aerial intercept [Fig. 1]; Sidle et al. 2001, White et al. 2005, Odell et al. 2008). The ratio between the lengths of aerial intercepts of colonies and total intercept surveyed yields an estimate of the proportion of area occupied by colonies.

If prairie dogs do not currently live in any portion of a colony site, it is straightforward to exclude intercepts of such areas from the estimate of prairie dog colony area (Sidle et al. 2001, White et al. 2005, Odell et al. 2008). Providing an adjustment becomes more complex, however, when an aerial intercept includes both areas of colony and areas of uninhabited colony site (Fig. 1). Given the difficulty of distinguishing inhabited versus uninhabited colony sites from aerial platforms, visiting a subset of aerial intercepts on the ground allows observers to more slowly and carefully classify intercepts as colony versus uninhabited colony site using a suite of indicators such as fresh scat and recent disturbance at burrow mounds, the presence of vegetation cropped close to the ground surface, and visual confirmation of prairie dogs.

Several approaches have attempted to adjust aerial-survey estimates of prairie dog colonies. The Single Activity Category Adjustment (SACA) classifies an intercept as "active" or "inactive." The SACA defines the entire intercept as "colony" if any of it intersects a portion with prairie dog sign (e.g., White et al. 2005, Odell et al. 2008). The SACA does not utilize information on the relative amounts of colony versus uninhabited colony site along the intercept.

Another approach is to classify intercepts into different categories that represent different levels of prairie dog activity along a given intercept. For example, during ground surveys of intercepts that were detected during an aerial survey, Odell et al. (2008) classified intercepts based on the level of prairie dog sign along the intercept as ">50% active" or "<50% active." These classifications can then be used to adjust the estimate derived from the aerial survey. We refer to this approach as the Multiple Activity Category Adjustment (MACA; Fig. 2).

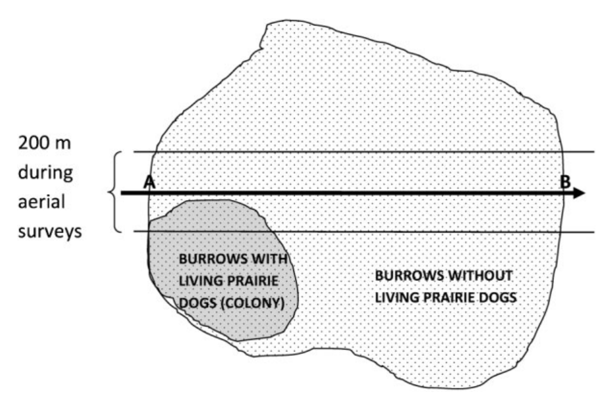

Figure 1. Illustration of a method for estimating the extent of black-tailed prairie dog colony sites used in Colorado, USA (White et al. 2005, Odell et al. 2008). During aerial surveys, the observer looking out of the right side of the aircraft as far as 100 m sees the prairie dog colony (burrows with living prairie dogs) and upon arrival at B records the entire intercept AB as "active" colony. During ground surveys the entire length AB would also be used to calculate estimates as long as any part of the colony was within 10 m of the transect line. In this paper we refer to this as the Single Activity Category-maximum approach.

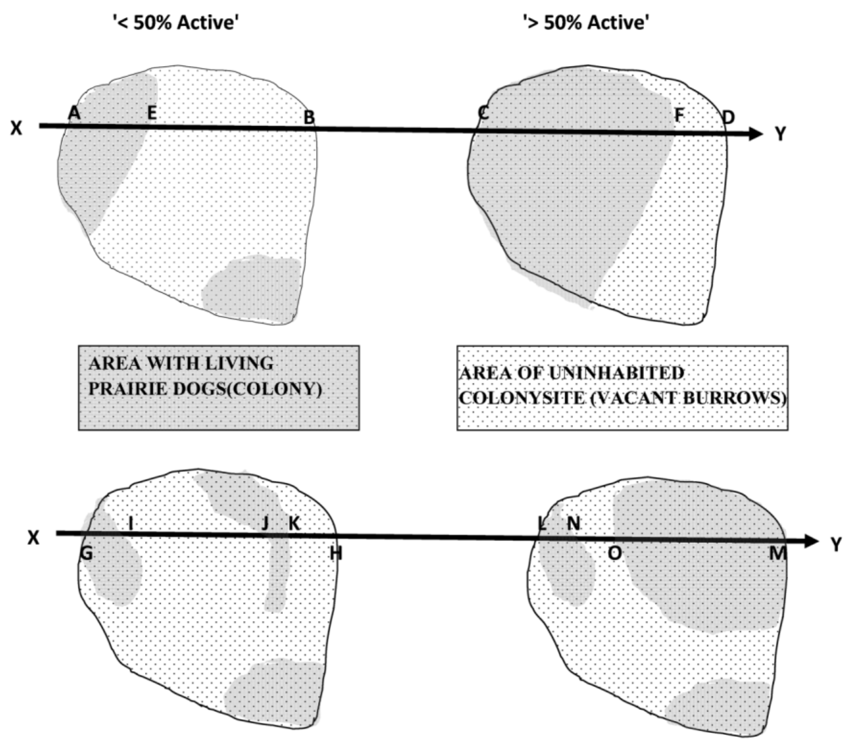

Figure 2. Illustration of various approaches for ground-truthing black-tailed prairie dog colonies to derive adjustment probabilities for aerial-survey results. With the Single Activity Category-maximum approach, the segment lengths A–B, C–D, G–H, and L–M would all be entirely counted as prairie dog colonies ("active"). With the Multiple Activity Category Adjustment-midpoint approach using the 2 categories in the Colorado Division of Wildlife database (<50% and >50% active), 25% of A–B and G–H and 75% of C–D and L–M would be counted. With the Proportional Activity Adjustment, the segments A–E, C–F, G–I, J–K, L–N, and O–M would be measured and used to adjust the aerial-survey data. The line *X*–*Y* represents the transect walked during ground surveys (along the aerial flight line).

Proportional Activity Adjustment

Another approach is to measure the length of segments of the aerial-intercept line that overlaps the prairie dog colony and uninhabited colony site. We refer to this as the Proportional Activity Adjustment (PAA; Fig. 2). From the air, data are obtained on lengths of transects classified as colony (C*: at least some evidence of living prairie dogs), uninhabited colony site (U*: an area containing burrows without any observed evidence of living prairie dogs), and noncolony (N*: areas without burrows). Sidle et al. (2001) used the SACA for small colony sites, but they used the PAA for larger colony sites where the aircraft could be maneuvered appropriately to record the point of transition between active and inactive portions of the colony site.

Because some transect segments classified as colony from the air may include some uninhabited colony sites, it is necessary to conduct ground surveys of a subsample of the intercepts used to calculate C*, U*, and N*. When a given intercept in a given class is visited on the ground, segments of that intercept or the whole intercept are classified as either colony (C) or noncolony (N). For each aerially classified intercept that is visited on the ground, the ground surveyors measure the portion that is colony and the portion that is uninhabited colony site and/or noncolony. The proportions of one aerial class that turn out to be in a specific ground class are estimates of classification probabilities. For example, the proportion of lengths deemed to be a colony from the air that are classified as colony on the ground (p_{C^*C}) is an estimate of the probability that a point on a transect segment deemed to be a colony was correctly classified, based on the assumption that the ground assessments are totally accurate (Table 1). Similarly, p_{U^*C} is an estimate of the proportion of uninhabited colony site aerial-intercept length that is determined to be a colony, and p_{N^*C} is an estimate of the proportion of noncolony intercept length that is determined to be a colony (Table 1).

The estimated total area of active colony based on the PAA ($\hat{C}$) is given as

$$\hat{C} = \mathrm{C}^* \times p_{\mathrm{C^*C}} + \mathrm{U}^* \times p_{\mathrm{U^*C}} + \mathrm{N}^* \times p_{\mathrm{N^*C}}$$

The above is the length of segments in an aerially determined class multiplied by the probability that a length of that class is classified on the ground as colony, summed over all aerial classes. Our analysis of the aerial and ground surveys of

Table 1. Matrix of estimated probabilities for each possible combination of aerial classification (C*, U*, and N*) and ground classification (C and N) of black-tailed prairie dog colonies.

	Assessment from ground	
Assessment from air	**Active colony (C)**	**Noncolony (including inactive colony site) (N)**
Active colony (C*)	p_{C^*C}	$p_{C^*N} = 1 - p_{C^*C}$
Uninhabited colony site (U*)	p_{U^*C}	$p_{U^*N} = 1 - p_{U^*C}$
Noncolony (N*)	p_{N^*C}	$p_{N^*N} = 1 - p_{N^*C}$

the National Grasslands in Colorado indicated that it is not necessary to conduct ground surveys of the segments classified as N* (noncolony site) from the air because this source of error is extremely small. Specifically, we found that out of 694,402 m of total transect length classified as noncolony (N*) from the air, only 101 m was actual active colony when surveyed on the ground ($p_{\mathrm{N^*C}} = 0.00015$). As long as this proportion is negligible, then

$$\hat{C} = \mathrm{C}^* \times p_{\mathrm{C^*C}} + \mathrm{U}^* \times p_{\mathrm{U^*C}}$$

The accuracy of this estimate is influenced both by the aerial estimates of C* and U*, and by the ground-based estimates of probabilities ($p_{\mathrm{C^*C}}$ and $p_{\mathrm{U^*C}}$). Estimates of variances of C* were given by Sidle et al. (2001); the variance of U* is estimated similarly. The conditional variances of $p_{\mathrm{C^*C}}$ and $p_{\mathrm{U^*C}}$ are calculated directly from the subsample of aerially classified intercepts classified on the ground as active. Bootstrap procedures can be used to compute the estimated variance (standard error) for $\hat{C}$ (Manly 2006); see McDonald et al. (2011) for examples.

Below, we first illustrate the MACA based on an aerial and ground survey of prairie dogs conducted by the Colorado Division of Wildlife (CDOW) in eastern Colorado, USA. We then examine the PAA by comparing the CDOW aerial survey and an independent ground-based survey of prairie dog colonies on the 2 National Grasslands in eastern Colorado.

Aerial Line-Intercept Survey

An aerial transect survey of eastern Colorado was conducted by CDOW in 2006 (Odell et al. 2008). The portions of this aerial survey overlapping Comanche National Grassland (CNG) and Pawnee National Grassland (PNG) were conducted during November 2006 and September 2006, respectively. While flying along a transect, an observer recorded the beginning and end point at which the transect intersected areas with visible prairie dog burrows (Fig. 1). The SACA was used by recording intercepts as being "active" (prairie dog sign noted at some point within a 200-m-wide strip along the intercept) or "inactive" (no prairie dog sign; CDOW 2006).

Ground-Based Survey of Aerial Intercepts in Eastern Colorado

Following the aerial survey of eastern Colorado, CDOW personnel visited a subsample of the intercepts classified as "active" and "inactive" (Odell et al. 2008). Each intercept was classified into 1 of 3 categories: <50% active, >50% active, or inactive (Odell et al. 2008; Table 2). Odell et al. (2008) made adjustments for the entire colony site based on false positives (classified as active from the air but no activity seen during ground surveys) and false negatives (classified inactive from the air but activity found during ground surveys) but made no adjustments based upon the ground-survey categories, <50% active and >50% active. We used the CDOW intercept length data (CDOW, unpublished data) to compare the SACA and MACA. For SACA, intercepts classified as active during the aerial survey could vary anywhere from 1% to 100% active in reality, but the proportion is not measured and hence is assumed. We examined scenarios where we assumed that the proportion of the aerial intercepts inhabited by prairie dogs was either 100% (SACA-max.),

Table 2. Variation in estimates of black-tailed prairie dog colony area based on different assumptions concerning the percent of colony sites (areas with both inhabited and contiguous uninhabited burrows) that are actually inhabited by prairie dog. The Single Activity Category Adjustment (SACA)-maximum assumes that any given intercept (either aerial or ground-based) is either a colony or is an uninhabited colony site. The SACA-midpoint and SACA-minimum provide contrasts based on assumptions that 50% and 1%, respectively, of the SACA-maximum actually intersected prairie dog colony. The Multiple Activity Category Adjustment (MACA) comparisons use data from ground surveys during which observers examined entire intercepts designated as active (colony) from the air and then reclassified each as inactive (uninhabited colony site), <50% active, or >50% active (Odell et al. 2008). The MACA-maximum assumes 100% of intercepts in the >50% category and 50% of the intercepts in the <50% category overlapped prairie dog colony. The MACA-midpoint assumes 75% and 25% respectively, and the MACA-minimum assumes 51% and 1%, respectively.

	Intercept classification during aerial survey			Final estimate of prairie dog colony intercept length
	Colony		Noncolony	
Intercept classification for SACA ground survey:	**Colony**	**Noncolony**	**Colony**	
Total length of intercepts (m)	90,431	30,763	705	
Total length of SACA-max. intercepts (m)[a]	90,431	0	705	91,136
Total length of SACA-midpoint intercepts (m)[b]	45,216	0	353	45,569
Total length of SACA-min. intercepts (m)[c]	904	0	7	911

	Intercept classification during aerial survey					Final estimate of prairie dog colony intercept length
	Colony			Noncolony		
Intercept classification for MACA ground survey:	**>50% colony**	**<50% colony**	**Noncolony**	**>50% colony**	**<50% colony**	
Total length of intercepts (m)	37,872	52,560	30,763	0	705	
Total length of MACA-max. intercepts (m)[d]	37,872	26,280	0	0	353	64,505
Total length of MACA-midpoint intercepts (m)[e]	28,404	13,140	0	0	176	41,720
Total length of MACA-min. intercepts (m)[f]	19,315	526	0	0	7	19,848

[a] Assuming 100% of intercepts classified as colonies are actually colonies.
[b] Assuming 50% of intercepts are actually colonies.
[c] Assuming 1% of intercepts are actually colonies.
[d] Assuming max. levels of active colony (100% and 50%, respectively) for the 2 colony categories.
[e] Assuming midpoints (75% and 25%, respectively) for the 2 colony categories.
[f] Assuming min. levels of active colony (51% and 1%, respectively) for the 2 colony categories.

50% (SACA-midpoint), or 1% (SACA-min.). For MACA, aerial-intercept length is partitioned into 2 categories: <50% active and >50% active. For each category, the actual proportion that is active is not measured and hence must be assumed. We examined MACA scenarios where we assumed that the first category was either 1%, 25%, or 50%, and the second category was either 51%, 75%, or 100% of the intercepts classified as >50% colony intersected a colony. The lower percentages in each category (1% and 51%) yielded comparisons based on the worst-case scenario (MACA-min.) and the highest values (50% and 100% in each of the 2 categories) provided the best-case scenario (MACA-max.). The 25% and 75% categories illustrate results if the midpoint of each of the 2 categories (≤50% and >50%) intersected a colony (MACA-midpoint).

Ground-Based Surveys of National Grasslands in Colorado

In 2006, the U.S. Forest Service (USFS) mapped prairie dog colonies during June and August on CNG and during July and August on PNG, within 60 days of the aerial survey on PNG and 89–156 ($\bar{x} = 117$) days prior to the aerial survey on CNG. Colony boundaries were delineated based on 1) the locations of burrow entrances that showed evidence of recent prairie dog presence (digging–soil disturbance and/or presence of green or brown fecal pellets near the burrow entrance), and 2) sharp transitions between prostrate or recently cropped vegetation and zones of taller vegetation that did not show signs of cropping by prairie dogs (Johnson 2005, CDOW 2006, Augustine et al. 2008, Cully et al. 2010).

Using burrows alone can create uncertainty in the delineation of complex polygons, but the additional use of vegetation boundaries in combination with burrow entrances minimized uncertainty in boundary delineation. Areas lacking evidence of prairie dog activity but that were surrounded on all sides by areas with prairie dog activity were included within the area mapped as an active colony. In cases where a colony site contained both inactive and active burrow entrances, the observer walked or drove slowly with an all-terrain vehicle along systematic transects across the colony, with transects spaced at ≤50-m intervals. The observer examined burrow entrances for activity, and used pin flagging to demarcate burrows with signs of activity as well as zones of vegetation height transitions in spaces between the outermost burrows showing signs of activity. With this method, individual burrows that lack signs of recent activity can be (and frequently are) included within the mapped colony boundary because other nearby burrows show signs of activity and/or other signs (vegetation clipping, scat) indicate the use of the area by prairie dogs. Colony boundaries were mapped with handheld GPS receivers (Trimble, Sunnyvale, CA), and incorporated into a Geographic Information System (GIS).

We note that the boundary between cropped and adjacent uncropped vegetation is typically visually distinct at the edges of black-tailed prairie dog colonies, but this may not be true for other prairie dog species that affect vegetation structure to a lesser degree. Hence, our mapping method may not be appropriate for other prairie dog species. McDonald et al. (2011) proposed an alternative means of assessing the proportion of a colony site actively occupied by prairie dogs based on a determination of the proportion of burrow entrances within a colony site that have signs of recent prairie dog activity. Our objective was not to evaluate or advocate a particular ground-survey method, but rather to assess the degree to which such ground surveys may alter conclusions based on aerial surveys alone.

We have not tested the ability of different observers to replicate boundary delineation, either from aerial platforms or during ground surveys. We make the assumption that observers located 0–2 m above ground level who are moving slowly and have the ability to stop, move in any direction, and check for signs of scat, digging, and vegetation cropping are more accurate in delineating colony boundaries than are observers approximately 55 m above ground level traveling at 160 km/hour in a single direction without the ability to recheck their observations.

During 2000–2006, poisoning and shooting of prairie dogs were prohibited on CNG and PNG. Contractions in colony boundaries indicative of a plague epizootic affected a significant portion of CNG colonies between 2005 and 2007 (Augustine et al. 2008, Cully et al. 2010).

Comparison of Aerial and Ground-Based Surveys

In a GIS, we identified all CDOW aerial-survey transects, aerial intercepts classified as colonies, and aerial intercepts classified as uninhabited colony sites that occurred within the boundaries of CNG and PNG. We overlaid transects and aerial intercepts with the USFS ground-mapped colonies, and then calculated the length of transect surveyed and length of intersection with ground-mapped colonies on the National Grasslands. For each aerial intercept, we measured the portion of that intercept that was mapped as colony on the ground, and the portion mapped as uninhabited colony site or noncolony. In cases where the ground-mapped colony extended farther in one or both directions along the aerial transect, we measured the length of the flight path that extended into this portion of the ground-mapped colony, and added it to the length of aerial intercept overlapping the colony.

RESULTS

For the ground-based survey of aerial intercepts in eastern Colorado, a subsample of 150 intercepts (total length = 123,481 m) that had been classified as either prairie dog colonies or inactive colony sites from the air were examined on the ground by CDOW staff. One hundred nine of these intercepts with a total intercept length of 90,431 m were classified as colony (“active”) on the ground (Table 2). Of the total length of all aerial intercepts classified as colony from the air that were examined on the ground, 31.2% (37,872 m) was classified as >50% colony on the ground, 43.4% (52,560 m) as <50% colony on the ground, and 25.4% (30,763 m) as uninhabited colony sites on the ground. An additional 6 intercepts classified as uninhabited colony sites during aerial surveys were examined on the ground (total aerial-survey length = 2,286 m).

With the SACA, resulting estimates can vary by a factor of 100 based on the difference between SACA-minimum and SACA-maximum assumptions (Table 2). Using the MACA, assumptions are still made about the proportional occupancy in each category, but in this case the maximum estimate (82,813 m) is only 3 times greater than the minimum estimate (27,332 m). In this example from eastern Colorado, assuming the value is the mid-point of the class gives similar estimates for both the SACA and MACA (Table 2) because similar amounts of intercept lengths were classified as being >50% active (52,399 m) and <50% active (60,122 m), respectively.

Comparison of aerial and ground surveys of the National Grasslands revealed high concordance in the ability of both surveys to detect colony sites (Table 3; lines E, F, and G). However, the aerial surveys did not differentiate between colonies versus uninhabited colony sites along a given intercept. For CNG, 36,407 m of aerial intercepts were classified from the air as being active colony. In contrast, aerial-survey transects intersected only 15,352 m of ground-mapped colony, based on the 2006 USFS ground survey. Because of an extensive epizootic plague outbreak in the study area between 2005 and 2006 (Augustine et al. 2008, Cully et al. 2010), many prairie dog colonies were larger in 2005 than in 2006. A merge of the maximum extent of colonies mapped in 2005 and 2006 revealed that aerial transects intersected 32,895 m of combined 2005–2006 ground-mapped colonies, which is similar to the total length of aerial intercepts classified as being active from the air in 2006 (36,407 m; Table 3).

Intercepts classified as "colony" from the air yielded an estimate of 7.8% of CNG being occupied by prairie dog colonies. If this value is adjusted using the SACA-maximum based on findings reported by Odell et al. (2008) that 91% of intercepts deemed to be colonies from the air were colonies on the ground and 33% of intercepts deemed to be uninhabited colony sites from the air were colonies on the ground, then 7.2% of CNG is estimated to be occupied by prairie dog colonies (Table 3). In contrast, using the length of intersections of aerial transects with ground-mapped colonies (15,352 m) plus the length of aerially detected colony intercepts that were not detected on the ground (1,912 m) yielded an estimate that only 3.7% of CNG was occupied by prairie dog colonies. This difference suggests that for CNG, the SACA-maximum overestimated prairie dog colony occupancy by 94% (Table 3).

For PNG, 3,156 m of aerial transects was classified as being active colony from the air, while 2,051 m of aerial transects intersected ground-mapped colonies. Epizootic plague typi-

Table 3. Comparison of the length of black-tailed prairie dog colony intercepts detected during aerial and ground surveys of prairie dog colonies on Comanche and Pawnee National Grasslands, Colorado, USA. Ground surveys were conducted during 7 June–17 August 2006 on the Comanche and 17 July–9 August 2006 on the Pawnee. Aerial surveys were conducted during 8–22 November 2006 on the Comanche and 12–20 September 2006 on the Pawnee. Aerial-survey data were supplied by the Colorado Division of Wildlife.

Measurement	Comanche National Grassland (Carrizo Unit)	Pawnee National Grassland
Area of National Grassland in analysis (ha)	102,821	77,921
(A) Total length of aerial transects intersecting analysis area (m)	466,341	228,061
(B) Total length of aerial intercepts classified as "active" prairie dog colonies from the air (m)	36,407	3,156
(C) Total length of aerial intercepts estimated to overlap prairie dog colonies based on SACA-max (Table 1)[a]	33,508	3,356
(D) Total length of aerial transects that overlapped ground-mapped prairie dog colonies (m)	15,352	2,051
(E) Total length of aerial intercepts classified as "active colony" from the air, but not intersecting either ground-mapped colonies or ground-mapped inactive colony sites (m)[b]	1,912	61
(F) Total length of aerial intercepts classified as "inactive" from the air, but classified as active prairie dog colony during ground surveys (m)	68	33
(G) Total length of aerial transects with no aerial detection, but intersecting ground-mapped active prairie dog colony (m)	509	72
(H) Total length of aerial transects that intersected areas ground-mapped as prairie dog colony in 2005 and/or 2006 (m)[c]	32,895	3,466
(I) Percent of study area occupied by prairie dog colonies based on 2006 ground surveys[d]	3.30%	0.90%
(J) Percent of study area occupied by prairie dog colonies based on 2006 ground-survey intersection with aerial transects (D) plus "missed" colonies (E) detected during aerial surveys but not detected during ground surveys	3.70%	0.93%
(K) Percent of study area occupied by prairie dog colonies based on unadjusted aerial survey	7.81%	1.38%
(L) Percent of study area occupied by prairie dog colonies based on aerial survey plus SACA-max.	7.18%	1.47%
(M) Overestimation of prairie dog colony area by aerial + SACA method vs. ground survey ($[L - J] \times 100/J$)	94%	58%

[a] Assuming 91.3% of aerially classified active colony intercepts are actually colony, and assuming 33.3% of aerially classified uninhabited colony-site intercepts are actually active colonies (Odell et al. 2008).

[b] This value can be interpreted as being either active prairie dog colonies that were missed during the ground survey or as intercepts mistakenly classified as prairie dog colony during the aerial survey or a combination of both.

[c] This value includes the lengths of transects overlapping active prairie dog colonies mapped during ground surveys during either 2005 (prior to an outbreak of plague on the Comanche) or 2006 (yr of a plague outbreak on the Comanche). The percentage values reflect the proportion of ground-mapped active colonies that were captured by the aerial surveys if all the active area during 2005 and 2006 had still been active during the aerial surveys.

[d] The percentage of ground-mapped active colonies that were captured by the aerial surveys if all of the active area during 2005 and 2006 had still been active during the aerial surveys.

cally influences some prairie dog colonies within the PNG each year (Stapp et al. 2004). A merge of the maximum extent of colonies mapped in 2005 and 2006 revealed that aerial transects intersected 3,466 m of ground-mapped colonies, which is similar to the total length of aerial intercepts classified as being active from the air (3,156 m; Table 3). Intercepts classified as "colony" from the air yielded an estimate of 1.38% of PNG being occupied by prairie dog colonies. If this value is adjusted using the SACA-maximum based on findings reported by Odell et al. (2008) that 91% of intercepts deemed to be colonies from the air were also colonies on the ground, and that 33% of intercepts deemed to be uninhabited colony-sites from the air were colonies on the ground, then 1.47% of PNG is estimated to be occupied by prairie dog colonies (Table 3). In contrast, using the length of intersections of aerial transects with ground-mapped colonies (2,051 m) plus the length of aerially detected colony intercepts that were not detected on the ground (61 m) yielded an estimate that only 0.93% of PNG was occupied by prairie dog colonies. For PNG, the SACA-maximum of the aerial survey overestimated prairie dog colony occupancy by 58% (Table 3).

Based on 48 intercepts that were classified as colonies in the aerial survey of the National Grasslands and then compared with the ground survey, the PAA estimated that $p_{C^*C} = 0.38$. Based on 7 intercepts classified as inactive colony in the aerial survey of the National Grasslands, we estimated that $p_{U^*C} = 0.083$. The variance of the mean for p_{C^*C} based on 48 intercepts in our National Grassland analysis was 0.003 (SE = 0.057). The variance of the mean for p_{U^*C} based on 7 intercepts in our National Grassland analysis was 0.003 (SE = 0.056).

DISCUSSION

The PAA permits more accurate adjustments to the aerial-survey data than the SACA or MACA because adjustments are based on empirical data rather than assumptions about the proportion of colony-site intercepts that represent active prairie dog colony. The ground-based colony boundary surveys we used in our analysis were derived from 2 specific domains of interest (2 National Grasslands) within a much larger aerial survey, and do not represent a random subsample of the aerially detected intercepts. Our estimates of p_{C^*C} and p_{U^*C} are therefore not applicable beyond the 2 areas for which they were derived. Rather, our findings demonstrate that the extent of colony sites can be substantially larger than the extent of prairie dog colonies. In addition, when ground-based surveys are used to adjust aerial line-intercept classifications, the final estimate of colony area can be strongly influenced by the way in which ground-survey data are used to adjust estimates from aerial platforms. Disease, especially sylvatic plague, as well as poisoning and recreational shooting can create large areas of uninhabited burrows within colony sites, even though some portions of the colony site may be occupied by prairie dogs. Our analyses indicate that ground surveys used to adjust estimates of prairie dog colony area from aerial platforms will be substantially more accurate if they measure the proportion of each ground-checked intercept that is occupied by prairie dogs (colony) and the proportion that consists of uninhabited colony site and/or noncolony, as recently recommended by McDonald et al. (2011). Repeated estimates of prairie dog abundance by aerial surveys that define areas of uninhabited burrows as colonies may not accurately document colony trends because of temporal variability in the proportion of colony sites consisting of colonies.

We found that the SACA-maximum matched the estimate of colony sites based on intensive ground-mapping if we overlaid colonies mapped in both 2005 and 2006 (i.e., including colonies that contracted between 2005 and 2006) with aerial line-intercept survey data (Table 3). This shows that significant portions of intercepts classified as "colony" from the air in 2006 were actually inactive colony sites that had been colonies the previous year. This finding shows that the difference between aerial and ground-based surveys can be explained on the basis of the dynamic nature of prairie dog activity, rather than differences in resolution between the aerial and ground surveys.

The PAA could underestimate colony extent if ground surveys do not estimate the amount of colony intercepts that were missed during the aerial survey. However, we found that this source of error was extremely small. For the National Grasslands, the proportion of intercepts classified aerially as noncolony that were actually prairie dog colony on the ground was 0.00015. This indicates that where prairie dog colonies occupy >1% of the study area, this source of error will be ≥2 orders of magnitude smaller than the estimate of prairie dog colony area. Another potential source of bias may occur if landowners who poison their prairie dogs are less likely than others to allow access for ground-truthing. This bias would presumably be equivalent for all methods that require on-the-ground visits to verify prairie dog presence.

We do not address 2 key survey design questions: 1) the way in which an area is subsampled using an aerial survey or aerial imagery, and 2) the way in which potential colony sites identified in the aerial survey or imagery are selected for ground-based surveys. There are many ways to approach both levels of subsampling, which in turn affect the appropriate estimators of error surrounding the resulting colony area estimate. The aerial and ground surveys that we analyzed are not intended as examples of ideal survey designs, but rather represent a unique opportunity to compare the aerial and ground methods. Application of the PAA as described here assumes 1) random subsampling of the study area based on the aerial platform (line-intercept or otherwise), and 2) random subsampling of the population of objects identified by the aerial platform. See McDonald et al. (2011) for a detailed treatment of more complex survey designs, including spatially balanced sampling and/or stratification, cluster sampling, and stratification based on the size of potential colony sites.

Another important issue concerning the use of ground surveys to adjust aerial surveys is the length of time that elapses between the two. For the ground survey conducted by CDOW, the probability that an aerially classified active colony intercept was subsequently reclassified as uninhabited colony site on the ground increased with increasing time between the aerial and the ground survey (Odell et al. 2008). Because aerial surveys of southeastern Colorado (including the CNG) occurred in November and were followed by a large winter storm in December of 2006, intercepts in that region could not be ground-checked until the following spring. The finding that many aerially classified active intercepts in southeastern Colorado were subsequently classified as inactive on the ground was attributed to the effects of this winter storm (Odell et al. 2008). However, ground-mapping by USFS staff on CNG occurred prior to the aerial survey and the winter storm. Rather than attributing this discrepancy to effects of winter storms on prairie dog populations after the aerial survey, we note that epizootic plague caused a large decline in colony area in this region between 2005 and 2006 (Augustine et al. 2008, Cully et al. 2010).

Line-transect surveys conceptually are based on transects of zero width, although in practice, a strip of specified width is often used to facilitate decisions concerning the start and end of an intercept while flying. The likelihood that a strip overlaps a prairie dog colony increases with wider strips in cases where a colony site includes both colony and areas of vacant burrows. To meet the assumptions of line-intercept sampling, one approach is to map the boundaries of the inhabited portion of a colony site during a ground visit using a GPS receiver, and then overlay the mapped polygon with the aerial intercept in a GIS. The intersection of ground-mapped colonies with the aerial intercepts would use a ground-based strip width of zero. Using a strip width of zero during ground surveys in combination with the PAA allows for the influence of the aerial strip width to be removed from the final prairie dog colony area estimate.

Another ground-based approach to estimate the proportion of colony sites that are actively occupied by prairie dogs was recently proposed by McDonald et al. (2011). In their method, a subset of colony sites classified as active during the aerial survey and a subset of sites classified as unoccupied colonies are visited on the ground. For each of these sites, all or a subset of the burrow entrances are surveyed to determine the proportion showing signs of prairie dog activity versus the proportion that do not. This approach is conceptually similar to the proportions derived from our overlay of aerial intercepts with ground-mapped colonies (i.e., p_{C^*C} and p_{U^*C}) in that both methods adjust the aerially obtained estimate using estimates of proportional activity, rather than categories of activity. If the McDonald et al. (2011) ground-survey protocol were to be used in combination with an aerial line-intercept survey, this would also remove any effect of aerial strip width from the final estimate of occupied colony area. We are unaware of studies that compare the accuracy of the colony boundary delineation–mapping approach that we used versus the method of measuring the proportion of burrow entrances with activity. Such evaluation remains an important research need. We hypothesize that the method proposed by McDonald et al. (2011) may produce slightly lower estimates of proportional activity because our method of colony boundary mapping allows for individual burrows that lack signs of recent activity, but that are surrounded by other burrows with signs of activity, to be included within the area mapped as an active colony (see the Methods Section). Overall, our findings support the recommendation (McDonald et al. 2011) that surveys based on aerial platforms do indeed need to be adjusted on the basis of ground surveys to effectively estimate the area occupied by prairie dog colonies.

In South Dakota, USA, Kempema (2007) estimated 253,000 ha of prairie dog colonies in 2006 based solely upon an examination of aerial imagery from the U.S. Department of Agriculture's National Agriculture Imagery Program. She noted that her estimate may be an overestimate due the inability to differentiate between active colonies and inactive colony sites. Plague affected over 11,000 ha on the Pine Ridge Indian Reservation in 2005 and continues to affect thousands of additional ha on and outside the Reservation through 2010. During 2004–2006, 12–16,000 ha of colonies were poisoned annually by South Dakota agencies (Kempema 2007). Such extensive effects of plague and poisoning on prairie dogs underscore the need to account for inactive colony sites when estimating prairie dog colony area from aerial platforms. Where ground-based estimates of proportional activity are applied to aerial surveys or to remotely sensed imagery, the PAA can result in meaningful estimates of prairie dog abundance and trends.

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