Black-tailed prairie dogs (Cynomys ludovicianus) are both ecologically important and socially contentious on the grassland and shrub–grasslands in central and eastern portions of Montana, USA (Foresman 2001). Described as "ecosystem engineers" (Miller et al. 2002), they influence landscapes by extensive burrowing, grazing, and selective removal of tall plants (Whicker and Detling 1988, Kotliar et al. 2006). Prairie dog colonies also provide habitat for several species (Lomolino and Smith 2004), including the endangered black-footed ferret (Mustela nigripes; Cahalane 1954, Campbell et al. 1987), burrowing owls (Athene cunicularia; Desmond et al. 2000, Sidle et al. 2001a), and mountain plover (Charadrius montanus; Knowles 1982, Dinsmore et al. 2005, Tipton et al. 2007). In addition to their conservation role in grassland ecosystems, prairie dogs are often found in conjunction with livestock grazing, which triggers debates about forage competition between prairie dogs and livestock (Stoddard and Smith 1955, Hansen and Gold 1977, Guenther and Detling 2003, Derner et al. 2006). Conflict over the role of prairie dogs in grassland ecosystems requires management agencies to accurately assess the current status of prairie dogs and response to management for this species.

In addition to the ecological and social interest in prairie dogs, the species has experienced extensive population declines over the past 2 centuries (Miller et al. 2007). In the past, the reduction in prairie dog populations was mainly due to aggressive eradication programs aimed at reducing or eliminating prairie dog populations. More recently, sylvatic plague (Yersinia pestis) has decimated populations throughout the species’ range (Cully and Williams 2001). These anthropogenically induced declines in prairie dogs have led to the decline of the black-footed ferret and difficulties in restoring ferrets to the wild. Black-footed ferret recovery efforts have focused on maintaining complexes of prairie dogs colonies to provide sufficient prey and habitat for ferrets (Miller et al. 1990). Currently, the amount of suitable habitat for potential ferret reintroductions in Montana is unknown.

Despite their keystone ecological role, public interest, their legal status, and the fact that this species has been a focus of conservation agencies and other interest groups, no rigorous estimate of the area occupied by prairie dogs in Montana...
exists. The Conservation Plan for Black-tailed and White-tailed Prairie Dogs in Montana (MPDWG 2002) and Montana’s Comprehensive Fish and Wildlife Conservation Strategy (MFWP 2005) both have identified the need for a comprehensive, rigorous assessment of the status of the prairie dog. The Montana Prairie Dog Working Group identified an objective of 42,105 ha of active prairie dog colonies and recommended management actions to achieve this objective (MPDWG 2002). However, the lack of a current and rigorous estimate of active prairie dog acreage has precluded evaluation of any management actions. Additionally, a reliable estimate is needed for interstate, collaborative conservation efforts, such as the WAFWA Prairie Dog Conservation Team (B. Van Pelt, Western Association of Fish and Wildlife Agencies, personal communication), a species status review by the U.S. Fish and Wildlife Service (USFWS 2008), and to assist in black-footed ferret recovery planning efforts. Current estimates of occupied prairie dog colony area in Montana are known to be underestimates (MPDWG 2002), yet these estimates are currently the only available data for federal species status review. Using a low estimate to represent status may result in a conservative federal listing decision, perhaps causing resources to be diverted away from species in more dire need of conservation attention and unnecessary restrictions on land uses.

Previous efforts to quantify the area of occupied prairie dog area have not covered the full range of prairie dogs in Montana. The first statewide inventory of prairie dog colonies in Montana was conducted in the mid-1980s and produced an estimate of 48,562–52,609 ha of occupied habitat (Campbell 1989). A cooperative statewide inventory effort between 1996 and 1998 yielded a minimum estimate of 26,709 ha (FaunaWest 1999). However, this inventory did not include areas where access was denied or results of other prairie dog survey efforts by various entities, including those conducted on tribal lands. Prior to our effort, the only established estimate of occupied prairie dog acreage was 36,422 ha, and this estimate was a combination of FaunaWest (1999) surveys, data from a statewide prairie dog observation database (Montana Fish, Wildlife and Parks, unpublished data), various other small surveys, and professional opinion. In 2002, the Montana Prairie Dog Working Group estimated that there were approximately 21,101 ha of active prairie dog colonies on non-tribal lands based on the best available information, which was known not to include all prairie dog colony area in the state (MPDWG 2002). None of these previous efforts provided sufficient rigor, repeatability, or confidence to evaluate management actions, develop a monitoring program, or adequately inform a federal status review.

To fill this information gap, we conducted a landscape-level aerial survey of prairie dog acreage in Montana. We adapted and updated peer-reviewed aerial survey methods originally developed by Sidle et al. (2001a) and further refined by the Colorado Division of Wildlife, USA (White et al. 2005, Odell et al. 2008) to estimate occupied prairie dog acreage in the state. Here we describe the updated methods and results of our prairie dog survey, discuss potential biases in the methodology, and the relevance of our findings for prairie dog management in Montana and elsewhere.

STUDY AREA

Prairie dogs throughout their northern range, including Montana, select relatively level sites that are generally <6% in slope and found in wide valley bottoms, rolling prairies, and tops of broad ridges (Reading and Matchett 1997, Avila-Flores et al. 2010). In Montana, prairie dogs occupy areas that are also suitable for livestock grazing; and therefore, prairie dog colonies are often associated with intensively grazed valley bottoms. The most frequently used habitats in Montana are dominated by western wheatgrass (*Pascopyrum smithii*), blue grama grass (*Bouteloua gracilis*), and big sagebrush (*Artemisia tridentata*); and silty overflow sites dominated by Nuttall’s saltbrush (*Atriplex gardneri falcate*) and dwarf stands of big sagebrush were also used (FaunaWest 1999).

METHODS

In the summer of 2008, we estimated the area of active and inactive prairie dog colonies using aerial line–intercept methods similar to Sidle et al. (2001a), White et al. (2005) and Odell et al. (2008). We adapted their methods to distinguish black-tailed prairie dog colonies from other mound-building animals. We did not establish a minimum number of burrow mounds or burrow entrances to define a prairie dog colony. However, a single mound or few mounds bearing prairie dog characteristics was not considered a colony. Because the range of Richardson’s ground squirrels (*Spermophilus richardsonii*) overlaps the range of prairie dogs in Montana (Foresman 2001), we distinguished Richardson’s ground squirrel colonies by their generally smaller, less conical mounds, entrances located at the edge of the mound rather than the center, lack of distinct vegetation differences between the colony and adjacent grassland, and vegetation occurring at the edge of the mound (Brown and Roy 1943; G. R. Michener, University of Lethbridge, personal communication).

We stratified the survey by county within the historical range of prairie dogs in Montana, as defined by Hoogland (1996) and records in the statewide observation database (Montana Fish, Wildlife and Parks, unpublished data). We excluded tribal lands and Jefferson County from the sampling frame (Fig. 1) because the state of Montana does not have management authority for wildlife on tribal lands and only a single prairie dog colony is known to exist in Jefferson County. Montana’s conservation plan for prairie dogs (MPDWG 2002) clearly dictates that statewide targets for distribution and abundance do not include tribal lands until a tribal agreement can be reached. No such agreement was in place at the time of this survey, so our efforts were concentrated on the portion of Montana covered by the current plan. We estimated the proportion of active prairie dog colonies in each county by summing the area of prairie dog colonies within each county per records in the existing Montana prairie dog observation database (Montana
Fish, Wildlife and Parks, unpublished data). Multiple records for the same colony existed, so we randomly selected one record in the database for those colonies recorded within 400 m of other colonies to minimize duplication of acreage. As in previous surveys (White et al. 2005, Odell et al. 2008), we predicted the proportion of lines in each county \(i\) that would intersect prairie dog colonies, \(r_i\), as the area of prairie dog colonies in county \(i\) divided by the total area of county \(i\).

To estimate the standard deviation of \(r_i\), we used data points from Colorado Division of Wildlife surveys (White et al. 2005, Odell et al. 2008). We estimated an approximate relationship between the standard deviation of \(r_i\) and the value of \(r_i\) as a linear relationship of \(SDI = 0.0031 + 0.7968r_i\).

We used our \(a\ priori\) estimates of SDI for each county to optimally allocate our fixed number of aerial transects (i.e., fixed budget) to each county to minimize the variance in our total acreage estimate (Cochran 1977). To estimate the cost of flying transects in each county, we assumed an average flight speed of 200 km/hr and US$ 250/flight-hr. We then defined the sampling frame in each county as 1.6-km increments along maximum north–south axis of each county to better distribute effort across the sampling frame. To further spatially balance the sampling effort within each county, we selected the transect locations along this axis using generalized random tessellation sampling (Stevens and Olsen 2004). Using the selected points along each north–south line, east–west flight lines were constructed for each county by extending lines out in a due east and due west direction to the point of intersection with each county boundary (Fig. 2). Flight line start and end points were located at these points of intersection and were uploaded into aircraft navigational Global Positioning System (GPS) units and flight routes constructed for each county. The actual path of the airplane was recorded so that deviations of the flight path off of the intended transect could be assessed.

We followed aerial survey protocols of White et al. (2005) and Odell et al. (2008). The pilot flew the aircraft at about 50 m above ground level and approximately 160–200 km/hr. We adapted a custom ArcGIS extension originally developed for the Colorado Division of Wildlife (Imap Solutions, Fort Collins, CO). We recorded intercepts for both active and inactive prairie dog colonies on a tablet personal computer with an integrated GPS unit (Xplore 76 Technologies Rugged iX104 Tablet PC and xGPS Module; Xplore Technologies, Fort Collins, CO).

Figure 1. Counties (slashed) in Montana, USA, surveyed for black-tailed prairie dogs in 2008 and records of prairie dog colony locations (dots).

Figure 2. Example of construction of aerial flight lines (transects) for Fergus County, Montana, USA, using generalized random tessellation sampling.
Technologies, Austin, TX). While in flight, the observer recorded the beginning and end point of pre-defined flight transects and the beginning and end points of prairie dog colony intercepts. The beginning point of a prairie dog colony intercept was marked when the prairie dog colony was visible by both the pilot and observer on their respective sides of the airplane. The intercept end point was marked when the prairie dog colony was no longer visible by either the pilot or the observer.

We classified an entire colony intercept as either active or inactive using criteria developed by White et al. (2005) or Odell et al. (2008). Odell et al. (2008) discussed classifying colony intercepts into 4 categories and determined that the classification of entirely active intercepts or entirely inactive intercepts was the most useful metric to monitor the area of prairie dog colonies. Prairie dog intercepts were classified as active if we observed prairie dogs, or observed fresh diggings around burrows (Sidle et al. 2001b). Other indications of an active colony included intact, unobstructed mounds clear of vegetation and presence of distinctive colony zonation from clipped vegetation, lighter colored subsoil brought to the surface by burrowing, and bare ground. The distinction of prairie dog colonies that were observed to be in close proximity to another on the flight path as either a single colony or multiple colonies was left to the discretion of the pilot and observer.

We adapted ground-truthing methods to correct estimates of prairie dog colony intercepts (Odell et al. 2008). We attempted to ground-truth 1 of 10 recorded prairie dog colony intercepts and a minimum of 1 prairie dog colony intercept in each county to ensure a wide distribution of the ground-truth sample. We selected the prairie dog colony intercept(s) in counties with >1 intercept into the ground-truth sample with probability equal to their proportional length; hence, longer intercepts were assigned a higher probability of being selected for ground-truthing. We attempted to obtain land owner permission to visit selected colony intercepts on the ground. During the ground visit, we recorded length of the colony intercept with GPS units, and classified the intercept as active or inactive within approximately 100 m of the transect line flown, because this is approximately the area reliably classified during the aerial portion of the survey. The ground visit occurred within 60 days of the aerial survey. We did not measure the proportion of active intercepts that might have been inactive or had a lower density of prairie dogs than the most active portions of the intercept. If an aerial intercept was determined to be misidentified through ground-truthing (e.g., Richardson’s ground squirrel colony), then all intercepts within that county were inspected and all non-prairie dog colony intercepts were removed from further analysis.

We recognize GPS error exists and may not always accurately represent ground-truthing and/or aerial intercepts. An error of 17 m can be experienced among various GPS units (Ginsburg 2002). Therefore, a potential error of 34 m between each aerial and ground-truthed intercept point exists, for a total possible error of 68 m/intercept. To minimize such an error, ground-truthed intercept points that were not within 34 m of the associated aerial intercept line were removed from analysis. Likewise aerial and ground intercepts that proved to not be approximately parallel were removed from analyses.

We offer a Bayesian alternative to the White et al. (2005) and Odell et al. (2008) methods for estimating the area of active prairie dog colonies (see on-line supplementary material: Appendix and R-code). This approach allows us to easily propagate error in our estimates of derived quantities (such as area of active prairie dog colonies), and calculate uncertainty in our estimates (Kéry 2010) without using approximations such as the delta method (Williams et al. 2002). Additionally, the Bayesian approach allows us to generate credible intervals that are exact for our sample sizes rather than relying on maximum likelihood approaches that are best for large sample sizes. We used WinBUGS (Lunn et al. 2000) and R2WinBUGS (Sturta et al. 2005) for all calculations.

To evaluate claims that inactivity along long transect intercepts classified as active lead to marked overestimates of active prairie dog colony acreage (Miller et al. 2005), we conducted a sensitivity analysis by classifying the longest 10% of our recorded active intercepts (>1,100 m, \( n = 64 \)) as 10–50% inactive to determine the effect on the acreage estimates. We adjusted estimated transect lengths for “long” transects occupied by prairie dogs by 10–50% to account for portions of the colony that may have been inactive. We defined long as >1,100 m for our first set of estimates and >750 m for our second set because these represented the approximate 90th and 80th quantiles of our observed colony-intercept lengths, respectively. We then calculated new \( r \), under both definitions of “long” and repeated the previously described analysis.

**RESULTS**

From 23 June 2008 to 12 August 2008, we surveyed 771 transects totaling 56,530 km in 32 counties in central and eastern Montana. We intercepted 667 prairie dog colonies in 21 counties. Intercept length varied from 55 m to 3,262 m \( (\bar{x} = 505, SD = 442) \). Uncorrected estimates of active and inactive colony areas from the aerial surveys were 81,766 (SE = 3,269) and 1,142 (SE = 603) ha, respectively.

From 20 July 2008 to 12 September 2008, we attempted to ground-truth 65 randomly chosen black-tailed prairie dog colony intercepts. Access was granted to 59 prairie dog colony intercepts for complete ground-truthing. Activity data (i.e., active or inactive) were collected for the remaining 6 intercepts. Eight of 65 ground-truthed intercepts were incorrectly classified as active from the air. During ground-truthing, intercepts in 6 counties were misidentified as being prairie dog colonies. Two ground-truthed intercepts met the criteria for exclusion from the final analysis because intercept points were not within 34 m of the associated aerial intercept line.

The corrected estimate of area occupied by active prairie dog colonies was 77,430 ha (95% credible intervals = 69,480–83,380; Fig. 3). Area of inactive colonies was
estimated at 12,990 ha (95% credible intervals = 7,039–20,970). The ground-to-air ratio of colony length was 1.091 (95% credible intervals = 1.087–1.094), and estimated percent of colonies classified as active from the air that were active on the ground was 86.8% (95% credible intervals = 77.9–93.5%).

Of 667 intercepts, 63 (9.5%) were >1,100 m and 133 (20%) were >750 m. Under the assumption that active colonies with transect lengths >1,100 m were not occupied on 50% of their length, our estimates of occupied area were 67,964 ha (95% credible intervals = 61,047–73,130; Fig. 3), or 9,480 ha less (95% credible intervals = 8,515–10,200) than our original estimate (Fig. 4). Given that our margin of error on the active prairie dog acreage estimate was 15%, 50% inactivity along all of our observed active prairie dog colony intercepts >1,100 m in length would result in an estimate that falls within our margin of error. In practical terms, we find it highly unlikely that ≥50% of all long intercepts >1,100 m are inactive.

Intercepts >750 m accounted for nearly half (48%) of the summed total intercept length. By assuming 50% of active colonies with transects >750 m were unoccupied, we estimated an occupied area of 61,470 ha (95% credible intervals = 55,520–66,140; Fig. 3), or 15,957 ha (95% credible intervals = 14,410–17,170) less than our original estimates (Fig. 4). This estimate is only slightly outside our realized margin of error and approximates our desired level of precision. A 50% reduction in the length of the longest active intercepts is the equivalent of saying 1 out of every 2 prairie dog colonies with an intercept >750 m was misclassified as active when it was indeed inactive. Thus, even relatively large inactive segments of active transects would have minimal effect on the active acreage estimate compared with the intended uses of these results. The resulting estimates would still represent a substantial increase in acreage over previous estimates.

DISCUSSION

We estimated considerably more area of active prairie dog colonies in Montana than previously thought. Our use of survey protocols developed by Sidle et al. (2001b), adapted by White et al. (2005), and further refined by Odell et al. (2008) contributes to the reliability and repeatability of our estimates. In contrast to previous surveys of prairie dogs in the Great Plains, we used a spatially balanced probability sample (generalized random-tessellation sampling), corrected our estimates based on ground-truthing, established a protocol to identify aerial intercepts that had been misclassified as prairie dog colonies, used a Bayesian approach to improve our estimates of uncertainty, and completed a statewide survey in a relatively short time period. Additionally, we examined potential systematic biases and alternate methods as suggested by Miller et al. (2005) through our sensitivity analyses.

Our estimate of active prairie dog area in Montana exceeds recent estimates by >2-fold. We attribute this to the difficulty of surveying a widely distributed species inhabiting expansive landscapes with multiple landownership patterns from the ground, as was attempted in previous efforts. To alleviate access issues and complete a survey in a reasonable amount of time with a fixed amount of manpower, we chose an aerial survey requiring <3 months. Therefore, our resulting estimate provides much needed information to inform evaluations of the status of prairie dogs in Montana.
Additionally, for the first time, we produced an estimate of the area of inactive prairie dog colony area in Montana. Misclassifications of intercepts may influence the estimate of the area of active prairie dog colonies, so we took great care to minimize the effects of misclassifications on our estimates. Intercept misclassifications can be due to species misidentifications and/or the classification of the activity level of an observed colony (Miller et al. 2005). Odell et al. (2008) used ground-truthing to correct estimates of prairie dog colony area in Colorado but made no mention of aerial intercepts being misclassified due to species misidentification. In our survey, if a landscape feature was misidentified as a prairie dog colony during ground-truthing, we inspected all intercepts within that county and eliminated misidentified intercepts from the analysis. Of 21 counties we observed with active colony intercepts, intercepts were misclassified in only 6 counties. Many intercept misclassifications were attributed to Richardson's ground squirrel colonies, a species not found in other states of the Great Plains.

We did not attempt to ground-truth transects for overlooked prairie dog colonies (i.e., false absences). An observer and pilot are unlikely to systematically misidentify large prairie dog colonies. Small colonies, however, are more likely to be missed or misidentified. Even if small colonies were frequently overlooked, it would have minimal impact on the estimate and result in a small under-estimation bias (White et al. 2005).

White et al. (2005) demonstrated that long intercepts have a greater proportional influence on the estimate than numerous shorter intercepts. Long intercepts may also be more likely to have portions that are inactive due to the effects of plague or poisoning. Previous studies have suggested stratifying long intercepts by activity level to account for inactive portions rather than focusing on activity level stratifications in smaller colonies (Miller et al. 2005). During our survey, only one small colony examined was known to be poisoned. Additionally, prairie dog mortality from a plague epizootic exceeds 95% (Pauli et al. 2006) and often exceeds 99%, which results in local extirpation in a relatively short time (Cully et al. 1997, Cully and Williams 2001, Lomolino and Smith 2001, Stapp et al. 2004). plague and poisoning impacts would only be noted during the same growing season as the event. Vegetation regrowth would occur during the following growing season after a plague epizootic event and these inactive colonies would lack prairie dogs, fresh digging, or vegetation zonation, which is a criterion used to identify inactive colonies (Sidle et al. 2001b). Only extremely recent plague events would contribute to misidentification of inactive, plague-affected colonies as active from an aerial survey, and this impact would most likely be seen in larger colonies where numerically more individual prairie dogs might survive plague events to be noticed in aerial surveys. Rather, we suspect that some active prairie dog colonies intercepted may have experienced plague events after the aerial survey and prior to ground-truthing efforts. In this case, the estimated activity correction factor would further reduce the active acreage estimate, yielding an under-estimation bias. As a result of our expectations that few plague-affected colonies would be misidentified as active, that activity-level classifications are ambiguous and difficult to quantify because of the inherent variability and fluctuations in prairie dog activity, and that our transect lengths would be shorter than those encountered in Colorado and elsewhere, we did not classify portions of long intercepts as active or inactive during the aerial survey. Further, Odell et al. (2008) examined the utility of subjective, multiple activity classifications from the air and determined that classification of entire intercepts as active or inactive was most useful.

Therefore, we believe that the established protocol of classifying an entire long intercept as active or inactive based on observing ≥1 prairie dog or fresh diggings and vegetation zonation is justifiable for landscape-level surveys. Studies of the temporal and spatial variation of burrow use and therefore activity also provide support for such a classification scheme. Prairie dog distributions within a colony are naturally dynamic, resulting in shifting areas of high-density active burrows and inactive burrows (Jachowski et al. 2008). Jachowski et al. (2008) attributed the shift in activity within colonies to the availability of forage; however, despite the shifting distribution of prairie dogs during the Jachowski et al. (2008) study, the overall extent of area covered by prairie dogs did not change. Hoogland (1995) found similar results. Although the number of individuals varied by >270% in his study area over a long period of time, the number of burrows remained almost constant.

MANAGEMENT IMPLICATIONS

Our methodology delivers a reliable estimate of the area of active prairie dog colonies in Montana. Given that our acreage estimate is more than twice previous estimates, the status of prairie dogs in Montana is more secure than previously thought. Our estimate can also be combined with estimates produced with similar methods in the Great Plains (e.g., Sidle et al. 2001b, Odell et al. 2008) for multi-state evaluations of the status of prairie dogs. Further, previous work suggested active prairie dog acreage fluctuated greatly (MPDWG 2002). Using our methodology, changes in active prairie dog acreage in response to management actions, disease, or natural phenomena can be quantified over time, and wildlife managers can evaluate alternative management actions in light of changing area estimates. We recognize that the estimates we produced are only appropriate for evaluations of management actions conducted at a landscape level. Finer scale surveys would be needed for evaluation of prairie dog colonies at a local level.

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SUPPORTING INFORMATION

Additional supporting information may be found in the online version of this article at the publisher’s web-site.

Appendix. Description of WinBUGS code to estimate correction factors for prairie dog transect lengths and misclassification errors. Digital Supplement.R—copy of code