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Dallas Virchow

University of Nebraska - Lincoln

Scott E. Hygnstrom

University of Nebraska-Lincoln, shygnstrom1@unl.edu

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ESTIMATION OF PRESETTLEMENT POPULATIONS OF THE BLACK-TAILED PRAIRIE DOG: A REPLY

Dallas R. Virchow and Scott E. Hygnstrom

*School of Natural Resource Sciences
University of Nebraska-Lincoln
Lincoln, NE 68583-0759*

Determination of the historical distribution and abundance of the black-tailed prairie dog (*Cynomys ludovicianus*) is important as a component of the science underlying decisions on the future management of this species. Clearly, we differ from Knowles and colleagues (2002) in our interpretation of those data (see below). In addition, Knowles et al. (2002) introduce other lines of evidence rather than focusing on the historical record as we did. The new lines of evidence they present include physical evidence, contemporary knowledge of prairie dog ecology, and distribution of the black-footed ferret, *Mustela nigripes*. Unfortunately, these new lines of evidence are incomplete and not sufficient to refute our interpretation of the historical evidence we presented.

Our position is not that "prairie dogs were not abundant prior to settlement," nor is it that prairie dogs were not a "widespread and common species on the Great Plains," as Knowles et al. (2002) attributed to us. Instead, we interpret the evidence to suggest that, while prairie dogs were abundant in the Great Plains west of the tallgrass prairie region, including superabundant in some areas of the shortgrass plains region prior to or during Euro-American settlement, numbers in tallgrass prairie were much lower (Virchow and Hygnstrom 2002). To reiterate, we found that the data available in the historical record do not support the idea of a *rangewide* superabundance of the black-tailed prairie dog nor do they support the high estimates for the abundance and occupancy rates of the species that some have suggested. In addition, we think that the historical record suggests the black-tailed prairie dog was much less abundant in the *tallgrass* prairie region than in other regions of the Great Plains, and that the eastward range expansion of the black-tailed prairie dog was facilitated by live-stock grazing.

The view presented by Knowles et al. (2002) that the black-tailed prairie dog was abundant, that is, "occupied 2% - 15% of the landscapes (400,000 ha or more)" during the presettlement period is supported only by evidence from one area (Montana). Others have presented estimates of occupancy rates that are much different for the presettlement period. For

instance, the US Fish and Wildlife Service used estimates made by the Black Footed Ferret Foundation (32 million ha) and by Knowles (45 million ha) to determine a range of estimates for occupied habitat of the black-tailed prairie dog (US Department of Interior 2000). In the same report the Service cited Seton's estimate of 155.5 million ha of historical range for the black-tailed prairie dog (Seton 1953 in US Department of Interior 2000). Based on these estimates, the historic occupancy rates for the black-tailed prairie dog were between 21% and 29% of their historical range. Furthermore, Wuerthner (1997) attributed a 283 million ha estimate of occupancy for all prairie dog species in the United States "in the late 1800s" to Merriam (1902). This estimate would represent a minimum occupancy rate of 91% for the black-tailed prairie dog across its entire historical range, given that the black-tailed species "probably occupied more area than all other [prairie dog] species combined" (Hoogland 1995 in US Department of Interior 2000).

The great differences between the estimates noted above indicate that the rate at which the black-tailed prairie dog occupied its rangewide habitat has not been determined unambiguously from the historical record. Neither have historical occupancy rates been determined from physical evidence or ecological principles. For example, the physical evidence, even within Montana, suggests that there is "considerable regional variation in prairie dog abundance" (Knowles et al. 2002). Furthermore, we believe that the physical evidence of "expansive" historical prairie dog towns that Knowles et al. (2002) present is insufficient because it consists of surveys of abandoned prairie dog burrows. Since neither the spatial nor temporal relationship of these abandoned burrows is presented, there is no way to evaluate the inference that the abandoned burrows represent remnants of large historical colonies. Furthermore, the ecological inferences need better data. An underlying but unevaluated assumption is that current distribution and dispersal patterns of prairie dogs also were characteristic of the presettlement period. Yet, historic colony sizes fluctuated in response to unknown environmental changes (Knowles et al. 2002). Also, we need more evidence on the biological factors, such as disease pathogens, that may have limited the historical abundance of the species.

It was not our intent to argue that early explorers of the western continent, such as Lewis and Clark, reported every prairie dog colony while en route. It is our contention, however, that the Lewis and Clark expedition and other expeditions, particularly those that contained naturalists Say and Peale (Long in 1820), Maximilian, Townsend, and Nuttall (Wyeth in 1834),

or Audubon (1843), or noted authors such as Washington Irving or Francis Parkman, would have recorded the most extensive, impressive, and notable colonies (Maximilian 1834; Irving 1835; Parkman 1846; Thwaites 1905; Fuller and Hafen 1957; McDermott 1965). These accounts seem to contradict the modern estimates of occupancy rates (Knowles et al. 2002; US Department of Interior 2000) or implications of Wuerthner (1997).

Additionally, one current view is that a colony or complex of prairie dogs >4,500 ha is needed for a viable population of black-footed ferrets (Knowles et al. 2002). Thus, Knowles et al. (2002) use the geographic distribution of extant specimens of the black-footed ferret, an obligate predator of prairie dogs, to infer that there existed a historic superabundance of the black-tailed prairie dog. Unfortunately, the data they present are inconclusive; these data include both presettlement and postsettlement specimens, differences in scale between counties, and no reference to the size of associated prairie dog colonies.

Our determination of the presettlement time frame is challenged (Knowles et al. 2002). We agree that the accounts by Messiter (1890) and Hayden (1863) represent presettlement conditions. Only one citation (Strong 1960) appears to contradict our interpretation of the lower presettlement abundance of black-tailed prairie dogs within tallgrass prairies than in mixed-grass prairie or shortgrass plains. Knowles et al. (2002) cite the information on the Oklahoma prairie dog colony from Strong (Strong 1960 in Lewis and Hassien 1973). However, we found that Strong (1960) was not discussed in Lewis and Hassien (1973) but was only cited. Instead, Lewis and Hassien (1973) cited four sources to note that the historical habitat for the species existed in Oklahoma within the "short-grass and mixed-grass types" and that prairie dogs were considered as "invaders in [the] shinnery oak grassland, [and] tall-grass prairie" (Carpenter 1940; Osborn 1942; Osborn and Allan 1949; Koford 1958). Although one 43-km-long colony apparently existed in central Oklahoma in 1878 (Strong 1960), we conclude that there is no evidence to support the suggestion that similarly large colonies occurred elsewhere across the various tallgrass prairies of the Great Plains.

Another issue of disagreement is the effects of grazing on the distribution of prairie dogs in the early settlement period. Knowles et al. (2002) note that it is "not possible to make generalizations about prairie dog population trends." We agree, but note the literature (Osborn and Allan 1949; Hall 1955; Lewis and Hassien 1973; Clark 1973) that suggests livestock grazing during the early settlement period probably caused an increase in the abun-

dance and distribution of black-tailed prairie dogs, especially along the easternmost extent of their range.

The point that prairie dog numbers are “significantly below those of the late 1800s” is not at issue. However, we question the reliability of estimates of the exact magnitude since estimates differ so widely and are based on an incomplete historical record. The large differences that exist among estimates of current populations of the black-tailed prairie dog statewide (US Department of Interior 2000) testify to the difficulty in establishing reliable numbers. For example, current estimates of black-tailed prairie dogs for Colorado range from 18,000 ha (Knowles 1998) to “well over 550,000 acres (220,000 ha)” (Francie Pusateri, Colorado Division of Wildlife, personal communication, 30 October 2002). These two estimates represent a twelve-fold difference. Knowles (1998) estimated that the *original range* of the black-tailed prairie dog had declined by 98% “within only a half century of plains settlement.” We conclude by the full compilation of the data available that the geographic range of the black-tailed prairie dog has changed little from the presettlement period, and the data on presettlement abundance are insufficient to create percentages or rates of decline. We believe over-interpretation of the data available influenced the US Fish and Wildlife Service in its determination to list the black-tailed prairie dog as a “threatened species” under the “warranted but precluded” proviso (US Department of Interior 2000).

Finally, we disagree that “the question now is not how far prairie dog [numbers] have fallen, but how we should restore them to numbers” that will “function on an ecosystem level as they once did” (Knowles et al. 2002). Instead, we suggest that the more relevant question is “How many prairie dogs (and bison, for that matter) are needed to function at an ecosystem level?” We believe that this is the question of most consequence to current policy and management, and it needs to be addressed from the ecologic, social, economic, and historical perspectives.

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