The Mixing Pot: Observations of Hybridization between Sharp-tailed Grouse and Greater Prairie-chicken in North Dakota

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Abstract - The Greater Prairie-chicken (*Tympanuchus cupido*) population in Grand Forks County, North Dakota has declined since 2005, after initial success following restoration efforts from 1992–1998. During this period, Sharp-tailed Grouse (*T. phasianellus*), which co-occupy the area, have increased. We provide a case study demonstrating shifts in the 2 populations, the occurrence of hybrids, and the potential indicators hybrids may play in populations where these 2 species co-occur. We conducted annual spring lek counts (15 March to 15 May 2019–2022) to monitor the population trends for both prairie grouse species. Within 2 study blocks, we attempted to identify all leks of both species through listening surveys and then return to count the number of birds on each lek by species and sex. We counted between 24 and 38 active leks annually. We observed steady decreases in Prairie-chickens (only 7 male Prairie-chickens were observed in 2022); increases in Sharptails; and increases in hybrid Greater Prairie-chicken x Sharp-tailed Grouse (8/31 leks in 2022). Previously, managers assumed that hybrids were relatively rare, but we documented as many as 16 hybrids that could be identified morphologically in a single year. Future work will be needed to evaluate the genetics of grouse where they co-exist to further determine accurate hybridization rates within the population.

Introduction

Hybridization is widespread among bird species (Grant and Grant 1992) and common within groups such as Galliformes, Anseriformes, Passeriformes, and Charadriiformes (Ottenburghs et al. 2015). It can occur when barriers are removed that results in overlapping ranges. In recent years, habitat fragmentation and modification as well as climate change have been identified as drivers of range shifts, facilitating interactions among species that were previously separated (Allendorf et al. 2001, Ottenburghs 2021). The occurrence of hybridization where species co-exist can result in the loss of one or both of the original populations (Allendorf et al. 2001, Todesco et al. 2016). Hybridization among prairie grouse (grouse species of the genus *Tympanuchus*), specifically the *Tympanuchus cupido pinnatus* Brewster, W (Greater Prairie-chicken; hereafter Prairie-chicken) and *T. phasianellus* Linnaeus (Sharp-tailed Grouse; hereafter Sharptails), has been documented when their ranges overlap (Johnsgard and Wood 1968, Augustine and Trauba 2015).

Both Prairie-chickens and Sharptails have similar niche requirements and can survive in the same habitats. However, Sharptails can be more tolerant of woody vegetation and in some areas found in association with some brush cover (Connelly et al. 2020). The 2 species require vast, connected grasslands and are sensitive to development (Runia et al. 2021). Prairie grouse have been shown to avoid areas with trees in grassland landscapes (Lautenbach et al. 2017, Olsen et al. 2021); however, researchers have documented higher nest survival for Sharptails in woody habitats (Goddard et al. 2009, Goddard and Dawson 2009).

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Associate Editor: Don Wolfe, George Miksch Sutton Avian Research Center.

Past site occupancy research on the 2 species has shown that their occurrences are positively correlated with increasing grassland area and decreasing in and around developed areas (Runia et al. 2021). After settlers started working land for agriculture, Prairie-chickens and Sharptails had overlapping ranges due to an increase in fragmented grasslands. This resulted in increased interactions between the species and opportunities for hybridization to occur (Johnsgard and Wood 1968).

On grouse breeding grounds or leks, it is common for one or few alpha males to perform all the matings. An alpha male can mate with as many as 75% of the females that visit the lek (Lumsden 2005). This hierarchy might lead to an increase in Prairie-chicken x Sharptails hybrids (hereafter, hybrids) on mixed leks where one of the species, usually Sharptails, is more aggressive than the other (Johnsgard and Wood 1968). Additionally, in sparse populations, it is hypothesized that females may choose males of similar species if they do not encounter males of their own species in order to reproduce (Randler 2006).

Counts of displaying males on leks are widely used for monitoring grouse population trends (Cannon and Knopf 1981, Hamerstrom and Hamerstrom 1973). When leks become mixed and hybridization occurs, it can be difficult to discern individual species from hybrids, particularly when ground observers are counting from a distance. This can result in inaccurate counts of each species. Augustine and Trauba (2015) compared vocal and non-vocal sounds in Prairie-chickens, Sharptails, and apparent hybrids. They found that when they compared the hybrids' sound to both Prairie-chickens and Sharptails, the hybrids' sounds were similar to the "coo" vocalization of the Sharptails. However, the vocalizations of hybrids have generally been described as in-between the 2 species (Augustine and Trauba 2015). While hybrids may appear visually similar to either Sharptails or Prairie-chickens from a distance, Augustine and Trauba (2015) found that the foot-stomping varied between the hybrid individuals and their parental species. Sharptails, Prairie-chickens, and hybrids had similar intensity and aggressiveness in their displays when females were not present on the lek and the level of aggressiveness was key to which males successfully attracted females for breeding opportunities.

In North Dakota, Prairie-chickens are thought to have expanded into the state in the 1870s and 1880s, but see Ross et al. (2006), and quickly spread throughout most of it. The population peaked between 1890 and 1930 and then drastically declined to 4,000 to 5,000 birds by the 1960s (Johnson and Knue 1989). Since the 1950s, the Prairie-chicken population in North Dakota has been decreasing drastically. By the 1970s Prairie-chickens were limited to the western edge of the Red River Valley and along the eastern edge of the Missouri Coteau in North Dakota (Johnson and Knue 1989). Sharp-tailed Grouse are native to North Dakota. Due to Sharptails being considered "commonplace" on the prairie, people did not usually detail sightings of them (Johnson and Knue 1989). However, Johnsgard and Wood (1968) emphasized how the species was most likely encountered when settlers moved to the prairies.

Prairie grouse populations in Grand Forks County, North Dakota have been monitored annually since 1954 (Huschle and Toepfer 2020). Prairie-chickens were not present in Grand Forks County from 1980 until 1992, when biologists translocated them back to the area. Translocation efforts continued until 1998, and the population continued to increase naturally until 2004. Populations have declined in the area since 2008 (Huschle and Toepfer 2020). Although Sharptails were not abundant when translocations began (<10 males on <2 dancing grounds found in 1990–1991; Kobriger 1991), they increased in abundance beginning in 1996 as translocations were ongoing and climbed through the early 2000's (Huschle and Toepfer 2020). Hybrids were observed sporadically, but lek counts were conducted from a distance, and their prevalence may have been underestimated. There is a need for

biologists to have information on the prevalence of hybrids and characteristics useful in distinguishing hybrids from Sharptails and Prairie-chickens during surveys. The goal of our study is to document the increased numbers of mixed compositions of Sharptails and Prairie-chickens and the resulting increase in hybrids in northeastern North Dakota. Furthermore, to provide information on the scenario that has led to this increase as a case study and share characteristics of hybrids found at leks to demonstrate challenges in detecting them from traditional roadside surveys.

Materials and Methods

Study area

We surveyed 2 study plots in Grand Forks County, North Dakota. The Bry Block (centroid: 48.0728 -97.3467) is 212.9 km^2 (82.2 mi^2) in size and includes the Bry and Prairie-chicken State Wildlife Management Areas, Kelly's Slough National Wildlife Refuge, and the Stewart Lake Waterfowl Production Area. The Grand Forks Block (centroid: 47.8611 -97.2668) is 124.1 km^2 (47.9 mi^2) and includes the University of North Dakota's Oakville Prairie Biology Field Station and Wildlife Management Area.

Field methods

Listening surveys. From 15 March to 30 April each spring, researchers conducted listening surveys to locate leks from 30 minutes prior to sunrise until 1.5 hours after sunrise (the first 2 hours of daylight) on mornings with wind less than 24 kph (15 mph). For each survey block, researchers would stop every 0.8 km (½ mile), get out of the vehicle, listen and, when possible, visually scan for 5 minutes looking for active leks (i.e., displaying grouse). When birds were detected, the species and location were recorded so the birds present would later be counted during lek counts.

Count survey. We conducted at least 2 counts on each lek located during the listening surveys following the same protocols with winds not exceeding 24 kph and surveys occurring in the first 2 hours of daylight. Birds on each lek were counted and recorded by species (Sharptail, Prairie-chicken, and hybrid) and sex, when possible. In cases where there were no birds present, the area was scanned to see if the birds had moved to another location and if so, the location was adjusted. If predators chased grouse off a lek prior to or during the survey, we would wait for them to return. If observed, predator species were also recorded. Predators that were regularly observed were Coyotes (*Canis latrans* Say), Red Foxes (*Vulpes vulpes* L.), Red-tailed Hawk (*Buteo jamaicensis* Gmelin, JF), and Rough-legged Hawk (*Buteo lagopus* Pontoppidan, E). If possible, counts were made from the roadside; however, when poor visibility prohibited accurate counts or concerns of species identity existed, researchers approached leks. In some cases, complete counts could only be obtained by flushing the grouse from the lek. When possible, we captured videos of flushed leks to confirm counts post hoc.

All observers had training in the protocols to identify species and discern between sexes prior to the start of the field season. Observations were always conducted in teams of 2 when observers had less than 1 year of bird identification experience, and in most cases for safety reasons during early morning surveys, teams included 2 observers to allow for accurate counts and confirm species identification. Leks that had prairie chickens, hybrids, or large numbers of grouse were confirmed with multiple observers, and often a third lek count was conducted.

Ground blind observations. We set up 2 ground blinds close to 2 of the larger mixed leks to record the behavior of the grouse on camera and photograph the individuals suspected to be hybrids. Technicians in the blinds entered 30–60 minutes before sunrise to avoid walk-

ing through the lek during peak activity. Furthermore, technicians waited for birds to flush or after our 2-hour, after-sunrise observation period before exiting to avoid unnecessary disturbance on the grouse. Observations occurred within the first 2 hours of sunrise and with winds less than 24 kph. Counts and species identifications were conducted during these blind observations and compared to the traditional lek counts, described above. We used window-mounted or tripod-mounted spotting scopes (20–60x) for much of our counting. However, to identify or confirm hybrids, we sat in pop-up ground blinds to enable observers to view grouse from 5–40 m. In the blinds, observers used 10x42 or 10x50 binoculars to classify grouse by species. In addition, observers took photographs using digital single-lens reflex cameras with telephoto lenses to freeze details and examine patterns post hoc.

Apparent Hybrid Identification. Overall, Sharptails are lighter in plumage, especially on the belly, than Prairie-chickens (Connelly et al. 2020). Those considered "pure" Sharptails have white breasts with brown-bordered, white chevrons. Tails of Sharptails have 2 central tail feathers ¼ longer than the rest of the tail (Fig. 1).

Prairie-chickens have very long bars extending from the lower neck to lower bellies and are much darker with thinner white lines overall (Fig. 2). Prairie-chickens have tail feathers with similar lengths forming a smooth, rounded tail fan. Long, black pinnae feathers are useful for identifying Prairie-chickens from Sharptail, although Sharptails have shorter feathers that they lift to reveal their air sacs (Fig. 3). For more detailed descriptions see Johnson et al. (2020).

Generally, Sharptail vocalizations are described as "chuckles" or "clucks" loudly while in flight (Johnson and Knue 1989, Connelly et al. 2020) compared to the "boom" of Prairie-chickens on the lek (Johnson et al. 2020), although Prairie-chickens also "chuckle" in flight (Johnson and Knue 1989). Prairie-chicken booming was identified as "oo-loo-woo" or "*zooooo...woooo...youoo"* sound as summarized in Johnson et al. (2020). They make softer sounds when fighting that sounded less intense or mature.

Results

General observations

During the 2019–2022 surveys, we found as few as 2 and as many as 16 hybrids in a single season (Table 1). We visited 24–38 active leks annually and 2–8 of these included hybrids. Further, the hybrids appeared viable, as observations were recorded that suggested hybrids were breeding based on morphological characteristics we observed from the blinds (Fig. 2–3).

During this same period, we observed increasing numbers of Sharptails, increasing mixed leks, and declining Prairie-chickens (Table 1). However, it is important to mention that in the first survey year the exact number of Sharptails were not reported as the work focused mostly on Prairie-chickens so 2019 Sharptail numbers may be underestimated. Specifically, Prairie-chickens decreased from 29 booming males to 7 over the 4 survey periods.

Description/identification of hybrids

Using observations from the blinds, the research team was able to confirm descriptions of behaviors exhibited by hybrids that would be more difficult to detect and accurately attribute to specific individuals from more distant road surveys. Hybrids portrayed a mix of traits, with darker breast barring extending further down the bellies. Breast feather patterns were inconsistent and varied among hybrids. Hybrids had more barring than pure Sharptails, but barring was broken, unlike pure Prairie-chickens (Fig. 2). Some hybrids had longer central tail feathers (we estimated as much as a ¼ longer), but never

Figure 1. Sharp-tailed grouse. Hybrid Sharp-tailed Grouse x Greater Prairie-chicken (hybrid), and Greater Prairie-chicken. Chevrons on the underside of a sharptail were dense on the upper breast, but thinned out to pale bellies. Dark bars on prairie-chickens were relatively unbroken and continued down the entire belly. Hybrid patterns were intermediate with broken barring on the breast and dark v's on the belly. Photography by Jesse Kolar.

Figure 2. Sharp-tailed grouse, hybrid, hybrid, Greater Prairie-chicken. The tails are helpful in these photos to see irregular shapes that do not fit the light, pointed sharptail tails nor the dark, rounded prairie-chicken tails. The second photo appears to be a F1 hybrid of prairie-chicken and sharp-tailed grouse. The third photo shows a hybrid that had speckling on the belly. We suspect that this hybrid could be a backcross between a hybrid and prairie-chicken. We do not know how much variation is natural in first generation hybrids. Photography by Jesse Kolar.

Figure 3. Sharp-tailed grouse, hybrid, hybrid, Greater Prairie-chicken. The range of pinnae feather length and air sac color from a pure sharp-tailed grouse (left) to a pure greater prairie-chicken (right) and hybrid expressions (middle photos). Photography by Jesse Kolar.

Table 1. Hybrids, prairie-chickens, and sharp-tailed grouse observed in Grand Forks County, 2019–2022, during spring lek surveys. Mixed leks are those with both sharp-tailed grouse and prairie-chickens present. Total individuals includes a maximum count of all male, female, and unknown grouse observed.

Leks	2019	2020	2021	2022
Number of leks with hybrid	4	2	5	8
Number of leks with prairie-chickens	10	9	9	4
Number of leks with sharptail	20	28	31	32
Number of mixed (sharptail and chicken) leks	4	8	10	9
Total active leks surveyed	24	31	38	33
Individuals				
Total number of hybrids	6	2	12	16
Total number of male hybrids	4	2	10	14
Total number of sharptail	289	376	498	544
Total number of male sharptail	132	217	368	294
Total number of prairie-chickens	42	32	39	7
Total number of male prairie-chickens	29	27	30	7

as long as Sharptails, and most hybrid tails appeared more rounded. Hybrids had various sizes of pinnae feathers, but they were never as long as a pure Prairie-chicken (Fig. 1). Hybrids showed variation in air sac coloration, from purple to yellow with purple borders. The "pure" Prairie-chickens usually have a deeper yellow or orange air sac with darker purple borders. In early morning sunlight colors can appear brighter, so it is difficult to identify the birds by air sacs alone (Fig. 3). Sharptails always had purple air sacs.

In flight, Prairie-chickens had very dark and square tails, their bellies were dark and barred, and overall they appeared large and slow in flight. Sharptail appeared lighter in flight, and the longer tail retrices gave the tails a pointed "sharp" shape in flight. Hybrids had slightly pointed tails; however, they did not have notably longer central rectices. Hybrids had thick speckling on pale bellies and a faint barring on the neck. Hybrids were likely to be confused with a darker Prairie-chicken if seen from the side or top, or if only looking at the tail, but from below, the paler bellies of hybrids appeared more like Sharptail.

In our study area, Sharptails and hybrids were more aggressive at the leks compared to Prairie-chickens. The appearance of hybrids varied significantly depending on their posture. Because of this, hybrids could be misidentified by ground observers as Prairie-chickens from certain angles and farther distances from the lek (e.g., > 400 m). Given visibility challenges, we confirmed species identification from walking in or from blind observations conducted, but unfortunately, we did not conduct formal analysis of frequency misidentification would have occurred if additional inspection had not occurred.

From a distance, dancing Sharptails appeared to ground observers to have a wedge shape, with their necks and heads stretched toward the ground and tails pointing straight up; whereas Prairie-chickens were squarer, or H-shaped, with vertical pinnae feathers standing parallel to vertical tails. Hybrids can show multiple expressions, but pinnae feathers never appeared taller than the tail (Fig. 1). Interestingly, hybrids with more Prairie-chicken traits rarely erected their pinnae feathers, but hybrids with Sharptail traits had "cat-ear" pinnae feathers consistently raised while dancing (Fig. 1).

Auditory descriptions

Hybrids attempted a Prairie-chicken boom but, instead of the consistent "oo-loo-woo" or "*zooooo...woooo...youoo"* described by Johnson et al. (2020), they made abbreviated booms which sounded like they were "catching their breath" in the middle of booming. In the field, the cooing sounds were most useful for distinguishing hybrids by sound. Further, the sound of hybrids rarely carried as far in that detection often occurred closer to a lek than the louder "oo-loo-woo" boom of pure Prairie-chickens, which could be detected over a kilometer away, on a calm day.

Discussion

We documented increasing hybridization among Sharptails and Prairie-chickens in a population that historically was dominated by Prairie-chickens. Hybridization between Sharptails and Prairie-chickens has been observed for decades (Johnsgard and Wood 1968, Lumsden 2005) and likely started when settlers started working the land in North Dakota which caused an expansion in the Prairie-chickens' range (Svedarsky et al. 2000; but see Ross et al. 2006) that suggests the prairie chicken range may have been larger prior to European settlement than most records report. Hunter-harvested hybrids have been observed in Nebraska, North Dakota, Minnesota, and South Dakota (J. Kolar, North Dakota Game and Fish, Bismarck, ND, 2022, pers. comm.). Huschle and Toepfer (2020) documented as many as 3 hybrids in a single year but admitted that they did not approach all booming grounds close enough to detect hybrids. We observed up to 16 hybrids in a single year, and at least 8 of those were initially identified as Prairie-chickens due to their darker appearance compared to nearby Sharptails using distant, traditional survey techniques. In fact, the establishment of a blind near the lek was the only way many of the hybrids were identified and confirmed as hybrids. Based on our findings, we suspect that hybridization in areas where Prairie-chickens and Sharptails overlap is underestimated.

Hybridization is most likely to occur when numbers of each species are low, facilitating the selection of similar species matings over same species (Augustine and Trauba 2015). The Grand Forks populations provided an ideal scenario with decreasing Prairie-chicken numbers and increasing Sharptail as habitat changes such as increased woody vegetation became more common across the landscape (Sharptails are often more tolerant of brush).

According to Huschle and Toepfer (2020), the recent Grand Forks Prairie-chicken population was at its peak in 2004, with 330 males recorded. After this, the population started decreasing and by 2018, only 13 male Prairie-chickens were observed in the area (Huschle and Toepfer 2020). Huschle and Toepfer (2020) suspected Conservation Reserve Program (CRP) declines and winter weather as reasons for declines in Prairie-chicken populations. However, they only considered increased interactions with Sharptails as a plausible driver in Prairie-chicken population declines. We have observed increases in woody vegetation, primarily *Elaeagnus angustifolia* Linnaeus (Russian Olive), on many of our study areas. These are likely a result of the prolonged wet period the Dakotas have experienced since the 1990s and a general shift in grasslands that promotes woody vegetation as result of reduced disturbances such as fire and grazing (Springsteen et al. 2010). With rapidly increasing Sharptail populations that are more tolerant to some woody vegetation, this resulted in more mixed leks. Further, we observed Sharptails to be more aggressive than Prairie-chickens, similar to other work (Johnsgard and Wood 1968, Sparling 1981). This aggressiveness often leads to male Sharptails being the individuals females choose for mating (Johnsgard and Wood 1968). Our observations confirm a slow takeover by Sharptails in Prairie-chicken boom-

ing grounds; however, we do not know whether behavioral or environmental factors allow Sharptails to express their dominance. In areas of overlap in Nebraska, Prairie-chickens appeared to be more dominant than Sharptails on leks. This differs from our observations where Sharptails were more aggressive than Prairie-chickens (J. Laux, Nebraska Game and Parks Commission, Alma, NE, 2021, pers. comm.).

From observations made in the field conducting grouse surveys, it is clear that some hybrids are significantly harder to identify than others. Certain hybrid individuals will stand out due to their atypical vocalizations or behavior. Other individuals cannot be properly identified without help from spotting scopes and cameras that will allow careful inspection of morphological subtleties.

We warrant caution in using roadside surveys to classify Sharptails from Prairie-chickens in areas of overlap, due to the possibility of hybrids in these populations. Although roadside surveys are commonly used for logistic simplicity, we observed that it was difficult to differentiate hybrids from either species from a distance. In one instance, we counted a mixed lek multiple times from ~200 m using a spotting scope, but we did not confirm hybrids until using a blind for closer observation. On our distant, roadside count, we grossly overestimated Prairie-chickens because the hybrids on the lek appeared darker than nearby Sharptail. Similar mistakes could result in over- or underestimating the misidentified species, and impact population or trend estimates.

One caveat to our study is that all grouse were identified phenotypically, and we did not confirm the identity of Sharptails, Prairie-chickens, or hybrids using genetics. Future work using genetic analysis could provide additional information on the role of hybridization and population declines in Prairie-chickens and better understand reproduction by hybrids.

Sharptails are more tolerant of some woody vegetation encroachment across the grasslands whereas Prairie-chickens are more sensitive to these (Goddard et al. 2009, Lautenbach et al. 2017). Absence of disturbances (e.g., fire, grazing, mowing/haying) could result in benefits for Sharptails in areas where both species exist, making the Sharptail become more prevalent and Prairie-chickens less common. As the number of Prairie-chickens decline, Sharptails are more likely to breed with remaining females resulting in increased opportunities for hybridization. Augustine and Trauba (2015) and others have noted that hybrids are viable; however, hybrid males are less likely to have breeding opportunities given their unique behaviors that do not align with either species.

Acknowledgements

We wish to thank the North Dakota Game and Fish for funding the prairie grouse surveys. We also want to thank dedicated field technicians: Mackenzie Jensen, Noah Raitz, Seth Owens, Ean Malchow, Allicyn Nelson, Grant Kapaun, and Chris Felege for helping collect valuable data. Jim Job (NDGF) secured landowner permission and set up observation blinds used in this study. Initial assistance with survey locations was provided by David Lambeth, Erik Fritzell, Gary Huschle, and Mike Jacobs.

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