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Geographic and Seasonal Patterns of Ptarmigan and Grouse Harvest in Rural Alaska

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ABSTRACT. We estimated harvest of ptarmigan (*Lagopus* spp.), grouse, and their eggs by Alaska's rural residents and described seasonal and geographic patterns. In Alaska, subsistence is a way of life centered on harvest and use of wild foods. Subsistence is typical in remote regions where Indigenous people are an important contingent of the population. Harvest estimates were based on a large dataset (753 community-years) from household surveys conducted as in-person interviews. We used a parts collection (biological samples) to infer the species composition of the harvest. The estimated annual average harvest of ptarmigan by rural residents was 49,707 birds/year (CI = 46,725–52,689) and 848 eggs/year (CI = 755–941) in the 2004–15 reference period. The estimated grouse harvest was 23,897 birds/year (CI = 20,790–27,004) and 35 eggs/year (CI = 19–51). About half (51%) of the ptarmigan harvest occurred in spring, while grouse harvest occurred primarily in fall–winter (82%). Most of the ptarmigan harvest occurred in western regions. Most of the grouse harvest occurred in regions in interior Alaska, where the per capita harvest was relatively high. Based on the parts collection, the ptarmigan harvest was composed of 88% Willow Ptarmigan (*Lagopus lagopus*), 11% Rock Ptarmigan (*L. muta*), and 1% White-tailed Ptarmigan (*L. leucura*). The grouse harvest was composed of 60% Spruce Grouse (*Canachites canadensis*), 22% Sooty Grouse (*Dendragapus fuliginosus*), 14% Sharp-tailed Grouse (*Tympanuchus phasianellus*), and 4% Ruffed Grouse (*Bonasa umbellus*). Ptarmigan represented 13% and grouse represented 6% of the total number of birds annually harvested by Alaska's rural residents, including migratory birds. Results from this study can inform harvest management and help strengthen collaboration with rural residents.

Keywords: Alaska; grouse; harvest assessment; management; harvest survey; hunting; ptarmigan (*Lagopus* spp.); subsistence

RÉSUMÉ. Nous avons estimé le nombre de lagopèdes (*Lagopus* spp.), de tétras et d'œufs de ces oiseaux récoltés par les habitants ruraux de l'Alaska, puis nous avons décrit le caractère saisonnier et la répartition géographique des récoltes. En Alaska, la subsistance est un mode de vie centré sur les récoltes et sur l'utilisation d'aliments issus de la nature. La subsistance est typique dans les régions éloignées où les peuples autochtones représentent un important segment de la population. Les estimations de récoltes ont été effectuées à partir d'un vaste ensemble de données (753 communautés-années) découlant d'enquêtes auprès des ménages réalisées sous la forme d'entrevues en personne. Nous avons utilisé un ensemble de parties d'oiseaux (échantillons biologiques) pour déduire la composition des espèces récoltées. L'estimation des récoltes moyennes annuelles de lagopèdes par des habitants ruraux s'est élevée à 49 707 oiseaux/année (IC = 46 725–52 689) et à 848 œufs/année (IC = 755–941) pendant la période de référence de 2004-2015. L'estimation des récoltes de tétras s'est chiffrée à 23 897 oiseaux/année (IC = 20 790–27 004) et à 35 œufs/année (IC = 19–51). Environ la moitié (51 %) des récoltes de lagopèdes s'est faite au printemps, tandis que les récoltes de tétras se sont faites principalement en automne et en hiver (82 %). Le plus gros des récoltes de lagopèdes a été effectué dans les régions de l'Ouest, tandis que le plus gros des récoltes de tétras a été fait dans des régions intérieures de l'Alaska, où les récoltes par habitant étaient relativement élevées. D'après l'ensemble de parties d'oiseaux, les récoltes de lagopèdes étaient composées de lagopèdes des saules (*Lagopus lagopus*) dans une mesure de 88 %, de lagopèdes alpins (*L. muta*) dans une mesure de 11 % et de lagopèdes à queue blanche (*L. leucura*) dans une mesure de 1 %. Pour leur part, les récoltes de tétras étaient composées de tétras du Canada (*Canachites canadensis*) dans une mesure de 60 %, de tétras fuligineux (*Dendragapus fuliginosus*) dans une mesure de 22 %, de tétras à queue fine (*Tympanuchus phasianellus*) dans une mesure de 14 % et de gélinotte huppée (*Bonasa umbellus*) dans une mesure de 4%. Les lagopèdes ont représenté 13 % du nombre total d'oiseaux récoltés annuellement par les habitants ruraux de l'Alaska, tandis que les tétras ont représenté 6 %, oiseaux migrateurs y compris. Les résultats de cette étude peuvent éclairer la gestion des récoltes et aider à renforcer la collaboration avec les habitants ruraux.

Mots-clés : Alaska; tétras; évaluation des récoltes; gestion; enquête sur les récoltes; chasse; lagopède (*Lagopus* spp.); subsistance

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INTRODUCTION

> We who live in the marshlands were taught that forests were places where we could try to survive, that trees are places where we could always try to find food. Because those ptarmigan that they call aqesgit never go away all winter, including snowshoe hares and Arctic hares. They wanted us to keep that in mind.
> Nicolai Pavilla, Atmautluak (Fienup-Riordan, 2020:317)

Across Alaska's vast expanse in Arctic and subarctic western North America, ptarmigan (*Lagopus* spp.) and grouse inhabit diverse ecosystems, including brushy tundra, coastal plains, alpine meadows, and forests. Willow Ptarmigan (*Lagopus lagopus*) and Rock Ptarmigan (*L. muta*) are broadly distributed, while White-tailed Ptarmigan (*L. leucura*) occur in southeast and interior Alaska. Spruce Grouse (*Canachites canadensis*), Ruffed Grouse (*Bonasa umbellus*), and Sharp-tailed Grouse (*Tympanuchus phasianellus*) occur mostly in interior Alaska, with Spruce Grouse having the broadest range and extending into southwestern and southeastern Alaska. Sooty Grouse (*Dendragapus fuliginosus*) occur only in southeastern Alaska (Gabrielson and Lincoln, 1959; Weeden, 1965; Fink et al., 2023). Grouse are generally absent from the Arctic Slope, Kodiak Archipelago, and Aleutian Islands. We use the terms ptarmigan and grouse following English names for species adopted by the American Ornithological Society (Chesser et al., 2025).

Among a limited set of yearlong resident birds, ptarmigan and grouse impart a sense of place for Indigenous and non-Indigenous people of Alaska. The Willow Ptarmigan is one of the most characteristic accompaniments of the scenery in northern Alaska (Nelson, 1887:132). It is the all-important game bird for many Alaskans and contributes greatly to the food supply in remote localities (Gabrielson and Lincoln, 1959:301). Fittingly, thousands of school children chose the Willow Ptarmigan as Alaska's state bird (Armstrong and Hermans, 2004).

For millennia, Alaska's Indigenous people—Iñupiaq; St. Lawrence Island Yupik; Central Alaskan Yup'ik; Athabascan; Alutiiq-Sugpiaq and Aleut-Unangam; and Eyak, Tlingit, Haida, and Tsimshian—have harvested wild foods, including ptarmigan and grouse, yearlong following their seasonal availability (Fienup-Riordan, 2007; Langdon, 2020). Although birds are a small part of the total harvest of wild foods, bird harvesting is culturally and socially important, improves food security, and adds diversity to the diet (Fall, 2016; Schwalenberg et al., 2023). For Indigenous people in western and northern Alaska, the Willow Ptarmigan is an important food and historically was a critical resource in times of food shortage (Nelson, 1887). Ptarmigan and grouse are some of the few fresh foods available in winter. Through intentional observation and use over generations, Indigenous people have accumulated knowledge about ptarmigan and grouse ecology and behavior (Irving et al., 1967; Nelson, 1983; Fienup-Riordan, 2007, 2020).

Ptarmigan and grouse are also important for non-Indigenous people in Alaska for both consumptive and non-consumptive uses. Organizations such as the Ruffed Grouse Society, Alaska Waterfowl Association, Founding Forty, and Safari Club International have supported habitat enhancement, hunter education, transplant attempts to supplement hunting opportunities, and research on ptarmigan and grouse in Alaska (Paul, 2009; Merizon and Carroll, 2023).

There is no dedicated annual harvest monitoring for ptarmigan and grouse in Alaska. Early harvest data primarily represented Alaska's urban hunters (Weeden, 1963, 1965). Ptarmigan and grouse harvest data have been collected in annual bird harvest surveys in rural Alaska, primarily focused on migratory birds (Wentworth, 2007a, b; Naves et al., 2021), and in discrete studies conducted in selected years and locations addressing diverse wild foods (e.g., Patterson, 1974; Tahbone et al., 2004; Bacon et al., 2011; ADF&G, 2026a) and small game harvest (Merizon and Carson, 2013; Merizon et al., 2015).

This study integrated, and built upon, the available information while specifically applying the geographic framework used for ptarmigan and grouse harvest management. The objective of this study was to estimate the seasonal harvest of ptarmigan and grouse and their eggs by residents of rural regions in Alaska. Based on available data, we provided harvest estimates for rural regions only (Fig. 1). We combined multiyear data to depict the average annual harvest in the 2004 – 15 period. A quantitative characterization of patterns of harvest of ptarmigan and grouse is important to better understand uses, inform harvest management, and strengthen collaboration with rural residents in research and harvest management.

Socio-Economic and Regulatory Context

In Alaska, definitions of rural and urban spaces relate to differences in geographic, economic, demographic, and ethnic factors that translate into diverse patterns of fishing and hunting (Wolfe and Ellanna, 1983; Aslaksen et al., 2009; Fall, 2016). About 250 small, remote communities are accessible only by aircraft, boat, and in winter by snowmobile. Just a few urban centers concentrate more than half of the state's total human population (~730,000 people). About half of the rural population is Indigenous, and in many communities this percentage approaches 100% (U.S. Census Bureau, 2012, 2026). Reliance on wild foods is a primary characteristic of rural communities. Subsistence is defined in law as a way of life centered on customary, non-commercial uses of wild resources for food, shelter, fuel, clothing, tools, crafts, transportation, sharing, and bartering (Alaska Statutes 16.05.940[34]), Alaska National Interest Lands Conservation Act Title VIII section 803). This definition derives from the values, traditions, and local economies of Indigenous people and other rural residents with similar resource use patterns. State law identifies nonsubsistence areas as those where dependence upon

subsistence is not a principal characteristic of the economy, culture, and way of life (Alaska Statutes 16.05.258[c], 5 Alaska Administrative Code 99.015). Recreational hunting in Alaska is usually associated with urban residents (Brown and Burch, 1992).

The State of Alaska manages harvest of ptarmigan and grouse under the general hunting regulations (5 Alaska Administrative Code 85.065). Under state regulations, all hunters are eligible to participate (Alaska residents and nonresidents) unless otherwise noted. The U.S. Department of Interior Office of Subsistence Management manages harvest of ptarmigan and grouse in areas federally defined as rural on federal public lands in Alaska (U.S. Fish and Wildlife Service, National Park Service, Bureau of Land Management, and U.S. Forest Service) (36 Code of Federal Regulations 242, 50 Code of Federal Regulations 100). Eligibility in federal subsistence regulations refers to all qualified Alaska rural residents unless otherwise noted. State and federal regulations may differ on eligibility criteria, geographic boundaries, season dates, and bag and possession limits, although wildlife managers attempt to coordinate these frameworks.

State subsistence regulations apply to game management units (GMUs), for which the Alaska Board of Game, the regulatory body that determines hunting regulations, has made a positive finding for customary and traditional (subsistence) use for defined fish and wildlife populations. For GMUs with a positive customary and traditional use finding, if harvest opportunities must be limited, preference in allocation is conferred to subsistence use (5 Alaska Administrative Code 99.030, Alaska Statutes 16.05.258). The Alaska Board of Game has made positive customary and traditional use findings for ptarmigan in parts of GMUs 1–5, 9–13, 15–19, and 20–26, and for grouse in parts of GMUs 1–5, 11–13, 15, 16, 19, and 20–25 (Fig. 1) (Ikuta and Balivet, 2011; Magdanz et al., 2011; Ikuta and Park, 2013; Wiita et al., 2018; Runfola and Naaktgeboren, 2020a, b).

State and federal regulations often refer to ptarmigan and grouse as multi-species categories. Hunting season dates for ptarmigan and grouse harvest extend from early August to March, and up to June in some GMUs. Harvest regulations tend to be more liberal outside of the nonsubsistence areas, in areas with a customary and traditional use finding, and in areas under federal subsistence regulations.

METHODS

Study Area

Based on data availability, we estimated harvest by residents of rural regions only (Table S1). We defined rural as communities and regions outside of nonsubsistence areas and the industrial enclave of Prudhoe Bay (Fig. 1, see also ADF&G 2026b) (Alaska Statutes 16.05.258[c], 5 Alaska Administrative Code 99.015, Fall 2016). Federal subsistence regulations identify similar nonrural areas. The nonsubsistence areas include the more populous areas of Alaska: Anchorage, a portion of the Kenai Peninsula Borough (excluding Beluga, Nanwalek, Port Graham, Seldovia, Seldovia Village Census-designated Place, and Tyonek), a portion of the Matanuska-Susitna Borough (excluding Glacier View, Lake Louise, Skwentna, Susitna, Eureka Roadhouse, and Chase), the Denali Borough (excluding Anderson and Cantwell), the Fairbanks North Star Borough, a portion of the Southeast Fairbanks Borough (including Big Delta, Delta Junction, Deltana, Fort Greely, and Whitestone Census-designated place), the Ketchikan Gateway Borough, Juneau, and Valdez.

We used 19 regions based on the GMUs defined in state regulations (Fig. 1) (5 Alaska Administrative Code 92.450, ADF&G 2026c). The GMUs 7 and 14 were excluded because all communities are within a nonsubsistence area. We combined GMUs 1–6 into the Southeast Alaska-Prince William Sound region because of limited harvest data. The 19 regions varied widely in the number of communities (median = 10; range = 3–41) and total human population (median = 3143; range = 126–29,163) (Table S1).

The survey data represented harvest by permanent resident households, including harvest that may have occurred outside the boundaries of their community of residence. Alaska Native people traditionally allocate use of resources within defined geographic areas among kinship groups. As the Indigenous population re-organized from a semi-nomadic way of life into yearlong communities at defined locations, land use areas evolved into community use areas (Wolfe and Ellanna, 1983). Thus, it is reasonable to assume that harvest occurred within the boundaries of the region of residence.

Harvest Estimates: Data Sources and Treatment

We compiled household survey data to estimate the annual average harvest for ptarmigan and grouse for each region and for the entire state for the 2004–15 reference period. The basic data unit was a community-year, that is, a harvest survey conducted in a specific community (city, census-designated place, unincorporated community, or population balance) and year (Table S1). The dataset (753 community-years) included data from the harvest survey of the Alaska Migratory Bird Co-Management Council (AMBCC) (n = 439 community-years) (Schwalenberg et al., 2023; AMBCC, 2026), the Community Subsistence Information System of the Alaska Department of Fish and Game, Division of Subsistence (n = 252) (ADF&G, 2026a), and research conducted by other entities (n = 62) (Brower and Opie, 1996, 1997; Fuller and George, 1997; Hepa et al., 1997; USFWS, 1997a, b; Brower Jr. et al.; 2000; Stovall, 2000; Tahbone et al., 2004; Ahmasuk et al., 2008; Bacon et al., 2011; Tahbone and Trigg, 2011; Harcharek et al., 2018). Sampling method (simple random sampling and stratified random sampling) and sampling rates varied depending on community size (total number of households). In all community-years, data collection

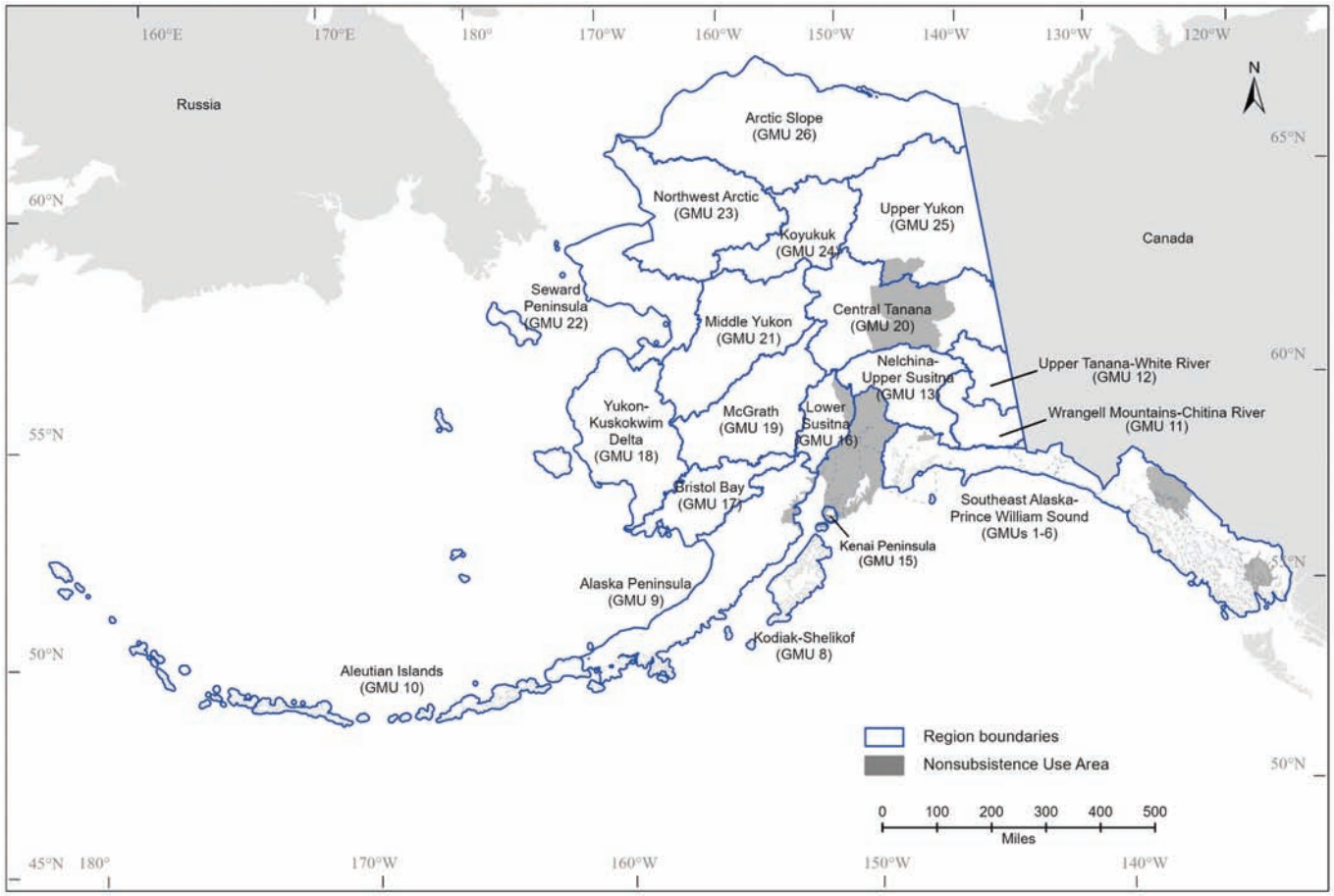

FIG. 1. Alaska's game management units (GMUs) used to estimate ptarmigan and grouse harvest. The GMUs 1–6 were combined into the Southeast Alaska-Prince William Sound region. The GMUs 7 and 14 (not shown in this map) were excluded because all communities are within a nonsubsistence area.

followed ethical principles, including informed consent, voluntary participation, anonymity, confidentiality, and community review of draft findings (Alaska Federation of Natives, 1993; U.S. National Science Foundation, 2018). Data were collected by in-person household interviews conducted in partnership with Indigenous organizations, and participation of households selected for sampling was typically greater than 80%. Sixty-nine percent of the dataset (517 community-years) pertained to the 2004–15 reference period, while older (166 community-years in 1982–2003) and more recent data (70 community-years in 2016–21) supplemented information for less frequently surveyed regions (Fig. S1).

Because of analytical constraints, the dataset did not include community-years from the AMBCC survey with missing data. Surveys conducted in the Yukon-Kuskokwim Delta and Bristol Bay in the 1980s to 1990s only reported results at the region level (Wentworth, 2007a, b) and were incompatible with the analytical approach we used. We excluded community-years for which the sample size was smaller than 30 households and the sampling proportion was less than 30% of total households (including some AMBCC data for 2016 and later, when methodological changes reduced household sampling rates) (Naves et al., 2021). This criterion did not cause under-representation of small communities in the dataset, as their sampling rate is typically above 30%.

For most community-years, harvest data were collected using the multi-species categories ptarmigan and grouse. Accordingly, we used these categories for the entire dataset, including for some community-years that collected data for individual species. Subsistence harvest surveys in Alaska use multi-species categories due to diverse study foci, challenges in species identification, limited understanding of local ethno-taxonomies by researchers, and a need for conciseness in surveys that include dozens to hundreds of animal and plant species.

We defined seasons as spring (April–June), summer (July–August), and fall–winter (September–March). The season of harvest was unknown for a small proportion of the community-years in the dataset. We presented only annual egg harvest estimates because eggs are available for about a month during spring–summer. Separately identifying fall and winter harvest is relevant for harvest management of resident ptarmigan and grouse (Sandercock et al., 2011). But we were limited to using seasons as in the AMBCC survey, as this source represented 58% of the community-years in the dataset. The AMBCC survey was designed with consideration of phenology and harvest management seasons for migratory birds, many of which are absent

from Alaska for a substantial part of the year. Resident ptarmigan and grouse were included in the AMBCC survey in recognition of their importance for rural residents.

The AMBCC survey collected winter harvest data (November–March) only for regions in Alaska used by migratory birds during their non-breeding period (Kodiak Archipelago, Aleutian-Pribilof Islands, Gulf of Alaska-Cook Inlet, and part of Bristol Bay). In addition, the AMBCC survey covered only spring and summer for the Arctic Slope, as many migratory birds start departing this region in late summer. Thus, it is possible that this study underestimated winter harvest. Nevertheless, this issue was partially alleviated because 42% of community-years in the dataset did include winter harvest (ADF&G 2026a and other data sources) and, in Alaska, inclement weather and short daylight hours in mid-winter (especially November–February) limit outdoor activities and harvest effort.

Harvest Estimates: Data Analysis

We estimated harvest by extrapolating data from surveyed households and communities to represent all rural households and communities in each region. For AMBCC data, we started with raw data at the household level and estimated community-level harvest (Cochran, 1977; Naves, 2018; Naves et al., 2019; Naves and Schamber, 2024) (Appendix S1: Equation 1). Then, we combined AMBCC community-level estimates with the other data sources that published community-level estimates. Although we used a large dataset, data were insufficient to estimate harvest for individual years while properly accounting for geographic patterns. For the many instances where a community was surveyed in more than one year, we averaged harvest and variance at the community level for all years surveyed before estimating harvest at the region level. Thus, estimates represented an annual average harvest in the 2004–15 period. To estimate harvest at the region level, we extrapolated community-level estimates to account for communities not represented in the dataset (Appendix 1: Equation 2). We summed the region-level estimates into a total for all rural regions. Harvest estimates did not account for crippling (i.e., birds shot but not retrieved).

Region-level harvest estimates were based on the average community harvest and the total number of communities in a region (Otis et al., 2016; Naves, 2018; Naves et al., 2019; Naves and Schamber, 2024). Data extrapolation did not account for community size (number of households). To minimize the risk of over-extrapolation, we excluded from the sampling frame nine communities that had 10 or fewer households as of the 2010 census and were not represented in the dataset (Portage Creek, Excursion Inlet, Hobart Bay, Aleneva, Pope-Vannoy Landing, Chicken, Livengood, and population balances for the Yukon-Kuskokwim Delta and Arctic Slope regions) (U.S. Census Bureau, 2012). Of 259 rural communities in the sampling frame, only 26 communities (10%) were not represented in the dataset (Table S1). Communities not represented in the dataset were dispersed in 12 regions, although almost half (n = 12) were in the Southeast Alaska-Prince William Sound region.

We calculated community-level variance for the AMBCC data based on raw data at the household level (Cochran, 1977) (Appendix S1: Equations 3a and 3b). For the other sources, we retro-calculated variance based on published confidence intervals at the community level. We assumed that these surveys used simple random sampling (Appendix S1: Equation 4). We calculated region-level variance using formulas for two-stage sampling: communities were primary sampling units, and households were secondary sampling units (Appendix S1: Equations 5a–c). We summed region-level variance into a total for all rural regions. We presented confidence intervals as a percentage of harvest estimates (Appendix S1: Equations 6a and 6b). We used the IBM Statistical Package for the Social Sciences (SPSS) version 27.

Species Composition

We combined harvest estimates for the multi-species categories ptarmigan and grouse with data from a parts collection (biological samples) to calculate the species composition of the harvest (e.g., Raftovich et al., 2025). Since 2011, the Alaska Department of Fish and Game Small Game Program has requested that hunters voluntarily provide wings, tails, and heads from harvested ptarmigan and grouse (ADF&G, 2026d). This parts collection has not included random sampling of hunters because of challenges in identifying a sampling frame. For example, hunters are not required to indicate if they intend to hunt ptarmigan and grouse when obtaining a hunting license.

We used the regional proportions of species from the 2011–23 parts collection for all years combined (Merizon, 2012, 2013; Carroll and Merizon, 2014, 2017, 2021; Merizon and Carroll, 2019, 2023). In 2011–23, on average, the parts collection yielded 978 parts/year (range = 721–1294), with participation of 71 hunters/year (range = 36–93). The number of hunters participating is a minimum because samples provided do not always include the hunter's name. The dataset included 6470 samples for ptarmigan and 6017 samples for grouse (Table S2). We combined parts collection data for GMUs 1–6; GMUs 1–13; and GMUs 19, 21, 24, and 25 due to small sample sizes (smaller than 30) in some GMUs where species of ptarmigan or grouse are likely to occur. For grouse harvest reported in GMUs 8 and 10, we used species composition from GMU 9; for grouse harvest reported in GMUs 22 and 26, we used species composition from GMU 23—grouse are uncommon in these six GMUs.

RESULTS

Ptarmigan

The total estimated annual average harvest of ptarmigan by Alaska's rural residents was 49,707 birds/year

TABLE 1. Estimated harvest of ptarmigan (species combined) by residents of rural regions in Alaska, annual average 2004–15.

Region and game management unit (GMU) of residence	Ptarmigan estimated harvest (number of birds/year)[1]					Ptarmigan egg harvest
	Spring (April–June)	Summer (July–August)	Fall-winter (September–March)	Unknown season	Annual total	
Arctic Slope GMU 26	1353	198	328	0	1879	15
Northwest Arctic GMU 23	1416	72	4807	6	6301	0
Seward Peninsula GMU 22	1196	85	2951	4	4236	77
Yukon-Kuskokwim Delta GMU 18	15,148	242	3527	3	18,920	676
Bristol Bay GMU 17	3113	62	1375	6	4556	20
Alaska Peninsula GMU 9	1094	534	2030	394	4052	35
Aleutian Islands GMU 10	102	67	599	1	769	14
Kodiak-Shelikof GMU 8	279	8	1253	60	1600	0
Southeast Alaska-Prince William Sound GMUs 1–6	183	295	2656	374	3508	0
Kenai Peninsula GMU 15	0	0	111	0	111	0
Lower Susitna GMU 16	6	0	129	37	172	0
Nelchina-Upper Susitna GMU 13	54	219	928	373	1574	0
Wrangell Mountains-Chitina River GMU 11	7	7	23	114	151	3
Upper Tanana-White River GMU 12	214	45	377	0	636	0
McGrath GMU 19	12	0	129	0	141	8
Central Tanana GMU 20	51	19	405	0	475	0
Middle Yukon GMU 21	13	0	133	0	146	0
Koyukuk GMU 24	132	5	196	5	338	0
Upper Yukon GMU 25	54	8	80	0	142	0
Total	24,427	1866	22,037	1377	49,707	848

[1] Confidence interval presented in Table S3.

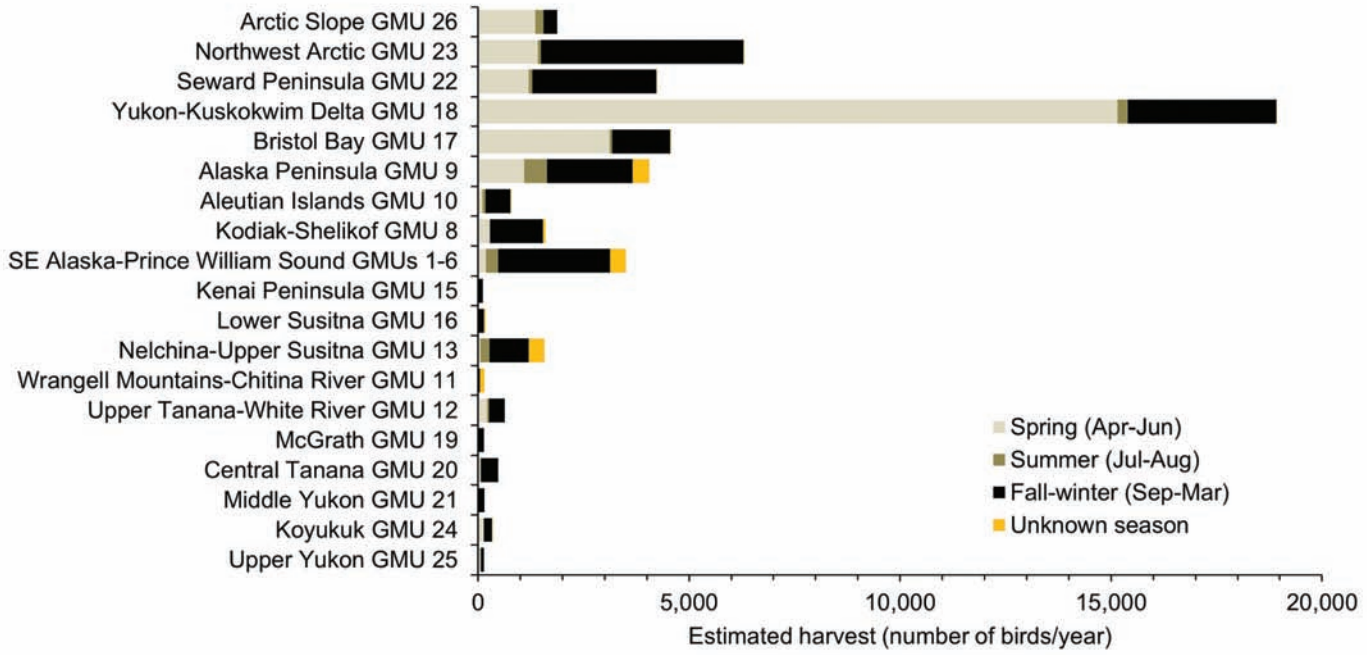

FIG. 2. Estimated harvest of ptarmigan by residents of rural regions in Alaska, annual average 2004–15. GMU: game management unit.

(CI= 46,725–52,689) in the 2004–15 reference period (Table 1, Fig. 2, Table S3). The Yukon-Kuskokwim Delta had the largest ptarmigan harvest (18,920 birds/year, or 38% of the total harvest). Ptarmigan harvest for the Northwest Arctic, Seward Peninsula, Bristol Bay, Alaska Peninsula, and Southeast Alaska-Prince William Sound regions (about 3000–6000 birds/year or 7%–13%) was intermediate relative to other rural regions. Ptarmigan harvest was relatively small (up to 1900 birds/year or 3%) for the remaining regions.

For all rural regions combined, the seasonal distribution of ptarmigan harvest was 51% in spring, 4% in summer, and 45% in fall–winter (harvest with documented seasons) (Table 1). Spring–summer accounted for at least 69% of the ptarmigan harvest for the Yukon-Kuskokwim Delta, Bristol Bay, and Arctic Slope regions. Harvest was about evenly split between spring–summer and fall–winter for the Alaska Peninsula and Upper Yukon regions. Fall–winter harvest was at least 59% of the annual total for the remaining regions.

TABLE 2. Estimated harvest of grouse (species combined) by residents of rural regions in Alaska, annual average 2004–15.

Region and game management unit (GMU) of residence	Grouse estimated harvest (number of birds/year)[1]					Grouse egg harvest
	Spring (April–June)	Summer (July–August)	Fall-winter (September–March)	Unknown season	Annual total	
Arctic Slope GMU 26	0	0	4	0	4	0
Northwest Arctic GMU 23	14	11	152	0	177	0
Seward Peninsula GMU 22	22	31	290	0	343	5
Yukon-Kuskokwim Delta GMU 18	62	11	584	0	657	0
Bristol Bay GMU 17	215	533	3248	32	4028	0
Alaska Peninsula GMU 9	225	136	504	217	1082	0
Aleutian Islands GMU 10	0	0	4	0	4	0
Kodiak-Shelikof GMU 8	1	0	0	0	1	0
Southeast Alaska-Prince William Sound GMUs 1–6	428	302	3765	852	5347	0
Kenai Peninsula GMU 15	5	18	153	0	176	0
Lower Susitna GMU 16	4	39	204	225	472	0
Nelchina-Upper Susitna GMU 13	109	598	1173	204	2084	0
Wrangell Mountains-Chitina River GMU 11	19	124	39	32	214	0
Upper Tanana-White River GMU 12	245	188	1324	0	1757	30
McGrath GMU 19	128	33	2453	0	2614	0
Central Tanana GMU 20	134	106	2451	0	2691	0
Middle Yukon GMU 21	52	40	1403	0	1495	0
Koyukuk GMU 24	48	12	191	0	251	0
Upper Yukon GMU 25	59	15	426	0	500	0
Total	1770	2197	18,368	1562	23,897	35

[1] Confidence interval presented in Table S4.

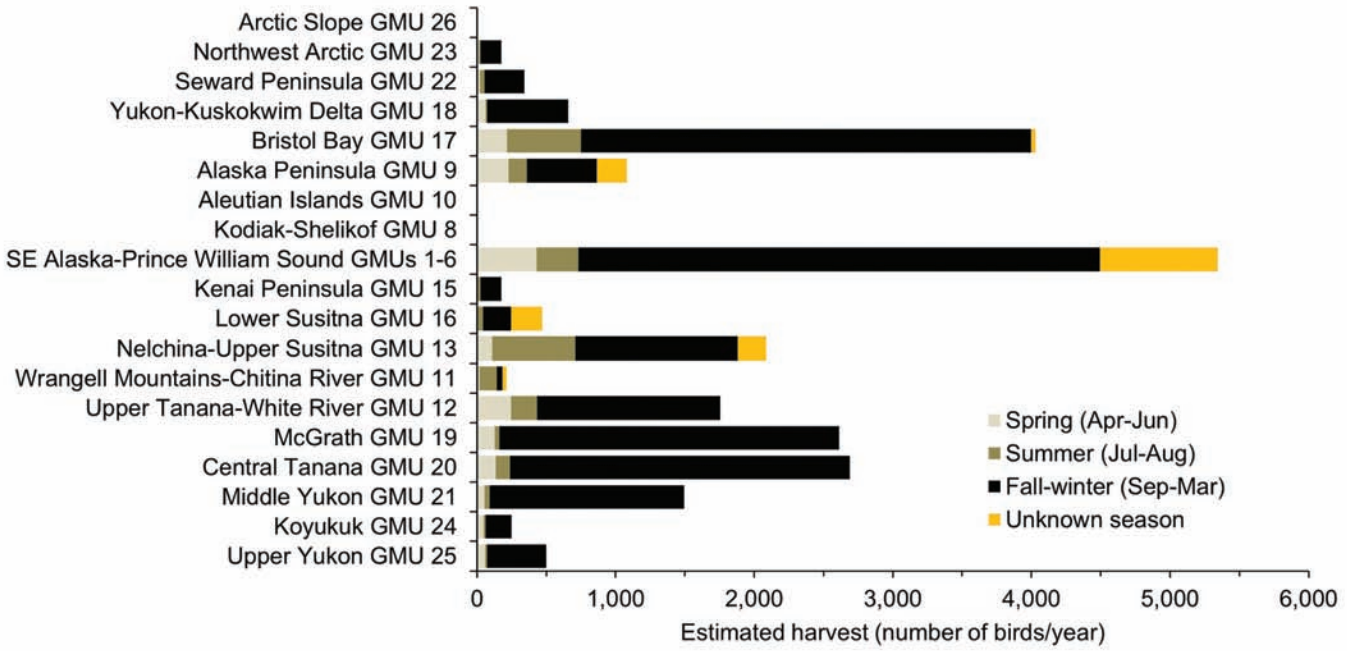

FIG. 3. Estimated harvest of grouse by residents of rural regions in Alaska, annual average 2004–15. GMU: game management unit.

The total estimated harvest of ptarmigan eggs was 848 eggs/year (CI = 755–941) (Table 1, Table S3). The Yukon-Kuskokwim Delta (80%) and Seward Peninsula (9%) accounted for most of the ptarmigan egg harvest. Harvest of ptarmigan eggs was documented for five additional regions.

Grouse

The total estimated annual average harvest of grouse by Alaska's rural residents was 23,897 birds/year (CI = 2 0,790–27,004) in the 2004–15 period (Table 2, Fig. 3, Table S4). For all rural regions combined, the seasonal distribution of the harvest was 8% in spring, 10% in summer, and 82% in fall–winter (harvest with documented seasons). Harvest of grouse eggs was documented for the Upper Tanana-White River and Seward Peninsula regions, averaging a total of 35 eggs/year (CI = 19–51).

Regions with the largest grouse harvest were the Southeast Alaska-Prince William Sound (22% of the total harvest by rural residents) and Bristol Bay (17%). Grouse

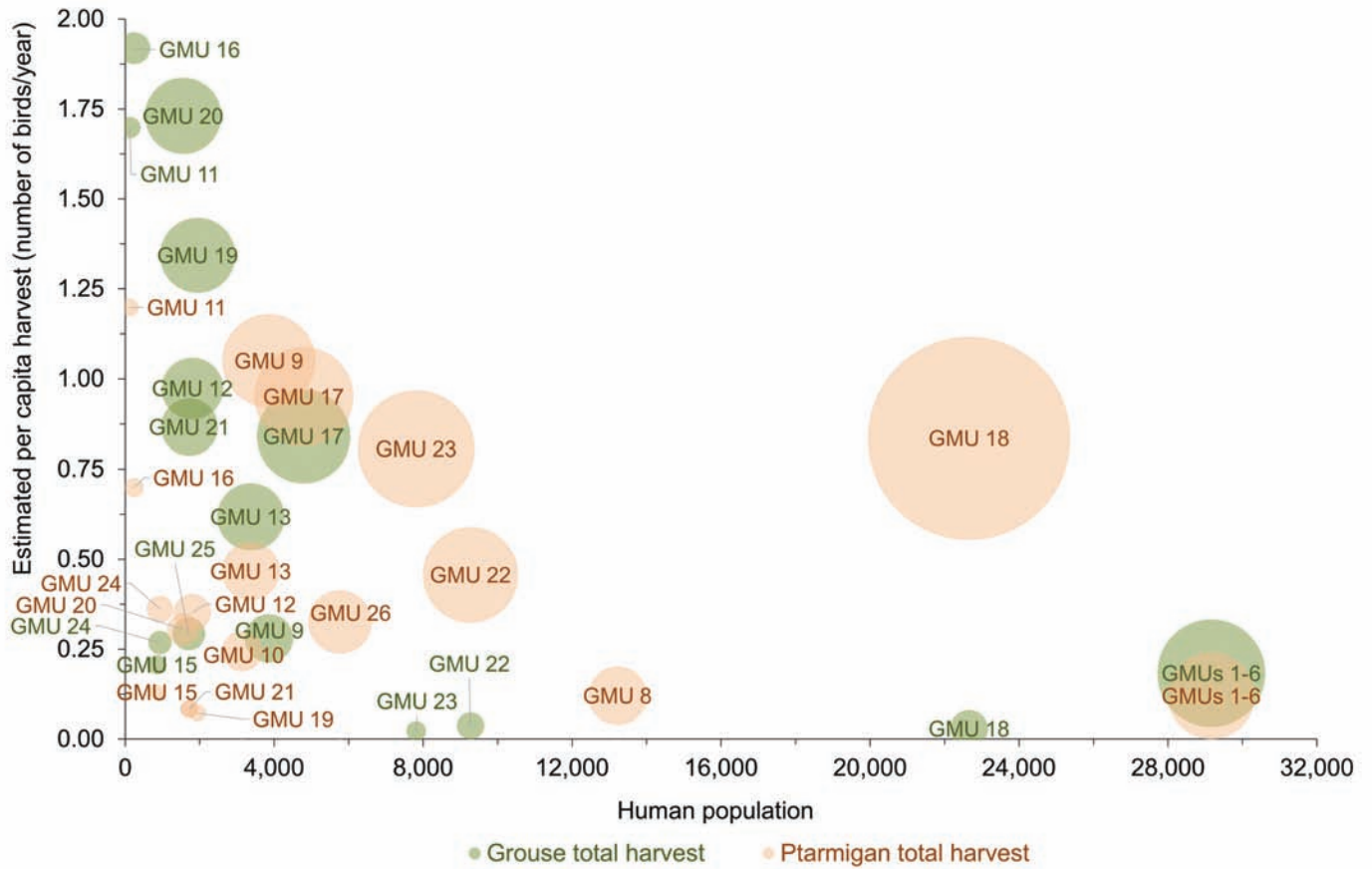

FIG. 4. Estimated per capita harvest of ptarmigan and grouse by residents of rural regions in Alaska, human population (U.S. Census Bureau, 2012), and total harvest (diameter of circles), annual average 2004–15. Regions or game management units (GMUs) are: (1–6) Southeast Alaska-Prince William Sound; (8) Kodiak-Shelikof; (9) Alaska Peninsula; (10) Aleutian Islands; (11) Wrangell Mountains-Chitina River; (12) Upper Tanana-White River; (13) Nelchina-Upper Susitna; (15) Kenai Peninsula; (16) Lower Susitna; (17) Bristol Bay; (18) Yukon-Kuskokwim Delta; (19) McGrath; (20) Central Tanana; (21) Middle Yukon; (22) Seward Peninsula; (23) Northwest Arctic; (24) Koyukuk; (25) Upper Yukon; and (26) Arctic Slope.

harvest was intermediate (5%–11%) for the Alaska Peninsula and for several regions in interior Alaska (McGrath, Middle Yukon, Central Tanana, Nelchina-Upper Susitna, and Upper Tanana-White River). Grouse harvest by residents of the remaining regions was small (1%–3%).

Geographic and Seasonal Patterns

The total ptarmigan harvest (49,707 birds/year) was nearly double the grouse harvest (23,897 birds/year) (Fig. S2a). Ptarmigan harvest occurred in all rural regions and had a strong component in western Alaska (Yukon-Kuskokwim Delta, Northwest Arctic, Bristol Bay, Seward Peninsula, and Alaska Peninsula). Harvest in western and northern Alaska was primarily composed of ptarmigan. In western Alaska, the Bristol Bay and the Alaska Peninsula also had a substantial grouse harvest. Across regions, the per capita harvest was more variable for grouse than for ptarmigan (Fig. 4). Grouse harvest had a strong component in interior Alaska, including some of the highest values for per capita harvest (Lower Susitna, Central Tanana, Wrangel Mountains-Chitina River, McGrath). Grouse harvest was virtually absent from the North Slope, Aleutian Islands, and Kodiak-Shelikof regions, reflecting species distribution.

Ptarmigan harvest in the North Slope, Yukon-Kuskokwim Delta, and Bristol Bay primarily occurred in spring (April–June) (Fig. S3a). Ptarmigan harvest in all other regions occurred primarily in fall–winter (September–March). Grouse harvest primarily occurred in fall–winter (Fig. S3b). In the Southeast Alaska-Prince William Sound, harvest consisted of equal proportions of grouse and ptarmigan, primarily occurring in fall–winter. This region had a relatively large total harvest and a relatively small per capita harvest (Fig. 4). Summer harvest (July–August) for both ptarmigan and grouse was more prominent in the Nelchina-Upper Susitna and Wrangell Mountains-Chitina River.

Species Composition

Applying the species proportions from the parts collection to the harvest estimates, the ptarmigan harvest was composed of 88% Willow, 11% Rock, and 1% White-tailed ptarmigan (Table 3). The grouse harvest was composed of 60% Spruce Grouse, 22% Sooty Grouse, 14% Sharp-tailed Grouse, and 4% Ruffed Grouse (Table 4).

Representation of individual species in the parts collection approximately aligned with species ranges in

TABLE 3. Estimated annual harvest of ptarmigan species by residents of rural regions in Alaska, annual average 2004–15.

Region and game management unit (GMU) of residence	Estimated annual harvest (number of birds/year)			
	Annual total harvest	Willow Ptarmigan	Rock Ptarmigan	White-tailed Ptarmigan
Arctic Slope GMU 26	1879	962	917	0*
Northwest Arctic GMU 23	6301	4501	1800	0*
Seward Peninsula GMU 22	4236	3986	250	0*
Yukon-Kuskokwim Delta GMU 18	18,920	18,920	0	0*
Bristol Bay GMU 17	4556	4556	0*	0*
Alaska Peninsula GMU 9	4052	3982	70	0*
Aleutian Islands GMU 10	769	0*	769	0*
Kodiak-Shelikof GMU 8	1600	533	1067	0*
Southeast Alaska-Prince William Sound GMUs 1–6	3508	3055	453	0
Kenai Peninsula GMU 15	111	87	0	24
Lower Susitna GMU 16	172	171	0	1
Nelchina-Upper Susitna GMU 13	1574	1457	86	31
Wrangell Mountains-Chitina River GMU 11	151	140	8	3
Upper Tanana-White River GMU 12	636	591	32	13
McGrath GMU 19	141	69	72	0*
Central Tanana GMU 20	475	188	281	6*
Middle Yukon GMU 21	146	72	74	0*
Koyukuk GMU 24	338	167	171	0*
Upper Yukon GMU 25	142	70	72	0*
Total	49,707	43,508	6121	77

Note: Species composition based on parts collection (Table S2) (Merizon, 2012, 2013; Carroll and Merizon, 2014, 2017, 2021; Merizon and Carroll, 2019, 2023).

* Species has limited occurrence or is unlikely to occur in this region.

TABLE 4. Estimated annual harvest of grouse species by residents of rural regions in Alaska, annual average 2004–15.

Region Game Management Unit (GMU)	Estimated annual harvest (number of birds/year)				
	Annual total harvest	Spruce Grouse	Ruffed Grouse	Sharp-tailed Grouse	Sooty Grouse
Arctic Slope GMU 26	4	4*	0*	0*	0*
Northwest Arctic GMU 23	177	177	0*	0*	0*
Seward Peninsula GMU 22	343	343	0*	0*	0*
Yukon-Kuskokwim Delta GMU 18	657	657	0*	0*	0*
Bristol Bay GMU 17	4028	4028	0*	0*	0*
Alaska Peninsula GMU 9	1082	1082	0*	0*	0*
Aleutian Islands GMU 10	4	4*	0*	0*	0*
Kodiak-Shelikof GMU 8	1	1*	0*	0*	0*
Southeast Alaska-Prince William Sound GMUs 1–6	5347	122	0*	0*	5225
Kenai Peninsula GMU 15	176	176	0	0	0*
Lower Susitna GMU 16	472	436	36	0	0*
Nelchina-Upper Susitna GMU 13	2084	1414	99	572	0*
Wrangell Mountains-Chitina River GMU 11	214	145	10	59	0*
Upper Tanana-White River GMU 12	1757	1192	83	482	0*
McGrath GMU 19	2614	1797	123	694	0*
Central Tanana GMU 20	2691	1184	581	926	0*
Middle Yukon GMU 21	1495	1028	70	397	0*
Koyukuk GMU 24	251	173	12	67	0*
Upper Yukon GMU 25	500	344	23	133	0*
Total	23,897	14,306	1037	3330	5225

Note: Species composition based on parts collection (Table S2) (Merizon, 2012, 2013; Carroll and Merizon, 2014, 2017, 2021; Merizon and Carroll, 2019, 2023).

* Species has limited occurrence or is unlikely to occur in this region.

Alaska (Gabrielson and Lincoln, 1959; Weeden, 1965; Fink et al., 2023). Absence of Rock and White-tailed ptarmigan in the parts collection for some regions may reflect participation in the parts collection, limited hunting effort, or access to the alpine habitats where these species usually occur. Proportions of ptarmigan and grouse (multi-species categories) in harvest estimates and in the parts collection were similar (0%–17%) for 11 of the 19 regions (Table S5, Fig. S4). Some regions showing less similar proportions (26%–60%) nevertheless had relatively large sample sizes for the parts collection (e.g., Nelchina-Upper Susitna n = 2082 and Kenai Peninsula n = 588). The species composition

should be considered as provisional at least for 11 of the 19 regions due to small sample sizes in the parts collection (Table S2) and/or a substantial mismatch in the proportion of ptarmigan and grouse (multi-species categories) between the harvest surveys and the parts collection (GMUs 1–6, 8, 11, 12, 13, 15, 16, 17, 21, 24, and 25).

DISCUSSION

Harvest Amounts

This study provided diverse refinements to the available information on ptarmigan and grouse harvest in Alaska (Table 5). We aligned the regions and sampling frame with the state GMUs used for harvest management. Some earlier harvest data incompletely represented rural regions (Weeden, 1963, 1965). More recently, while the AMBCC survey has provided much of the bird harvest data available for rural Alaska, its usefulness to inform ptarmigan and grouse harvest management has been limited because it has used region boundaries and a sampling frame defined for migratory birds (Naves et al., 2021). About 55 communities considered as rural in this study are ineligible to participate in the subsistence harvest of migratory birds, most of them in the Southeast Alaska-Prince William Sound and Nelchina-Upper Susitna regions. Also compared to the AMBCC survey, this study more completely accounted for fall and winter harvest by including additional data sources that fully represented these seasons.

By using household survey data, we were able to properly represent rural demographics. Surveys based on hunting license holders have tended to underrepresent Indigenous and rural residents. Up until the 1950s, Indigenous residents were not required to obtain a hunting license and thus were not included in the sampling frame for harvest assessments based on license holders (Buckley, 1954, 1957). Currently, most requirements pertaining to hunting licenses and harvest reporting apply to rural and urban residents alike. Participation by rural residents in these requirements tends to be lower than by urban residents (Schmidt and Chapin, 2014; Naves et al., 2023). Participation of rural residents in voluntary harvest surveys based on hunting license holders also tends to be lower than among urban residents (Merizon and Carson, 2013; Merizon et al., 2015).

Finally, the dataset we used represented most communities in all rural regions, except for the Southeast Alaska-Prince William Sound region (where 70% of the communities were represented). Thus, harvest estimates in this study relied on minimal extrapolation at the community level and properly accounted for diverse harvest patterns among communities and regions.

Based on surveys of hunting license holders in 2012 and 2014, the average estimated annual Alaska-wide harvest by both rural and urban residents were 127,103 ptarmigan and 83,946 grouse (Table 5) (Merizon and Carson, 2013; Merizon et al., 2015). These studies acknowledged challenges in identifying a sampling frame specific to small game hunters among all license holders, as well as low participation in the surveys, especially by rural license holders. Relative to the Alaska-wide estimates based on surveys of license holders (Merizon and Carson, 2013; Merizon et al., 2015), estimates from this study for rural residents only based on household surveys represented 39% of the ptarmigan harvest and 28% of the grouse harvest (Table 5). In contrast, rural residents accounted for 79% of the annual average Alaska-wide harvest of waterfowl and Sandhill Crane (344,282 birds/year in the 2004–15 period) (Naves and Schamber, 2024; USFWS, 2025). Future studies may further clarify harvest levels of ptarmigan and grouse by urban hunters, as well as whether harvest patterns by rural and urban hunters differ between resident and migratory birds in Alaska.

The AMBCC survey and earlier surveys related to the goose management plan provide an index for the annual variation of ptarmigan harvest for western Alaska (Wentworth, 2007a, b). For the Yukon-Kuskokwim Delta, annual ptarmigan harvest estimates were relatively large in the 1986–2019 period, except for 2007, 2008, and 2019 (Naves et al., 2021). For the Bristol Bay region, in the 1995–2019 period, relatively low ptarmigan harvest estimates occurred in 2016–19 (Naves et al., 2021). As reported by local residents, low ptarmigan abundance starting around 2016 and extending into 2022 was likely related to weather unfavorable for chick survival (cool and wet summers, followed by little snow in winter) (Merizon and Carroll, 2019, 2023). Annual variation in harvest estimates may reflect bird abundance, socio-ecological factors affecting harvest effort, and variable performance in the implementation of harvest surveys.

Overall, ptarmigan represented 13% and grouse 6% of the total number of birds annually harvested by Alaska's rural residents, including migratory birds (Fig. S5a) (Naves, 2018; Naves et al., 2019; Naves and Schamber, 2024). Ptarmigan and grouse are integral to the diverse fish and wildlife that have traditionally supported the subsistence way of life and the associated food security system.

Geographic and Seasonal Harvest Patterns

Large ptarmigan harvest in the Yukon-Kuskokwim Delta was a main feature of harvest patterns in rural Alaska (Fig. S2). This pattern may be related to ptarmigan abundance, hunting effort, and other cultural and ecological factors. The literature qualitatively characterizes Willow Ptarmigan as being most abundant along the barren coast of the Bering Sea and the Arctic Ocean. In the late 1800s, flocks of ptarmigan in the Yukon-Kuskokwim Delta often numbered several hundred, and sometimes several thousand, birds (Nelson, 1887:131–132). Among the sheer abundance and diversity of the avifauna of the Yukon-Kuskokwim Delta, the title of "tundra game king" reflects Willow Ptarmigan's role as food for people and wildlife (Brandt, 1943:199).

TABLE 5. Historic and current estimates for annual harvest of ptarmigan and grouse in Alaska.

Species	Harvest estimates for rural Alaska (based on household interview surveys)				Alaska-wide harvest estimates (based on survey of hunting license holders)			
	1954–57[1*]	1969–73[2*]	2004–15[3ǂ]	2004–15[4]	1952[5]	1954–61[6]	2012[7]	2014[8]
Ptarmigan	52,672	50,541	33,644	49,707	38,904	74,440	140,000	114,206
Willow Ptarmigan	–	–	–	43,508	–	–	–	–
Rock Ptarmigan	–	–	–	6121	–	–	–	–
White-tailed Ptarmigan	–	–	–	77	–	–	–	–
Grouse	3952	10,262	9802	23,897	51,694	52,018	69,000	98,891
Spruce Grouse	–	–	–	14,306	–	–	61,000	72,734
Ruffed Grouse	–	–	–	1037	–	–	5500	15,947
Sharp-tailed Grouse	–	–	–	3330	–	–	1800	5397
Sooty Grouse	–	–	–	5225	–	–	700	4813
Total	56,624	60,803	43,446	73,604	90,598	126,457	209,000	213,097

Source: [1] Olson (1956), Hansen (1957), Weeden (1963, 1965); [2] Patterson (1974); [3] Naves et al. (2021); [4] this study; [5] Buckley (1954, 1957); [6] Courtright (1968); [7] Merizon and Carson (2013); and [8] Merizon et al. (2015).

– Data unavailable.

* These surveys included different subsets of communities and incompletely represented rural regions.

ǂ The AMBCC survey used seasons, region boundaries, and sampling frame defined for migratory birds.

Compared to ptarmigan, grouse harvest estimates did not reach such high levels despite large per capita harvest in some regions in interior Alaska (Fig. 4). It is unclear if this pattern was due to grouse abundance, density, or behavior, or to factors related to harvesting practices. In the Southeast Alaska-Prince William Sound region, relatively large grouse harvest estimates were associated with intermediate per capita harvest, although harvest estimates for this region relied on a smaller dataset as compared to other regions in this study (Table S1).

Based on the parts collection and qualitative information, most ptarmigan are harvested in September–October and March–April (Weeden, 1965:84; Carroll and Merizon, 2014). Based on the household surveys, across all rural regions, about half (51%) of ptarmigan harvest occurred in spring. This overall pattern largely reflected harvest in the Yukon-Kuskokwim Delta, where 80% of the annual ptarmigan harvest occurred in spring (Fig. 2). Archiving records for a Yup'ik dance mask collected in the early 1900s in the lower Kuskokwim River seem to refer to seasonal harvest patterns: "Mask representing a valley ptarmigan. This spirit calls the ptarmigan in spring for food" (Museum of the American Indian 9/3402, Brooklyn Museum 44.34.7). Old Yup'ik dance masks were associated with Agayuyaraq, a communal ceremony conducted in late winter to request abundance in the upcoming harvest season (Fienup-Riordan, 1996). Seasonality of ptarmigan harvest may be related to flocking behavior, movements between wintering and breeding grounds, males' fearless behavior during the mating season (that makes birds susceptible to harvest), and environmental and ecological factors that may differ among regions (Nelson, 1887; Brandt, 1943).

In all rural regions, grouse harvest occurred primarily in fall–winter (82%), including some regions where ptarmigan harvest primarily occurred in spring, such as the Yukon-Kuskokwim Delta, Bristol Bay, and Alaska Peninsula (Fig. 3). Large proportions of harvest of waterfowl, Sandhill Crane, seabirds, and shorebirds in rural Alaska also occurred in spring (Naves 2018; Naves et al., 2019; Naves and Schamber, 2024) (Fig. S6). Some factors involved in seasonal patterns of grouse harvest may include incidental harvest during fall hunting for large mammals, such as moose and caribou, and grouse behavior in fall in search of grit near roads (Weeden, 1965).

Alaska is unique among U.S. states and other countries in extending hunting season dates for ptarmigan and grouse into late winter and spring (Dahlgren et al., 2021). Hunting mortality may be compensatory in fall and early winter due to high natural mortality of hatch-year birds, while it tends to be additive in other times of the year (Sandercock et al., 2011; Frye et al., 2022). Harvest management involves choosing preferred scenarios: ample time opportunity through a longer hunting season, with the possibility of lower bird densities on the landscape, or a shorter season, with the possibility of higher bird densities (Merizon and Carroll, 2019). Preferences in harvest management may differ among user groups and depend on temporal variation in bird abundance.

Informing Future Harvest Assessment and Management

Prior bird harvest assessment in rural Alaska has been largely based on methods developed for migratory birds, many of which are absent from Alaska for a substantial part of the year. Better accounting for ecological factors, geographic and seasonal harvest patterns, and the management framework specific to ptarmigan and grouse can improve the applicability of harvest data collected in diverse harvest assessment efforts without compromising their specific goals.

For GMUs with a customary and traditional use finding, the Alaska Board of Game determines the number of animals reasonably necessary for subsistence (ANS) consistent with sustained yield (5 Alaska Administrative

Code 99.025, Alaska Statutes 16.05.258[f]). The ANS is a regulatory guideline that reflects customary needs, it is not a quota or a guarantee of harvest. The ANS is usually defined as a range based on historical harvest data, if available. For example, the harvest estimate from this study for the Yukon-Kuskokwim Delta (18,920 birds/year) was close to the high end of the defined ANS range (3000–23,000 birds), and the harvest estimate for the Seward Peninsula (4236 birds/year) was well above the ANS range (125–900 birds) defined based on the previously available information (5 Alaska Administrative Code 99.025.12). Harvest estimates provided by this study clarified harvest levels for all rural regions and are useful to fine-tune management parameters and actions.

Consideration of socio-ecological contexts of rural regions is important to collaboratively develop harvest management approaches that are meaningful for rural residents. The Alaska Department of Fish and Game has closely collaborated with hunters to gather biological and harvest information (Merizon and Carroll, 2023). Nevertheless, studies on ptarmigan and grouse populations in Alaska have mostly addressed areas along road corridors within nonsubsistence (urban) areas (Weeden, 1972; Merizon, 2013; Merizon, et al., 2018; Frye et al., 2022, 2023). By characterizing harvest patterns for rural regions, this study supports engagement of, and collaboration with, rural residents in research and harvest management. Future efforts to document Indigenous knowledge and perspectives about ptarmigan and grouse can fill gaps in ecological knowledge and further strengthen collaboration with subsistence users in Alaska. Ongoing efforts to generate information on population abundance, ecology, and harvest create possibilities for the future implementation of adaptive harvest management (Dahlgren et al., 2021). Such investments in research and collaboration should reflect the high nutritional, cultural, and ecological importance of ptarmigan and grouse for all people in Alaska.

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