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# Effects of Control on the Dynamics of an Adjacent Protected Wolf Population in Interior Alaska

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**ABSTRACT** Long-term wolf (*Canis lupus*) research programs have provided many insights into wolf population dynamics. Understanding the mechanisms controlling responses of wolf populations to changes in density, environmental conditions, and human-caused mortality are important as wolf management becomes increasingly intensive. Competition with humans for ungulate prey has led to large-scale wolf control programs, particularly in Alaska, and although wolf populations may sustain relatively high (e.g., 22–29%) rates of conventional harvest, control programs are specifically designed to have lasting population-level effects.

Understanding the broader impacts of wolf control efforts on the surrounding area is of particular concern for conservation agencies such as the United States National Park Service, whose mandates generally preclude the artificial reduction of populations of native predators, particularly for the primary purpose of increasing available prey biomass for human harvest. Detailed assessments of the factors influencing population vital rates (i.e., survival, natality, dispersal) and population trajectory in the context of control efforts are critical for understanding complex ecological relationships between wolves and their prey and informing management of each. Using a long-term dataset and a powerful new integrated modeling approach, we assessed the effects of wolf control on the dynamics of a monitored wolf population residing primarily within an adjacent protected area where wolf control activities were prohibited.

We monitored wolf population dynamics in Yukon-Charley Rivers National Preserve (YUCH) in interior Alaska, USA for 22 years (1993–2014). During our study, 2 large-scale wolf control programs were implemented in the surrounding area with the primary goal of increasing the size of the Fortymile caribou herd. We used known-fate data based on relocations of marked wolves and repeated counts of associated pack mates to estimate survival, dispersal, and natality rates. We jointly analyzed these data using an integrated modeling approach, thereby providing inference to the entire resident, pack-dwelling population of wolves using YUCH. Apparent survival (i.e., including mortalities and dispersals) was lower in the study area during the lethal control period, indicating a direct additive effect of control despite the prohibition of control efforts inside YUCH boundaries. Apparent survival was higher in years following winters with above-average snowfall, corresponding with a predicted increase in ungulate prey vulnerability the following year. Extraterritorial forays were associated with lower apparent survival rates, particularly after the initiation of lethal wolf control in the surrounding area. In general, mortalities tended to occur evenly throughout the year, whereas dispersal rates increased during late winter and early spring. Dispersals accounted for approximately half of the observed losses in our collared sample across all age classes (excluding known breeders), although yearlings were the most likely to disperse.

Sustained reductions in wolf densities outside the YUCH boundary during both wolf control programs also allowed us to directly assess the effects of reduced density on vital rates. Natality rates (estimated number of individuals added to each pack over the May–Aug interval) increased sharply over the course of each control program, suggesting a strong reproductive response to large-scale reductions in wolf densities in the surrounding area. Natality rates dropped rapidly between the 2 control programs, further supporting this conclusion. Smaller pack sizes and losses of known breeders were associated with lower natality rates per pack in the following year, suggesting human-caused mortality could have direct short-term effects on productivity by reducing pack sizes and removing breeders. However, although control can reduce the fecundity of individual packs in the short term, adjacent populations quickly respond to reduced wolf density by increasing natality rates.

Estimates of wolf density based on relocations of marked individuals within packs were dependent on sample size and could not be used to reliably estimate population growth rate ( $\lambda$ ). As an alternative, we developed a new metric,  $\lambda^*$ , which assessed whether natality was sufficient to offset population losses on an annual basis, under the assumption that the minimum functional unit in a wolf population is a breeding pair. When  $\lambda^*$  decreased below 1.0

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because of a combination of loss of individuals and the dissolution of packs, the population of interest effectively became a population sink reliant on immigrants from surrounding areas for maintenance. Based on estimates of  $\lambda^*$ , we determined the YUCH study population was a source of wolves for the surrounding area in most years before implementation of lethal wolf control but became a population sink largely reliant on immigration from surrounding areas afterwards, despite the prohibition on control activities within YUCH. This finding has important implications for the management of protected areas, particularly in areas such as Alaska where wolf control is commonly implemented at large spatial scales. We expect  $\lambda^*$  will be a useful tool for understanding wolf ecology and managing populations in other areas as well.

Overall, wolf vital rates were quite dynamic and responded quickly to changing conditions. The rapid increase in natality in an apparent response to decreased density strongly suggests that density dependence plays an important role in regulating wolf populations. Flexibility in dispersal and natality rates likely allow wolf populations to respond to variation in prey resources, wolf density, and mortality. These findings also suggest that sustainable harvest rates depend on annual variation in population vital rates. The clear impacts of management schemes in the area adjacent to YUCH suggests that effective conservation of protected areas may require more active management decisions than are often employed, particularly if the maintenance of unaltered system dynamics is a primary objective. © Published 2017. This article is a U.S. Government work and is in the public domain in the USA. Wildlife Monographs published by Wiley Periodicals, Inc. on behalf of The Wildlife Society. This is an open access article under the terms of the Creative Commons Attribution License, which permits use, distribution and reproduction in any medium, provided the original work is properly cited.

**KEY WORDS** Alaska, *Canis lupus*, density dependence, harvest, individual heterogeneity, integrated model, known-fate, natality, *N*-mixture, population dynamics, predator control, survival, wolf.

## Los Efectos del Control sobre la Dinámica de una Población de Lobos en un Área Adyacente en el Interior de Alaska

**RESUMEN** Los estudios a largo plazo de lobos (*Canis lupus*) proveen mucha información sobre la dinámica poblacional. Es importante entender los mecanismos que controlan las reacciones de las poblaciones de lobos a los cambios de densidad, condiciones ambientales, y la muerte a causa de humanos a medida que el manejo de los lobos se vuelve más intensiva. La competencia entre lobos y humanos por presas unguladas ha llevado al desarrollo de programas de control a gran escala, sobre todo en Alaska. Aunque las poblaciones de lobos pueden aguantar un nivel alto (22–29%) de cacería, los programas de control están diseñados para afectar la población a largo plazo. Entender los impactos más amplios del control de lobos en los alrededores es de interés para las agencias de conservación como el Servicio de Parques Nacionales de los Estados Unidos, que tiene prohibido reducir artificialmente las poblaciones de depredadores nativos, sobre todo para aumentar las presas disponibles a los humanos. Investigaciones detalladas de los factores que influyen las tasas vitales (supervivencia, natalidad, y dispersión) y el trayecto de la población dados los esfuerzos de control son críticas para entender las relaciones ecológicas complejas entre los lobos y sus presas e informar el manejo de cada uno. Evaluamos los efectos del control de lobos sobre la dinámica de una población de lobos que viven principalmente dentro de un área protegida donde el control de lobos está prohibido. Para esto, usamos unos datos recolectados a largo plazo y un enfoque nuevo de modelos integrados.

Monitoreamos las dinámicas de población de los lobos en Yukon-Charley Rivers National Preserve (YUCH) en el interior de Alaska, USA por 22 años (1993–2014). Durante nuestro estudio, se implementaron 2 programas de control de lobos en las áreas rodeando el área protegida con la meta de aumentar el tamaño de la manada de caribú del Fortymile. Usamos datos de destino conocido generados por la reubicación de lobos marcados y conteos repetidos de miembros asociados de la manada para estimar supervivencia, dispersión, y natalidad. Analizamos estos datos usando un método de modelos integrados, así proporcionando inferencia a toda la población residente de lobos que viven en manadas en YUCH. La supervivencia aparente (incluyendo muertes y dispersión) era más baja en el área de estudio durante el periodo de control letal, indicando un efecto aditivo y directo de control a pesar de la prohibición de control dentro de los límites de YUCH. La supervivencia aparente era más alta en los años siguiendo a los inviernos con caídas de nieve más del promedio, correspondiente al aumento de vulnerabilidad de los ungulados en el siguiente año. Las salidas fuera del territorio estaban asociadas con tasas de supervivencia menores, particularmente después de empezar el control letal de lobos en la zona de los alrededores. En general, las mortalidades ocurrieron durante todo el año, mientras que las tasas de dispersión aumentaron durante el fin del invierno y el comienzo de la primavera. La dispersión representó aproximadamente la mitad de las pérdidas de lobos con collares de todas las

edades (con la excepción de los lobos que se saben son reproductores) aunque los de un año eran los más probables en dispersar.

Reducciones en las densidades de lobos fuera de los límites de YUCH durante ambos periodos de control nos permitió analizar los efectos de la densidad reducida en las tasas vitales. La tasa de natalidad (el número estimado de individuos sumados a cada manada de mayo a agosto) aumentó considerablemente durante cada programa de control, lo cual sugiere que había una fuerte respuesta reproductiva a las reducciones a gran escala de densidad de lobos en los alrededores. La tasa de natalidad disminuyó rápidamente durante el periodo entre los 2 programas de control, apoyando aún más esta conclusión. Manadas más pequeñas y la pérdida de reproductores conocidos estaban asociados con menores tasas de natalidad por manada en el siguiente año, sugiriendo que la muerte causado por los humanos podría tener efectos directos de corto plazo sobre la productividad por medio de reducir el tamaño de las manadas y quitar a los lobos reproductores. Sin embargo, aunque el control puede disminuir la fecundidad de las manadas individuales a corto plazo, las poblaciones adyacentes responden rápidamente a la reducción de densidad de lobos aumentando las tasas de natalidad.

Las estimaciones de la densidad de lobos a base de las reubicaciones de individuos marcados en manada dependían del tamaño de la muestra y no se podían usar para estimar confiablemente la tasa de crecimiento de la población ( $\lambda$ ). Desarrollamos una métrica nueva,  $\lambda^*$ , como alternativa para evaluar si la natalidad era suficiente para compensar las pérdidas de población anuales, asumiendo que la unidad mínima funcional en una población de lobos es una pareja reproductiva. Cuando  $\lambda^*$  llega a ser menos que 1.0 por la pérdida de individuos y el desbarato de las manadas, la población de interés se convierte en un sumidero poblacional que depende de inmigrantes de los alrededores para mantenerse. A base de los estimados de  $\lambda^*$ , determinamos que la población de estudio en el YUCH era una fuente de lobos para los alrededores en los años antes de implementar el control de lobos letal pero se convirtió en un sumidero poblacional que dependía de la inmigración de los alrededores, aunque las actividades de control estaban prohibidas dentro del YUCH. Esto tiene implicaciones importantes para el manejo de las áreas protegidas, particularmente en áreas como Alaska donde el control de lobos se implementa a grandes escalas espaciales. Esperamos que  $\lambda^*$  sea una herramienta útil para entender la ecología de los lobos y manejar las poblaciones en otras áreas también.

Las tasas vitales de los lobos eran muy dinámicas y respondieron rápidamente al cambio de condiciones. El aumento rápido en natalidad en respuesta aparente a la densidad disminuida sugiere fuertemente que la dependencia de densidad juega un papel importante en la regulación de las poblaciones de lobos. La flexibilidad en las tasas de dispersión y natalidad probablemente permiten que las poblaciones de lobos respondan a la variación en los recursos de presas, densidad de lobos, y mortalidad. Esto también sugiere que las tasas de caza sostenibles dependen de la variación anual en tasas de supervivencia anuales. Los impactos claros del manejo en el área alrededor de YUCH sugieren que la conservación efectiva de las áreas protegidas puede exigir decisiones administrativas más activas que las que actualmente se usan, particularmente si el objetivo principal es el mantenimiento de las dinámicas de un sistema inalterado.

## Les Effets du Contrôle sur la Dynamique D'une Population de Loups Protégés Adjacente à une Population Contrôlée au Centre de L'alaska

**RÉSUMÉ** Les programmes de recherche à long terme sur le loup (*Canis Lupus*) ont fourni de nombreuses idées sur la dynamique des populations de loup.

La gestion du loup devenant de plus en plus intense, il est important de comprendre les mécanismes qui contrôlent les réponses des populations de loup aux changements de densité, aux conditions environnementales et à la mortalité causée par l'homme.

La concurrence avec les êtres humains pour la proie d'ongulés a conduit à des programmes de lutte contre les loups à grande échelle, en particulier en Alaska et bien que les populations de loup puissent maintenir des taux relativement élevés de récolte conventionnelle (par exemple 22-29%), les programmes de lutte sont spécifiquement conçus pour avoir des effets durables sur la population.

La compréhension des impacts plus larges des efforts de lutte contre le loup sur les alentours est particulièrement préoccupante pour les organismes de conservation tels que le Service des parcs nationaux des États-Unis dont les mandats empêchent généralement la réduction artificielle des populations de prédateurs indigènes, en particulier dans le but principal d'accroître la biomasse de proie disponible pour la récolte humaine.

Des évaluations détaillées des facteurs qui influent sur les taux vitaux de la population (i.e., La survie, la natalité, la dispersion) et la trajectoire de la population dans le contexte des efforts de lutte sont essentielles pour comprendre les relations écologiques complexes entre les loups et leurs proies et en informer le gestion de

chacun. À l'aide d'un ensemble de données à long terme et d'une nouvelle approche de modélisation intégrée puissante, nous avons évalué les effets de lutte contre le loup sur la dynamique d'une population de loup surveillée résidant principalement dans une zone protégée adjacente où les activités de lutte contre le loup étaient interdites.

Nous avons surveillé la dynamique des populations de loup dans la réserve nationale de Yukon-Charley Rivers (YUCH) au centre de l'Alaska, aux États-Unis, pendant 22 ans (1993-2014). Au cours de notre étude, 2 programmes de lutte contre le loup à grande échelle ont été mis en place dans la région environnante dans le but principal d'augmenter la taille du troupeau des caribous de Fortymile. Nous avons utilisé des données sur le destin connu en fonction des relocalisations de loups marqués et de comptages répétés des groupes de loups associés pour estimer les taux de survie, de dispersion et de natalité. Nous avons analysé conjointement ces données en utilisant une approche de modélisation intégrée fournissant ainsi une inférence à l'ensemble de la population résidente des groupes de loups utilisant YUCH. La survie apparente (i.e., y compris les mortalités et les dispersions) était plus faible dans la zone d'étude pendant la période de contrôle mortelle ce qui indique un effet additif direct de contrôle à l'intérieur des limites YUCH. La survie apparente a été plus élevée dans les années qui ont suivi les hivers avec des chutes de neige supérieures à la moyenne, ce qui correspond à une augmentation prévue de la vulnérabilité aux proies d'ongulés l'année suivante. Les incursions extraterritoriales ont été associées à des taux de survie apparente plus faibles, en particulier après l'initiation du contrôle mortel du loup dans la région environnante. En général, les mortalités ont tendance à se produire de manière uniforme tout au long de l'année, alors que les taux de dispersion ont augmenté au cours de la fin de l'hiver et au début du printemps. Les dispersions représentaient environ la moitié des pertes observées dans notre échantillon à colliers dans toutes les classes d'âge (à l'exclusion des reproducteurs connus), bien que les nouveaux-nés de l'année (yearlings) étaient les plus susceptibles de se disperser.

Les réductions soutenues des densités de loup à l'extérieur de la limite YUCH au cours des deux programmes de lutte contre le loup nous ont également permis d'évaluer directement les effets de la densité réduite sur les taux vitaux. Les taux de natalité (nombre estimé d'individus ajoutés à chaque groupe au cours de l'intervalle de mai à août) ont fortement augmenté au cours de chaque programme de contrôle, ce qui suggère une forte réponse reproductive aux réductions à grande échelle des densités de loup dans la région environnante. Les taux de natalité ont chuté rapidement entre les 2 programmes de contrôle, ce qui a confirmé cette conclusion. Les groupes plus petits et les pertes de reproducteurs connus ont été associés à des taux de natalité inférieurs par groupe l'année suivante, ce qui suggère que la mortalité causée par l'homme pourrait avoir des effets directs à court terme sur la productivité en réduisant la taille des groupes et en éliminant les reproducteurs. Cependant, bien que le contrôle puisse réduire la fécondité des groupes individuels à court terme, les populations adjacentes répondent rapidement à la densité de loup réduite en augmentant les taux de natalité.

Les estimations de la densité du loup en fonction des déplacements d'individus marqués dans les groupes dépendaient de la taille de l'échantillon et ne pouvaient pas être utilisées pour estimer de manière fiable le taux de croissance de la population ( $Y$ ). Comme alternative nous avons développé une nouvelle métrique,  $Y^*$ , qui a évalué si la natalité était suffisante pour compenser les pertes de population sur une base annuelle, en supposant que l'unité fonctionnelle minimale dans une population de loup est un couple de loups reproducteurs. Lorsque  $Y^*$  a diminué en dessous de 1,0 en raison d'une combinaison de perte d'individus et de la dissolution des groupes, la population en question est devenue une population dépendante des animaux des zones environnantes pour son entretien. Sur la base des estimations de  $Y^*$ , nous avons déterminé que la population de l'étude YUCH était une source de loups pour la région environnante dans la plupart des années avant la mise en oeuvre du contrôle de loup mortel, mais est devenue une population largement tributaire du déplacement des animaux des régions environnantes malgré l'interdiction des activités contrôlées au sein de YUCH. Cette découverte a d'importantes implications pour la gestion des espaces protégés, en particulier dans des régions comme l'Alaska, où le contrôle du loup est couramment mis en oeuvre à grande échelle spatiale. Nous espérons que  $Y^*$  sera un outil utile pour comprendre l'écologie du loup et la gestion des populations dans d'autres endroits.

Dans l'ensemble, les taux vitaux du loup étaient plutôt dynamiques et ont réagi rapidement aux conditions changeantes. L'augmentation rapide de la natalité dans une réaction apparente à une diminution de la densité suggère fortement que la dépendance à la densité joue un rôle important dans la régulation des populations de loup. La flexibilité dans les taux de dispersion et de natalité permet probablement aux populations de loup de répondre aux variations des ressources de la proie, de la densité du loup et de la mortalité. Ces résultats suggèrent également que les taux de récolte durables dépendent de la variation annuelle des taux vitaux de la population. Les impacts clairs des systèmes de gestion dans la zone adjacente à YUCH suggèrent que la conservation efficace des espaces protégés peut nécessiter des décisions de gestion plus actives que celles souvent employées, en particulier si le maintien de la dynamique du système inchangé est un objectif principal.

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## INTRODUCTION

Our collective understanding of wolf (*Canis lupus*) population ecology and dynamics has benefitted greatly from long-term research programs based on continuous monitoring of wolf populations in North America over many decades (e.g., Mech 1966, 1986, 2009; Peterson 1977, 1999; Mech et al. 1998; Smith et al. 2003, 2010). Naturally occurring populations (Superior National Forest, Denali National Park and Preserve) and those areas where reintroduction or recolonization occurred after long periods of absence (Yellowstone National Park, Isle Royale National Park) have provided important insights into how wolves affect ecosystems through their interaction with their ungulate prey (Murie 1944, McLaren and Peterson 1994, Post et al. 1999, Smith et al. 2003, Ripple and Beschta 2004). Wolves influence prey abundance and distribution (Gasaway et al. 1983), thereby affecting vegetation structure and composition across the landscape (Ripple et al. 2001, Fortin et al. 2005, Ripple and Beschta 2012). However, perceived competition between wolves and humans for ungulate prey often leads to conflict and efforts to reduce wolf populations.

Increased wildlife conflict with humans, and the control measures that are often implemented in response, have important implications for managers of protected areas such as national parks. Managers of national park units are often mandated to conserve populations of a variety of species, including wolves, and in many cases are prohibited by policy from artificially reducing one native species to increase the abundance of another. In contrast, management policies of state wildlife management agencies often prioritize the reallocation of ungulates to human harvest, and predator-control programs may be implemented towards that goal. This strategy is particularly true in Alaska (e.g., Boertje et al. 1996, 2017; National Research Council 1997). Contrasting mandates such as these often result in conflicts among management agencies, although a commonly unstated assumption by managers of protected areas is that simply minimizing human-caused mortalities within management-area boundaries will meet conservation goals. This approach is often termed passive management. However, the efficacy of passive management strategies has rarely been tested and may unintentionally lead to declining populations (e.g., Rosenblatt et al. 2014). The propensity for wolves to travel large distances suggests that they may be exposed to substantial sources of human-caused mortality outside of a given management boundary, possibly leading to population-level effects. The

proximity of large-scale wolf control programs to the boundaries of many protected areas highlights the need to assess the true impacts of management actions in adjacent areas (Creel et al. 2015). If the effects of adjacent wolf harvest and control programs influence surrounding populations, managers of protected areas may need to consider these factors when determining appropriate conservation and management actions.

Wolves have been harvested, controlled, or extirpated throughout much of their historical range (Musiani and Paquet 2004), and the additivity of human-caused mortality has been a primary subject of management debate (Adams et al. 2008, Creel and Rotella 2010, Murray et al. 2010, Gude et al. 2012, Creel et al. 2015). Although conventional hunting and trapping can limit wolf populations (Peterson et al. 1984, Ballard et al. 1997, Person and Russell 2008), wolf populations appear to sustain conventional harvest at rates of  $\leq 22$ –29% of the annual fall population (Fuller et al. 2003, Adams et al. 2008, Creel et al. 2015). Because of difficulties in reducing populations through conventional hunting and trapping, more intensive wolf control programs have been implemented to further reduce densities in targeted areas with the goal of increasing ungulate abundance (Ballard et al. 1987; Gasaway et al. 1992; Boertje et al. 1996, 2012, 2017; National Research Council 1997; Hayes et al. 2003). Despite extensive harvest and broad implementation of wolf control programs, the effects of sudden and sustained reductions in density on wolf population dynamics are not fully understood. When studied, the effects are generally assessed only within the control area, and relatively little is known about the impacts over adjacent landscape segments. An understanding of these effects is of profound importance for the effective management of protected areas that are often located in close proximity to active control areas.

Vital rates may be altered during population reduction, allowing wolf populations to compensate numerically for increased mortality and changes in food supply. Change in dispersal rates has been suggested as the primary mechanism for short-term responses to changes in ungulate resources and low to moderate human exploitation (Fuller et al. 2003, Adams et al. 2008). Young wolves are most susceptible to conventional harvest and are also the most likely to disperse; therefore, conventional harvest may be partially compensated by reduced dispersal rates (Mech and Boitani 2003, Adams et al. 2008). Another possible mechanism for response to harvest is increased pup production, which is associated with increased prey availability (Boertje and

Stephenson 1992, Mech et al. 1998, Fuller et al. 2003). Conversely, loss of breeders, which may be increased by human exploitation, can lead to pack dissolution and decreased productivity (Brainerd et al. 2008, Sparkman et al. 2011, Borg et al. 2015). Similarly, extraterritorial forays during periods of low prey availability (Van Ballenberghe 1983, Ballard et al. 1997, Burch et al. 2005) may increase mortality through additional conflicts with established packs or exposure to human-caused mortality. In the context of the management of protected areas, where naturally functioning ecosystems and wolf populations are primary goals, active management decisions may be necessary when changes in vital rates due to control efforts occur in adjacent areas.

The detailed study of wolf population dynamics is logistically difficult. Wolves are inherently secretive and difficult to observe, occurring at low densities in clumped distributions (i.e., packs). Since the advent of radio-collars, a majority of wolf research has been based on data obtained through the relocation of radio-marked individuals. Although radio-marking has dramatically increased the amount of available data, representative marked samples are often difficult to obtain. In many areas, aerial observations of radio-marked individuals are required, leading to high study costs, and consequently, limited sample sizes. Due in part to cost and logistical limitations, inherent sampling challenges (e.g., unrepresentative samples, limited sample sizes) are often ignored at the analysis phase, resulting in biased estimates of population parameters. Inference is generally limited to the subsample of marked individuals and is heavily dependent on the number of relocations of marked individuals within packs. Although the consequences of these issues have been documented in some cases (e.g., Bekoff and Mech 1984, Burch et al. 2005), proposed solutions have been limited. However, recently developed analytical tools leveraging the large amount of information typically collected on unmarked pack-mates (Schmidt et al. 2015) can be used to address a majority of the sampling issues and resulting bias prevalent in wolf studies.

Yukon-Charley Rivers National Preserve (YUCH) is a protected area managed by the United States National Park Service (NPS), which was created, in part, to protect populations of wildlife, including wolves. Partially in response to proposed wolf control efforts adjacent to YUCH, the NPS initiated a wolf monitoring program to identify any effects such efforts might have on the wolf population using YUCH. During the course of our study, the Alaska Department of Fish and Game (ADF&G) implemented 2 wolf control programs during 2 different time periods along the border of YUCH, allowing us to investigate the effects of direct control-related mortalities and large-scale changes in surrounding wolf densities on the adjacent YUCH wolf population. We used data from a marked population of wolves in YUCH during March 1993–April 2014 and recently developed analytical techniques (Schmidt et al. 2015) to assess the impacts of adjacent wolf control activities on the population residing largely within YUCH, a protected management area. Our objectives were to 1) assess the impact of external wolf control on vital rates of wolves in YUCH, and 2) quantify the effects of breeder loss, winter conditions, extraterritorial forays, and pack size on wolf vital rates. We predicted that control efforts in the surrounding area would measurably alter the population

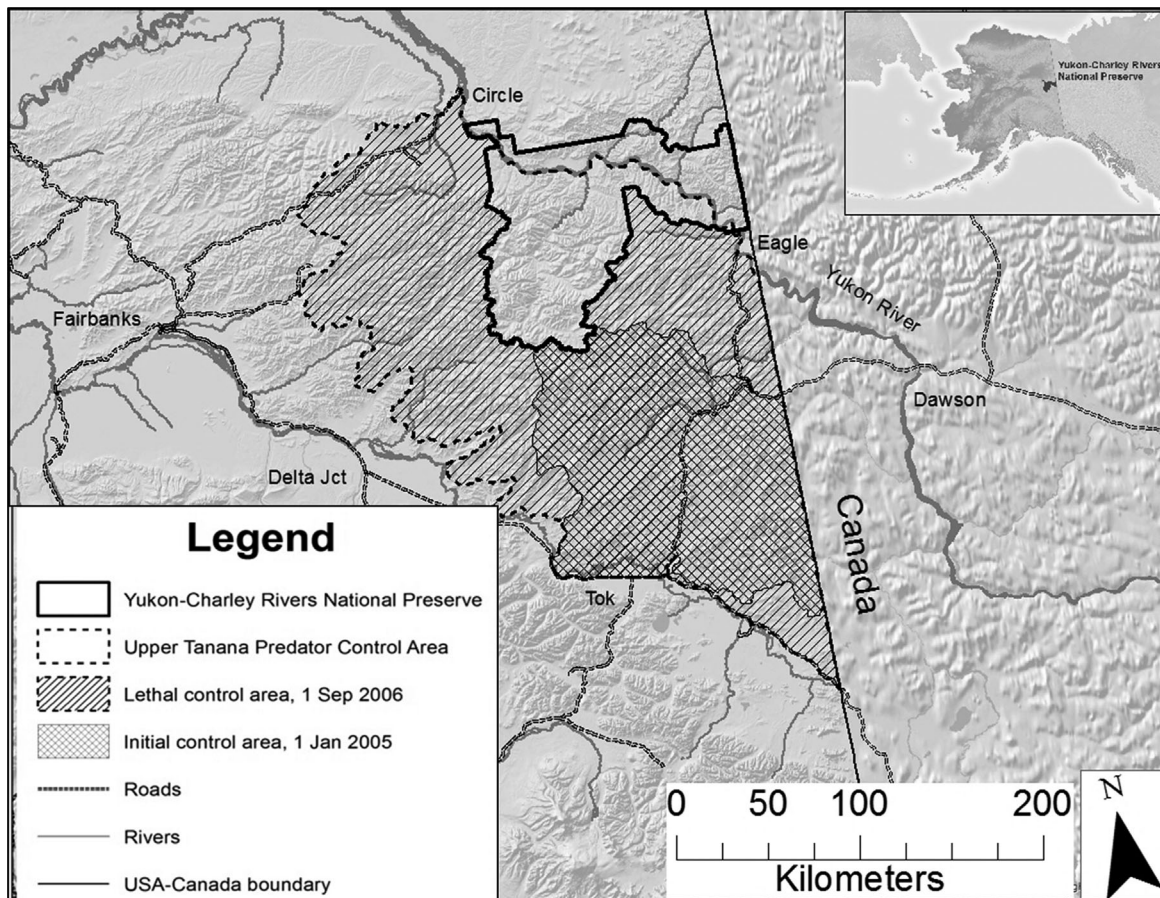
dynamics of wolves associated with YUCH. Specifically, we predicted that 1) control would be associated with reduced survival rates and interact with natality, resulting in larger population-level impacts when natality rates were low; 2) survival would be higher in years following winters with deeper snow because of increased prey vulnerability; 3) extraterritorial forays would result in reduced survival associated with large-scale movements; and 4) natality would be reduced for smaller packs and those experiencing breeder loss.

## STUDY AREA

The 10,220-km<sup>2</sup> study area included all of YUCH located in Interior Alaska bordering Yukon Territory, Canada (65°N, 143°W; Fig. 1). The study area included 184 km of the Yukon River and encompassed the entire Charley River watershed. The topography of the area consisted mainly of rolling hills and river bluffs. Some isolated rugged terrain occurred on several eroded mountains, with peaks generally <1,200 m. Vegetation at lower elevations was dominated by black spruce (*Picea mariana*) and several species of deciduous hardwoods including aspen (*Populus tremuloides*) and birch (*Betula papyrifera*). Ponds, sloughs, and large areas of tussock tundra were common in the flats along the Yukon River and lower parts of large tributaries such as the Charley and Kandik rivers. Wildfires were common throughout the study area, burning >400,000 ha (>40% of YUCH) since the mid-1980s. Winters in YUCH were long and cold, whereas summers were generally short and warm. The average annual temperature was −4.2°C and the maximum and minimum recorded values were 33°C and −51°C, respectively (Sousanes and Hill 2014). Little precipitation occurred annually (~315 mm), contributing to the propensity for large fires during summer months. The snow pack generally developed in mid-October and peaked in March at an average depth of 51 cm (Sousanes and Hill 2014).

The study area contained an intact predator-prey system where wolves were the primary predators of ungulates (Gasaway et al. 1983), although grizzly bears (*Ursus arctos*) were a significant source of calf mortality (Gasaway et al. 1992). The Alaska National Interest Lands Conservation Act led to the creation of YUCH in 1980 and included the stipulation that both sport and subsistence hunting and trapping were to be permitted in YUCH for a variety of game and furbearer species (including wolves). There were 3 ungulate prey species available to wolves in YUCH (Fig. 2): moose (*Alces alces*), Dall's sheep (*Ovis dalli*), and caribou (*Rangifer tarandus*). The moose population was a low-density (140 moose/1,000 km<sup>2</sup>), stable population of 700–1,300 moose that was concentrated primarily along the Yukon River (Burch 2012). Moose harvest in YUCH averaged 26 males/year (Burch 2012). Sheep occurred at low densities in the preserve, scattered among several small isolated mountains in the area. The last estimate of Dall's sheep abundance in the preserve during our study period indicated approximately 400 individuals were present in YUCH (Burch 2010). Harvest of sheep within YUCH averaged 4 males/year (Burch 2010). By far, the most numerous and widely available ungulate prey species was caribou.

The Fortymile caribou herd's home range overlapped the portion of YUCH south of the Yukon River, and calving primarily occurred in the hills surrounding the Charley River



**Figure 1.** Location of Yukon-Charley Rivers National Preserve (solid line) and the Upper Yukon Tanana Predator Control Area (dotted line), Alaska, USA. Wolf control activities occurred outside the boundaries of the preserve only (hashed areas). Although lethal wolf control began in January 2005, the initial area was restricted to the southeast portion of the final area.

drainage (Fig. 2). The herd's winter range covered a wide area from Steese Highway to the northwest and into the Yukon Territory of Canada to the east, including a majority of YUCH. Some portion of the Fortymile caribou herd wintered in or near the Charley River drainage in most years (Boertje et al. 2012), making caribou generally available to wolves in YUCH during the winter months. Approximately 1,000 caribou were harvested by humans annually from this herd, although there was high demand, and the season was often closed by emergency order to prevent overharvest (Gross 2015). Approximately half the wolf packs inhabiting YUCH were heavily dependent on caribou as their primary prey. The other packs preyed predominately on moose, although caribou were used by most packs. In fall 1920, Murie (1935) estimated the Fortymile caribou herd's size at 568,000 caribou; however, the methods used to generate this number were rudimentary, leading to repeated revisions of this estimate (e.g., Valkenburg et al. 1994, McDonald and Cooley 2004, Boertje et al. 2012). Since the 1930s, numbers have fluctuated from approximately 5,000 to 50,000, most recently increasing nearly 9-fold during the period 1973–2010 from approximately 6,000 to approximately 52,000 individuals (Valkenburg and Davis 1989; Valkenburg et al. 1994; Gross 2011; Boertje et al. 2012, 2017). Although the absolute value of Murie's estimate has been questioned, it continues to be used as a justification for the implementation of lengthy and intensive

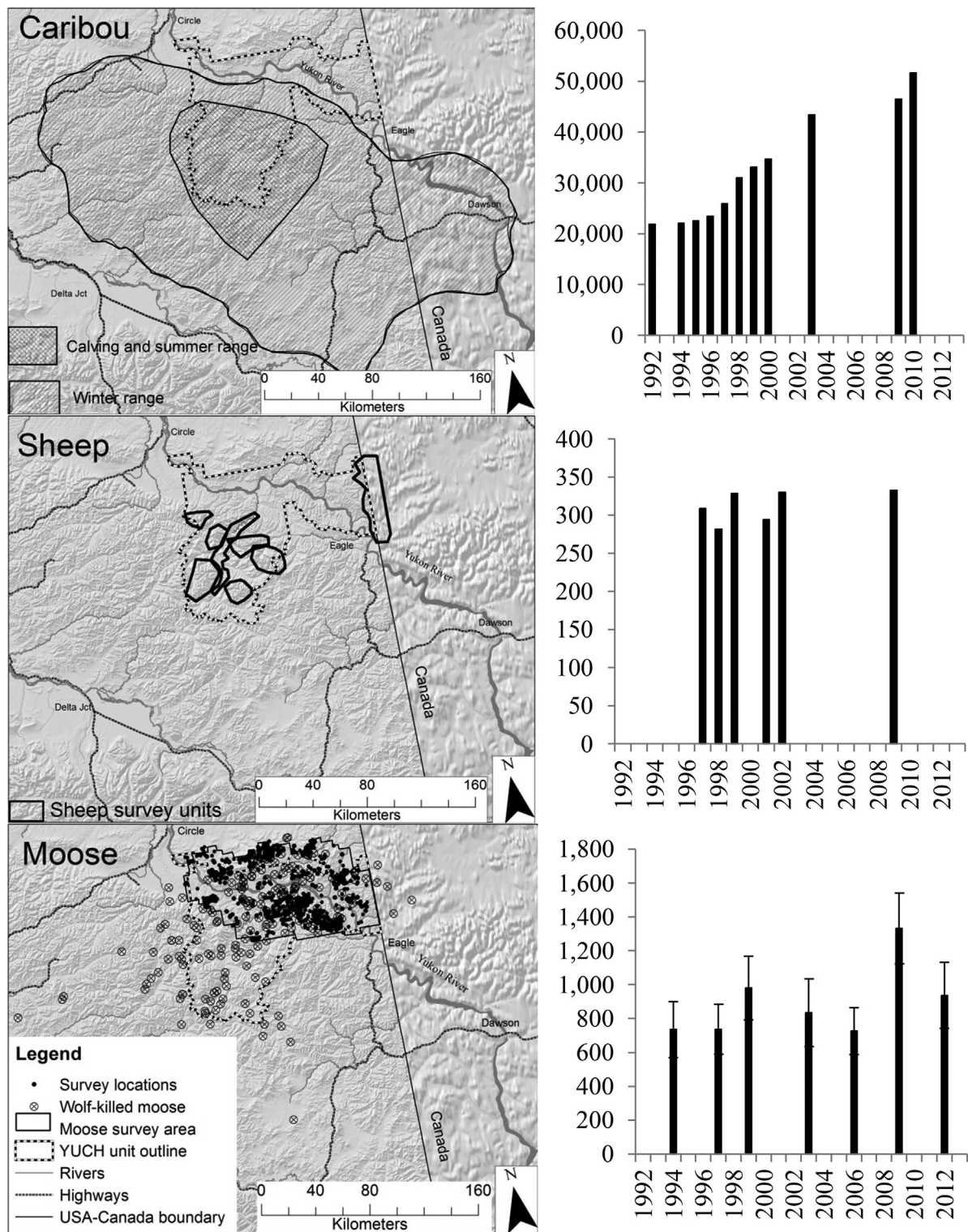
predator control programs in the area in an attempt to achieve higher caribou numbers.

### Wolf Control Programs

Historically, wolves were controlled by the federal government in the Fortymile area from the late 1940s until 1960 through poisoning, aerial shooting, trapping, and snaring (Gasaway et al. 1992, Valkenburg et al. 1994). Some poisoning of wolves continued in Alaska through the 1960s, and bounties on wolves continued through the late 1960s (McKnight 1970). A control program was also conducted in the Fortymile area by the ADF&G in the early 1980s (Gasaway et al. 1992). During our study, 2 wolf control programs, sterilization and translocation (non-lethal control) and aerial shooting (lethal control), were implemented at separate times by the ADF&G on the borders of YUCH with the goal of increasing the size of the Fortymile caribou herd to provide more opportunity for human harvest (Boertje and Gardner 2003; Boertje et al. 2012, 2017; Harvest Management Coalition 2012). Much of the caribou calving area lies within YUCH, and one of the goals of these programs was to reduce wolf predation on calves (Boertje and Gardner 2003, Boertje et al. 2017).

The first wolf control program conducted in the area during our study period was implemented between biological years (BY; May–Apr, based on the wolf reproductive cycle) 1997 and 2001.





**Figure 2.** Approximate distribution and estimates of abundance for the 3 ungulate prey species available to wolves in Yukon-Charley Rivers National Preserve (YUCH), Alaska, USA from 1992–2013. Bars are only shown for years with survey data. Caribou survey data were originally reported by Gross (2011) and Boertje et al. (2012), sheep survey data were originally reported by Burch (2010), and moose survey data were originally reported by Burch (2012). Error bars for the moose data represent 90% confidence intervals (Burch 2012). The polygons representing Dall's sheep range correspond to aerial survey units intended to cover a majority of sheep habitat in the area. Because moose also occur throughout the area, locations of known wolf kills and survey data are both shown to provide information on relative availability. Moose surveys were conducted only in close proximity to the Yukon River, where a majority of the moose are located in winter.

During this program, 15 packs along the border of YUCH were selected for reduction, and all pack members except the dominant pair were captured and translocated >160 km away (Fig. 3). The dominant pair was then surgically sterilized and released back into their territory. After sterilization, any wolves that were identified as having immigrated into the control area were translocated through the winter of 2000–2001 (Boertje and Gardner 2003, Gardner 2003, Boertje et al. 2008). Most treated pairs maintained their territories through BY 2001, although by the spring of 2003 approximately half of the sterilized packs remained. This effort reduced wolf numbers by approximately 78% along much of the border of YUCH (Fig. 3) for roughly 5 years (Boertje and Gardner 2003, Gardner 2003). No YUCH study packs were included in the sterilization program.

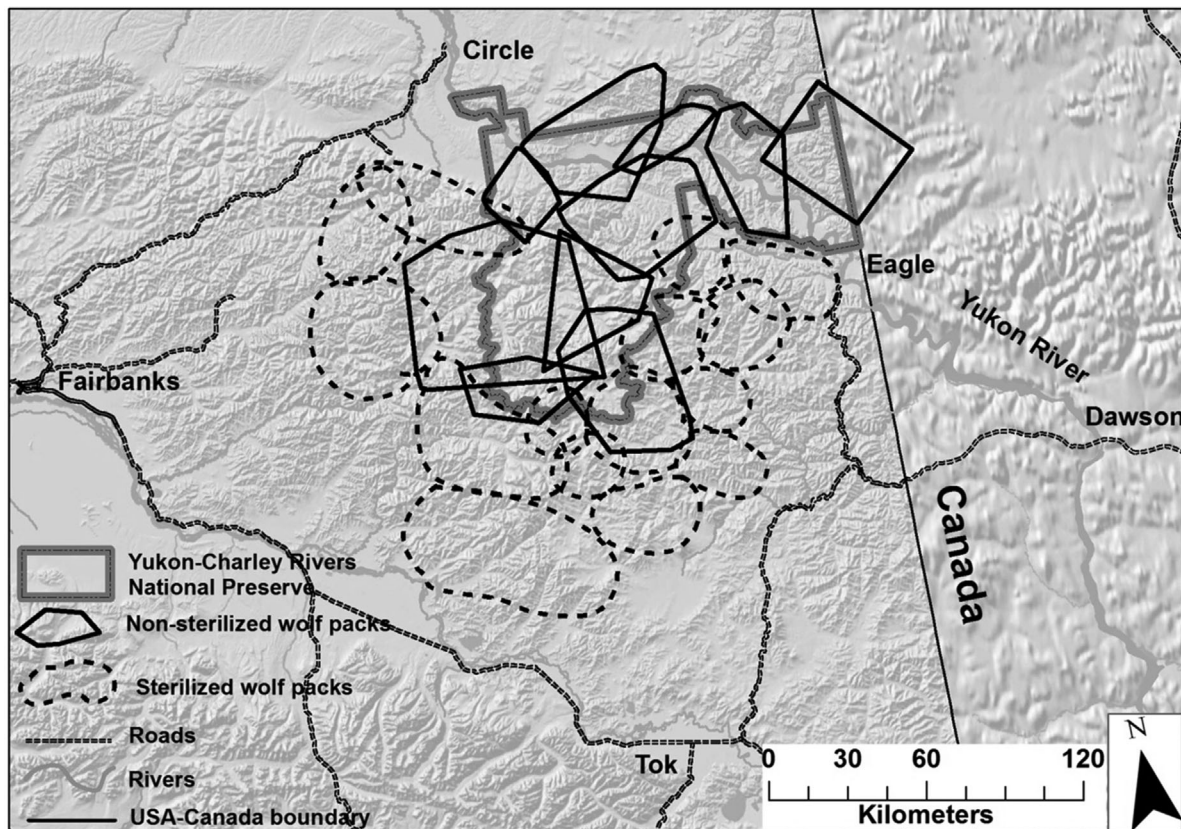
The second wolf control program was initiated in January 2005 as the Upper Yukon Tanana Predator Control Area (UYTPCA; Fig. 1). This predator control area was established southeast of the border of YUCH where private pilots were permitted to shoot wolves from fixed-wing aircraft (Gross 2012). The area was then expanded to 48,562 km<sup>2</sup> in September 2006 to include that portion of YUCH south of the Yukon River. Despite the inclusion of a portion of YUCH in the official control area, control activities were prohibited on NPS lands. This program was augmented from BY 2008 onwards to include the shooting of wolves from a helicopter by ADF&G staff (Gross 2012,

ADF&G 2014a). Although wolves were not killed within the boundaries of YUCH under this program, most YUCH study packs spent some portion of the year outside the YUCH boundary. Frequencies of collars deployed within NPS study packs were not used by ADF&G staff to aid removals; however, many packs used areas outside YUCH extensively in years when caribou were not locally available in large numbers, potentially exposing most packs to control activities. The number of reported mortalities from aerial control activities varied among years. Although lethal control was not uniformly applied to all YUCH study packs, many were directly affected during the course of the present study.

## METHODS

### Data Collection

We used relocations of marked individuals and counts of associated pack members to collect information on wolf vital rates for a sample of packs using our study area. We conducted wolf capture operations twice per year in most years, typically once in November or early December and once in February or March. Each capture operation usually lasted 5–7 days and was based from a remote field camp near the center of the study area. Captures targeted the breeding wolves from each pack whenever possible, primarily for budgetary reasons. Breeding wolves were



**Figure 3.** Spatial configuration of approximate wolf home ranges in and around Yukon-Charley Rivers National Preserve, Alaska, USA in 1997 when the non-lethal wolf control program was initiated. Dotted lines indicate approximate home ranges of the 15 packs that were identified for sterilization and relocation by the Alaska Department of Fish and Game. Subsequent removals reduced numbers in the treated area by 78% (Gardner 2003). Solid lines indicate home ranges based on minimum convex polygon methods for radio-marked packs that were excluded from treatments. The shaded line represents the boundaries of Yukon-Charley Rivers National Preserve.

the least likely to disperse or die, had greater den site and home range fidelity, and usually determined the travel patterns of the pack, thereby maximizing the life and benefit of each capture and radio collar. Over the course of the study, our abilities to pick out the breeding wolves and target them for capture improved, based primarily on body size, pelage appearance, and behavior. As a result, we expected that the collared sample alone would not be representative of the overall population. Therefore, we included counts of pack members in our analysis to augment the overall dataset and address the bias inherent in the marked sample (see Data Analysis section).

We initially located packs by searching for fresh wolf tracks in the snow from 2 or 3 small airplanes and following them until we located the wolves. We relocated packs containing marked individuals through radio tracking. Once we found a pack, we darted 1–3 pack members from a small helicopter and chemically immobilized them using a mixture of tiletamine hydrochloride and zolazepam hydrochloride (Telazol; 13.5 mg/kg). We recorded the sex and apparent age (Gipson et al. 2000, Adams et al. 2008) of each captured wolf, took a blood sample, and attached a mortality sensing very high frequency radio collar (VHF collar). Beginning in 2002, we instrumented most wolves with VHF radio collars also equipped with a global positioning system device (GPS collar) programed to record a single location per day. We identified pups via body size, behavior, canine length, and swelling of the epiphyseal closure of the distal end of the radius and ulna (Rausch 1967, Mech 1970, Adams et al. 2008). We identified breeding wolves using body size and weight, behavior, age assessment, pack composition (e.g., adult pair with pups), and testis or nipple size and pigmentation (Mech et al. 1993, Mech 2006). We also used den site attendance during the pup-rearing season to confirm breeding status. We monitored many packs over multiple seasons, providing further opportunities to confirm the identity of the breeding pair over time.

Once processing was complete, we left all captured wolves in a safe place to recover. We relocated each wolf later that same day or early the next day to confirm that it had recovered and rejoined its pack. We experienced no capture-related mortalities during the 22-year study ( $n = 225$  captures). Capture and handling procedures complied with guidelines established by the American Society of Mammalogists (Animal Care and Use Committee 1998), and this project was reviewed and approved by the NPS Institutional Animal Care and Use Committee (AKR\_YUCH.DENA\_Burch\_Wolves\_2013.A3). Study methods followed the standard operating procedures of the Central Alaska Network Vital Signs Monitoring Program (Meier and Burch 2009).

We relocated radio-marked wolves and their pack-mates from small fixed-wing aircraft approximately 20–45 times per year, although effort and success varied among years, months, and packs. Radio-tracking effort was concentrated in August–November and February–May with few locations in June–July or December–January for budgetary or logistical reasons (i.e., lack of light). We consolidated resighting histories for the collared wolves to monthly observations to help address the potentially large number of missing values caused by inconsistent relocation success. For each location, we recorded a latitude and longitude coordinate from the aircraft's GPS unit, as well as a general geographic description.

When we relocated a marked individual, we recorded the number of wolves seen, pelt colors, date, time, activity, and data on any prey killed or eaten. When conditions allowed, we counted the number of pups present in June–October based on body size, pelage appearance, and behavior. Counts varied in quality depending on sighting conditions (e.g., vegetation, turbulence, topography, snow conditions), and in most cases it was not possible to conclusively determine whether we detected the entire pack. However, under appropriate circumstances, observers could be confident that the count of pack members was complete. For example, packs may be found on open treeless slopes with good snow tracking conditions where observers could follow tracks and confirm that no other wolves associated with the pack had been missed. Under conditions when observers recorded that they were sure they had seen the entire pack, we assumed that detection probability was 1.0, providing a known count for that visit.

We assessed losses of wolves due to mortality or permanent dispersal from packs directly through the collared sample, and indirectly through decreases in counts of pack members. When we detected a mortality signal for a marked wolf, we used subsequent direct observations to confirm that a mortality had indeed occurred, and we collected carcasses for necropsy to determine the cause of death when possible. The most common causes of natural mortality were killed by other wolves, killed by prey (e.g., kicked by a moose, quilled by a porcupine), or starvation. A proportion of marked wolves were harvested through legal means in and around YUCH (wolf harvest is permitted on NPS preserve lands in Alaska), and we identified the harvest of marked wolves either through direct aerial observation (e.g., wolf observed in a trap or snare), harvest reporting, or the condition of the recovered collar (e.g., obviously cut off). We were unable to identify harvest of unmarked wolves, except on rare occasions. Therefore, we also summarized reported wolf harvest within the boundaries of YUCH based on ADF&G hide-sealing records to provide an overall estimate of harvest from the area. When we determined marked animals had permanently dispersed from a pack (initially based on  $\geq 1$  solitary locations outside the normal range of the pack, followed by lack of a VHF signal from that wolf's collar on multiple flights), we considered them to be lost from the study population for the purposes of analysis. Losses due to dispersal were more easily identified for wolves marked with GPS collars. Suspected dispersers were sometimes harvested long distances from the study area, confirming dispersal had occurred. We were unable to distinguish between mortalities and dispersals for unmarked individuals; therefore, we treated all losses equivalently when estimating apparent survival.

Extraterritorial forays (Van Ballenberghe 1983) occurred regularly throughout the study. We defined extraterritorial forays as temporary excursions from the pack's home range, usually including most or all of the pack members with locations  $\geq 20$  km from the majority of locations for a pack. Packs containing individuals marked with GPS collars were far more likely to be detected when on a foray. We identified the general home range for each pack in each year using minimum convex polygon (MCP) methods (Mohr 1947, Odum and Kuenzler 1955, White and Garrott 1990). The number of relocations used

in the MCP calculations varied widely, limiting our interpretations of home ranges and forays to qualitative descriptions only.

### Data Analysis

We modified the recently developed integrated modeling approach combining known-fate data from collared individuals with counts of unmarked pack mates (Schmidt et al. 2015) to allow the separate estimation of mortality and dispersal rates, in addition to apparent survival (losses due to mortality and dispersal combined) and natality (additions to packs over the May–Aug interval) for YUCH wolves. Our model was a combination of a known-fate sub-model (Royle and Dorazio 2008, Schmidt et al. 2010) and an open  $N$ -mixture sub-model (Dail and Madsen 2011) as described in Schmidt et al. (2015). To separately estimate survival and dispersal rates, we substituted a cause-specific known-fate survival model (Heisey and Fuller 1985) for the simple known-fate model used by Schmidt et al. (2015). Once an individual dispersed, we considered it to have been removed from the population; therefore, overall apparent survival probability is interpreted as the probability of surviving and not dispersing. Because we considered individuals to be lost from the population at the point in time at which they left their pack, dispersers that subsequently died did not influence estimates of mortality. We present separate estimates of mortality and dispersal rates (i.e., without covariates) to allow comparisons among methods and with previously published estimates. Because it was not possible to differentiate between dispersals and mortalities for unmarked wolves, we assumed covariates influenced both sources of loss equivalently and present covariate effects based on estimates of apparent survival throughout much of the rest of the manuscript.

Several advantages accrued to the application of the integrated approach in our study of wolf population dynamics. First, it allowed us to make direct inference to the entire population of resident, pack-dwelling wolves within the study area, avoiding bias caused by non-random selection of individuals for marking. Second, our sample sizes were dramatically increased by including counts of pack-mates because a majority of the individuals in the population were not part of the known-fate sample. Third, the integrated model allowed us to simultaneously estimate annual apparent survival and natality rates, while examining covariates thought to influence these parameters. Fourth, by incorporating a random effect at the pack level, we addressed heterogeneity in fates caused by correlation among individuals within packs, providing inference to a much larger theoretical population of wolves in interior Alaska. Finally, the ability to estimate the total number of wolves in the sample at any point during the biological year allowed direct estimation of the combined impact of annual variation in apparent survival and natality, regardless of differences in relocation intensity or sighting success. For comparison purposes, we also analyzed the data from the collared subsample using a basic known-fate approach. We fit our integrated model with and without the random-effects terms to explore the differences in population dynamics between our study population and a much larger theoretical population of wolves.

*General model structure.*—We structured our model in the context of the annual cycle of wolves (i.e., BY), starting in May in

year  $t$  and continuing through April of year  $t+1$ . To accommodate pack growth, we allowed packs to be open to additions only over the May–August interval. We used this 3-month period because pups were born during May, but observations were sparse during May–July. We expected that most of the additions during this period would reflect pups produced and recruited during the 3-month interval, although we could not be absolutely certain that all additions were pups. Therefore, we defined natality as additions to packs during the May–August interval as opposed to phrases such as pup production or pup recruitment.

We also estimated apparent survival over the May–August period accordingly. Losses of unmarked individuals from the monitored population included both dispersals and mortalities, although the specific cause of loss was usually unknown. Estimation of the relative contribution of dispersal versus mortality to apparent survival was therefore reliant on the marked sample. If dispersers joined packs within the study area during other months, bias could occur. However, this occurrence was rarely observed ( $n=6$ ), suggesting any bias would be negligible. Although it would be theoretically possible to modify the model to allow monthly additions to packs, we limited potential additions to the May–August interval based on the available data. Although direct observations and counts of pups existed for some packs during some months, we interpret estimates based only on our integrated model to avoid potential bias due to variation in the timing of pup observations or the level of resighting effort among years. Because packs are the main social unit for wolves and we targeted packs for marking, our inference was generally limited to the resident, pack-dwelling population of wolves in our study area. However, the incorporation of random-effects terms also allowed us to estimate apparent survival for a much larger theoretical population of wolves in general (see below).

Our model structure generally followed that of Schmidt et al. (2015). For collared individuals, the model for the observed state,  $Y_{i,t}$ , can be written as:

$$Y_{i,t} \sim \text{Bern}(Y_{i,t-1}\phi_{i,t-1}^A)$$

where the state for individual  $i$  at time  $t$  depends on the state at  $t-1$  and apparent survival probability,  $\phi_{i,t-1}^A$ . We modeled apparent survival as the product of the probabilities of surviving,  $\phi_{i,t-1}^S$ , and not dispersing,  $\phi_{i,t-1}^D$ ,

$$\text{logit}(\phi_{i,t-1}^S) = \mathbf{x}_{i,t-1}'\boldsymbol{\beta}$$

$$\text{logit}(\phi_{i,t-1}^D) = \mathbf{x}_{i,t-1}'\boldsymbol{\beta}$$

$$\phi_{i,t-1}^A = \phi_{i,t-1}^S \times \phi_{i,t-1}^D$$

where  $\mathbf{x}_{i,t}$  is a vector of covariates and  $\boldsymbol{\beta}$  represents the coefficients. Because cause-specific fates were unknown for the unmarked individuals, covariates were assumed to have the same effect on  $\phi_{i,t-1}^S$  and  $\phi_{i,t-1}^D$ . We used a multiplicative formulation because we treated dispersals as losses from the study population. For the counts of unmarked pack-mates, we modeled the surviving number of individuals,  $S_{j,t}$ ,

within each pack,  $j$ , as:

$$S_{j,t} \sim \text{Bin}(N_{j,t-1} - R_{j,t-1}, \phi_{j,t-1}^{A*})$$

where  $R_{j,t-1}$  indicates the number of individuals newly marked and then transferred to the known-fate sample. We modeled the apparent survival parameter,  $\phi_{j,t-1}^{A*}$ , in 2 parts as

$$\text{logit}(\phi_{j,t-1}^{S*}) = \mathbf{x}_{j,t-1}' \boldsymbol{\beta}^*$$

$$\text{logit}(\phi_{j,t-1}^{D*}) = \mathbf{x}_{j,t-1}' \boldsymbol{\beta}^*$$

$$\phi_{j,t-1}^{A*} = \phi_{j,t-1}^{S*} \times \phi_{j,t-1}^{D*}$$

where  $\mathbf{x}_{j,t}$  is a vector of covariates and  $\boldsymbol{\beta}^*$  represents the coefficients. Note that components of  $\boldsymbol{\beta}$  and  $\boldsymbol{\beta}^*$  were shared. The additions,  $B_{j,1}$ , to each pack,  $j$ , during the first interval (i.e., May–Aug) within a year can be written as:

$$B_{j,1} \sim \text{Pois}(\gamma_j)$$

where  $\gamma_j$  represents the number of individuals recruited into each pack during the May–August interval. To include covariate information,  $\mathbf{w}_j$ , natality can be parameterized as:

$$\log(\gamma_j) = \mathbf{w}_j \boldsymbol{\rho}$$

where  $\boldsymbol{\rho}$  represents the coefficients. The counts can be modeled as:

$$n_{j,t} \sim \text{Bin}(N_{j,t} - R_{j,t}, p_{j,t})$$

where the observed number of individuals,  $n_{j,t}$ , is a function of true abundance,  $N_{j,t}$ , minus any individuals transferred to the known-fate sample,  $R_{j,t}$ , and detection probability,  $p$ . For packs and months when counts were not certain, we modeled  $p$  as a random effect allowed to vary by month. Please see Schmidt et al. (2015) for additional details on model performance, implementation, and fitting.

*Sub-models.*—To better understand and quantify variation in survival and dispersal probabilities, we considered a suite of covariates (i.e.,  $\mathbf{x}_{j,t-1}'$ ) expected to influence these vital rates. We assumed that known breeders would tend to remain in a given pack at higher rates than other wolves. We assumed the remaining collared wolves had the same probabilities of survival and dispersal as unmarked wolves and we estimated these values jointly for these 2 groups. We also allowed survival and dispersal to vary by month, to account for general variation throughout the season, although we did not assume any trends or fixed patterns. To test for an additive effect of lethal control, we allowed apparent survival to be different between the BY 1992–2004 pre-lethal control period and the BY 2005–2013 lethal control period. Because lethal control was dependent on adequate snow cover for aerial tracking and landing to retrieve dead wolves, we restricted the potential lethal control effect to November–April. We also included a covariate indicating whether a pack was known to be on a foray during a given month, thereby accounting for the possibility of increased risks of mortality or dispersal when traveling outside a pack's typical home range. Forays occurred

primarily in fall and winter; therefore, we limited the effects to the September–April period. We also considered the effect of the previous winter's total snowfall as a proxy for increased prey vulnerability due to winter conditions, predicting that wolf apparent survival would be higher in years following deeper snow winters (Mech et al. 2001). We were unable to directly assess the effects of annual variation in ungulate abundance because of the sporadic collection of appropriate data. Through the inclusion of the aforementioned covariates, we expected to address major sources of variation in apparent survival within and among years. Estimates based on this fixed-effects version of the integrated model provided direct inference to the YUCH population of wolves.

We also fit a version of the integrated model including an overdispersion term in the form of a random effect at the level of the monthly observations of each pack. This accounted for correlated losses (e.g., all pack members died in the same interval), the random nature of the exposure to control efforts, and other potential differences in survival rates among packs and years. Accounting for heterogeneity in fates through the use of random effects provides unbiased inference to the larger population from which the sample is drawn (Cam et al. 2002, 2013; Link et al. 2002; Link and Barker 2009), which in most studies is the target population of interest. Our particular case was somewhat atypical in this context because a majority of the target population was included in our sample. Under this scenario, estimates based on the fixed-effects models provide direct inference to the target population (i.e., YUCH wolves). In contrast, estimates from models that explicitly account for heterogeneity provide inference to a larger theoretical population of wolves. Conceptually, these estimates can be thought of as representing the larger population of wolves in interior Alaska not directly exposed to lethal control, or similarly, a loose collection of wolf populations from protected areas throughout interior Alaska. Estimates would not apply within control areas such as the UYTPCA where the entire population is directly exposed to intensive control activities. The presentation of these estimates was useful because it provided context for our specific work in YUCH relative to the larger population of wolves in Alaska.

In addition to estimating survival, we were also interested in identifying factors related to variation in natality rates and therefore considered a suite of covariates (i.e.,  $\mathbf{w}_j$ ) expected to influence this vital rate. We began by assuming natality was influenced by covariates representing weather conditions, pack characteristics, and wolf control efforts. We expected total snowfall in the winter just before pupping would have a positive effect in the following spring because of increased prey vulnerability. We also considered 2 effects relative to pack stability: total pack size in the preceding April and whether or not a breeder was known to have been lost from the pack in the previous year. We expected that larger packs may produce more pups, representing either a response to a large food supply or >1 breeding female. Conversely, newly formed packs are often smaller, younger wolves may be less productive (Rausch 1967), or poor prey resources may exist in newly established home ranges. Loss of a breeder was expected to reduce pup production either directly (i.e., no pregnant female in the pack) or indirectly

through a disruption in pack dynamics resulting in poor pup survival or recruitment (Ausband et al. 2015, Borg et al. 2015). Both of these indicators were often related to lethal removal of wolves in later years of our study. Finally, to investigate the possibility of a density-dependent response to artificial reductions of wolf populations attributable to the control programs, we included a linear trend in natality during each control period, lagged by 1 year. We hypothesized that reductions in wolf density in the surrounding area would reduce competition for prey resources in our study area over time, resulting in increasing natality rates. We assumed a 1-year lag because the effects of reduced density would not be immediately realized because a majority of the reductions took place late in the biological year.

We limited our inference to the full model because model selection for integrated models is an active area of research and the time required to fit and compare multiple alternative models can be prohibitive (Hooten and Hobbs 2015, Letcher et al. 2015, Lindberg et al. 2015, Ver Hoef and Boveng 2015). Appropriate measures of goodness-of-fit for integrated models are also an active area of research (Besbeas and Morgan 2014); however, the basic integrated known-fate  $N$ -mixture model we used was evaluated through simulations by Schmidt et al. (2015) and was found to perform well. We fit our models in a Bayesian framework using OpenBUGS (Thomas et al. 2006) with program R 3.1.1 (R Core Team 2014) as an interface. We ran 2 Markov chain Monte Carlo chains for 10,000 iterations, discarding the first 5,000 as burn-in. We assessed convergence by a visual inspection of the chains and the use of the Gelman-Rubin diagnostic (Brooks and Gelman 1998) to ensure adequate mixing. All estimates are presented as means and 95% credible intervals.

In addition to the integrated analysis, we fit a basic (i.e., average rates across years, covariates not included) known-fate model (Heisey and Fuller 1985, Adams et al. 2008) to the data from our collared sample to produce estimates of survival, dispersal, and apparent survival rates. The intent of this analysis was to provide a contextual link between the type of known-fate approaches typically used in collar-based studies of wolf population dynamics and the integrated modeling approach we used. We compared the estimates generated using each approach and explained the resulting differences in inference and interpretation. We also used these comparisons to demonstrate the severity of the bias that can occur when collared samples are unrepresentative of the study population.

*Wolf population change.*—Reductions in wolf numbers by 78% along the border of YUCH during the non-lethal control period (Fig. 3) were clearly identified through sustained monitoring of sterilized pairs and removals of any immigrants into the control area (Gardner 2003). In contrast, although large numbers of wolves were removed from the UYTPCA through both conventional harvest and aerial shooting during the lethal control period, direct quantification of the effects on wolf densities was complicated because of a lack of consistent and rigorous monitoring efforts over the larger area. Between 2004 and 2013, large-scale wolf surveys were conducted outside of YUCH only during 2008 and 2009 (ADF&G 2015). However, these reconnaissance surveys apparently lacked a formal design and did not follow established wolf survey protocols (Becker et al.

1998, Gardner and Pamperin 2014), largely being conducted as part of aerial wolf control efforts during which the primary purpose was to remove wolves rather than estimate population size (Gross 2012). In addition, the numbers reported from these 2 surveys are presented without measures of uncertainty (ADF&G 2014b), making it difficult to assess their quality. In all other years during this period, wolf abundance was modeled using published vital rates, annual numbers removed, aerial observations, prey abundance, and anecdotal information (ADF&G 2015). Such model-based approaches are highly dependent on numerous untestable assumptions when empirical data are limited or absent. Although such approaches may be used to detect order-of-magnitude differences in wolf populations, their statistical error cannot be evaluated (Boitani 2003), limiting their utility.

Despite these issues, these annual abundance estimates represent the only source of information on the wolf population in the control area during the lethal control period. In an effort to provide some gross measure of the proportion of wolves removed, we used the published abundance, harvest, and removal information to calculate potential removal rates for YUCH and the portion of the UYTPCA outside of YUCH. To do so, we first separated the minimum number of wolves observed in YUCH study packs (plus 10% for lone wolves; Gross 2012) from the reported total wolf population size within the UYTPCA in each year (ADF&G 2015; 10% lone wolves already included). We also separated the number of wolves known to have been removed from YUCH by normal harvest or control efforts in each year from the total number removed annually from the UYTPCA (ADF&G 2015). We then divided the number of wolves removed from each subarea (inside YUCH vs. outside YUCH) by their respective population estimates to produce the potential proportion of the population from each area that was removed annually. These calculations can be represented by the following conceptual equations:

$$\begin{aligned} \text{Proportion removed}_{\text{Outside YUCH}} &= \frac{\text{Total removals} - \text{YUCH removals}}{\text{Total population} - 1.1 \times \text{YUCH minimum counts}} \\ \text{Proportion removed}_{\text{Inside YUCH}} &= \frac{\text{YUCH removals}}{1.1 \times \text{YUCH minimum counts}} \end{aligned}$$

We then assessed these proportions in the context of published levels of human-caused mortality expected to result in reductions in population size (Fuller et al. 2003, Adams et al. 2008, Creel et al. 2015) to ascertain their potential effects on wolf population densities. We assumed removal rates represented minimums because of the general absence of wolf population data in most years, additional unrecorded sources of mortality (e.g., wounding loss), carry-over effects between years, and the potential for decreased reproductive output and pack dissolution due to breeder loss (Brainerd et al. 2008, Creel and Rotella 2010, Sparkman et al. 2011, Borg et al. 2015). We then used these potential rates to provide context for our vital rate estimates and their effects on population dynamics in the YUCH population.

Assessing population growth rates ( $\lambda$ ) is often a management goal. Variation in wolf density estimates are commonly used to estimate  $\lambda$  in wolf populations and assess the effects of human-caused mortality (Ballard et al. 1997, Burch et al. 2005, Adams



et al. 2008). However, despite common usage, there is substantial evidence that estimates of  $\lambda$  based on densities reliant on relocations of collared individuals can be highly biased. Specifically, estimates are highly dependent on the number of relocations for each pack (Bekoff and Mech 1984, Burch et al. 2005), and the proportion of packs monitored within the area of interest. These dependencies lead to unquantifiable bias that cannot be resolved. In addition, home ranges of monitored packs in continuous populations overlap home ranges of surrounding unmonitored packs. Without estimates of total pack size and a measure of the degree of overlap with these adjacent packs, densities are further biased to an unknown degree because the edge of the total population area does not account for these packs. The effect of this source of bias on  $\lambda$  is expected to change with the number of monitored packs, their spatial distribution, and the shape of the study area.

The temporal extent of our dataset (22 yr), in addition to the shift from VHF to satellite-based radio-collars in the middle of our study, allowed us to evaluate the effect of variation in effort on density estimation. We assessed the validity, bias, and stability of density estimates (and the resulting estimates of  $\lambda$ ) based on standard home-range-estimation techniques. We also used these results to assess whether increasing the number of relocations per pack may alleviate dependencies between estimated density and sample size. We calculated annual densities by estimating the home range of each pack using MCP methods at the end of each biological year, calculating the area covered by all home ranges and then dividing the known number of wolves by the population area (Mech et al. 1998, Adams et al. 2008).

We used 2 different MCP approaches for comparison. For the first approach, we plotted the MCPs for each pack (after deleting all movements associated with dispersals and forays), and then subjectively removed any outlier locations. This approach left what we judged to be the best representation of the home range for each pack. For the second approach, in place of the subjective removals, we used the 95% MCP (i.e., removing the most extreme 5% of all locations) as a more objective representation of each home range. The population area was simply the aggregation of the individual home ranges each year. Because the study site was the same area each year, population growth rate between years,  $\lambda$ , could be estimated as

$$\lambda = \frac{\widehat{\text{density}}_t}{\widehat{\text{density}}_{t-1}}$$

We used multiple regression techniques (i.e., simple power, logarithmic, or exponential functions) to describe the general shape of the relationships between density metrics and sampling effort over time, selecting the curve with the highest  $R^2$  value as the best representation of each relationship. A trending or curvilinear relationship would indicate confounding between sample size and estimated density.

Based on our assessment of the home range-based density estimation approach, we developed an alternative metric,  $\lambda^*$ , a measure analogous to  $\lambda$ , to evaluate whether the population was self-sustaining each year. We calculated annual estimates of  $\lambda^*$  by dividing the estimated number of individuals existing in each study pack at the end of the biological year in April,  $\hat{N}_{\text{April}}$ , (a

derived estimate from the integrated model) by 2 times the number of packs monitored in that biological year,  $N_{\text{packs}}$ . We multiplied  $N_{\text{packs}}$  by a factor of 2 because a viable pack must consist of  $\geq 2$  individuals. The simple formula for the  $\lambda^*$  estimator can be written as:

$$\lambda^* = \frac{\hat{N}_{\text{April}}}{2 \times N_{\text{packs}}}$$

Estimates of  $\lambda^*$  summarize annual population changes due to additions (natality) and losses (mortality and dispersal) throughout the year, considering that the functional unit for wolves is the pack. The primary difference between estimates of  $\lambda$  and  $\lambda^*$  is that  $\lambda^*$  does not include gains due to immigration. Immigration is excluded by necessity because immigrants generally do not join established (i.e., monitored) packs, effectively making this rate unmeasurable without additional information. Although immigration is an important vital rate,  $\lambda^*$  may actually be a more informative measure of population sustainability because it integrates natality, mortality, dispersal, and pack integrity over the biological year, representing a value that approximates  $\lambda$  (minus immigration) for the sample population. Therefore, as estimates of  $\lambda^*$  approach 1.0, there is high risk of the population becoming a population sink (Pulliam 1988) reliant on immigrants from the surrounding area for maintenance. By definition, a pack cannot consist of  $< 2$  individuals; therefore, when  $\lambda^* < 1.0$ , it indicates that natality is insufficient to replace losses through death and emigration, including the loss of entire packs. When this occurs, the population becomes reliant on immigrants from surrounding areas to refill vacant territories and is no longer self-sustaining. Assuming the monitored packs are a reasonable representation of the overall population, this approach provides direct insight into the degree of local compensation present in relation to the potential for reliance on immigrants from other source populations (Creel et al. 2015).

## RESULTS

We marked and monitored 146 individual wolves and associated members of 42 packs (6–15 packs/yr) between spring 1993 and spring 2014 (Table 1, Figs. 4 and 5). Marked wolves remained in the sample for an average of 3.2 years for a total of 460 collared wolf-years in our sample. A majority of YUCH packs were likely sampled in most years (Fig. 4). All age classes were represented in our collared sample, although a large majority were estimated to be  $> 3$  years of age (Fig. 6). Older age classes tended to be more highly represented because of targeted collaring of known breeders and aging of collared individuals over time. Although most packs in our study population either denned in or had a substantial portion of their home range within YUCH, most packs also used areas outside the boundaries of YUCH (Fig. 4). Most study packs, particularly those with home ranges south of the Yukon River, were therefore potentially exposed to lethal wolf control activities after January 2005.

The percentage of human-caused mortalities in the collared sample increased from 19% to 29% after the implementation of lethal wolf control, whereas dispersals decreased from 34% to 22% (Fig. 7). The effect on observed dispersals may be underestimated because a majority of the collars deployed in

**Table 1.** Numbers of packs monitored and wolves marked with radio-collars for each of 22 biological years (May–Apr) in Yukon-Charley Rivers National Preserve, Alaska, USA. Initial number is the estimated number of wolves (model-based) in all monitored packs in August, and mean pack size = initial number/packs.

Biological year	Packs	Collared wolves	Initial number	Mean pack size
1992	7	12	37	5.3
1993	6	13	25	4.2
1994	7	13	44	6.2
1995	7	18	49	7.1
1996	9	23	69	7.7
1997	10	28	64	6.4
1998	9	25	42	4.7
1999	10	26	79	7.9
2000	15	30	108	7.2
2001	13	30	104	8.0
2002	7	17	88	12.6
2003	7	16	70	10.1
2004	7	16	57	8.1
2005	12	30	76	6.3
2006	10	23	54	5.4
2007	10	22	55	5.5
2008	7	23	55	7.8
2009	8	20	57	7.1
2010	10	23	74	7.4
2011	10	22	93	9.3
2012	9	19	89	10.0
2013	7	10	54	7.8

the second period were GPS collars, making it much easier to detect dispersing individuals. Caution is also warranted because the summaries of observed values do not account for variation in the proportion of young wolves in the collared sample. Despite increases in human-caused mortalities overall, the proportion of observed natural mortality in the collared sample remained consistent during both time periods (Fig. 7), whereas total conventional harvest within YUCH decreased during the lethal control period (Fig. 8). The effect of lethal control on uncollared pack-mates was likely much larger than was observed in the collared sample because multiple individuals were known to have been removed during some events (i.e., up to 24 wolves from 1 pack), and relatively few collared individuals were present in each pack.

### Survival, Dispersal, and Natality

Based on the basic integrated model (no covariates, no random effects), average annual apparent survival (the probability of surviving and not dispersing) for known breeders in the YUCH wolf population was approximately 50% higher (0.77 [0.72, 0.81]) than that of other wolves (0.35 [0.30, 0.40]). The mean annual survival rate estimate (dispersal excluded) was 0.81 (0.77, 0.85) for known breeders and 0.60 (0.54, 0.68) for other wolves. The mean estimated annual dispersal rate was much lower for known breeders (0.03 [0.02, 0.07]) than for other wolves (0.41 [0.34, 0.48]), in agreement with our general observations. The probability of detecting unmarked wolves during a count was highest in November and March, and lowest in December and August (Fig. 9A), corresponding with increased flight efforts during late fall and late winter when sighting conditions were better because of complete snow cover and adequate daylight. Monthly survival probabilities were high and consistent, showing no evidence of elevated mortality rates at any point throughout

the year (Fig. 9B). In contrast, dispersals were more likely to occur from early spring through the summer months but were less common during mid-winter (Fig. 9C). This result corresponded with our general observations of increased numbers of dispersals during the spring through summer period. We observed extraterritorial forays in most years and recorded many packs traveling outside of their typical home ranges over hundreds of kilometers throughout the surrounding area (Fig. 10). All packs returned to their territories for the following denning season unless they were killed.

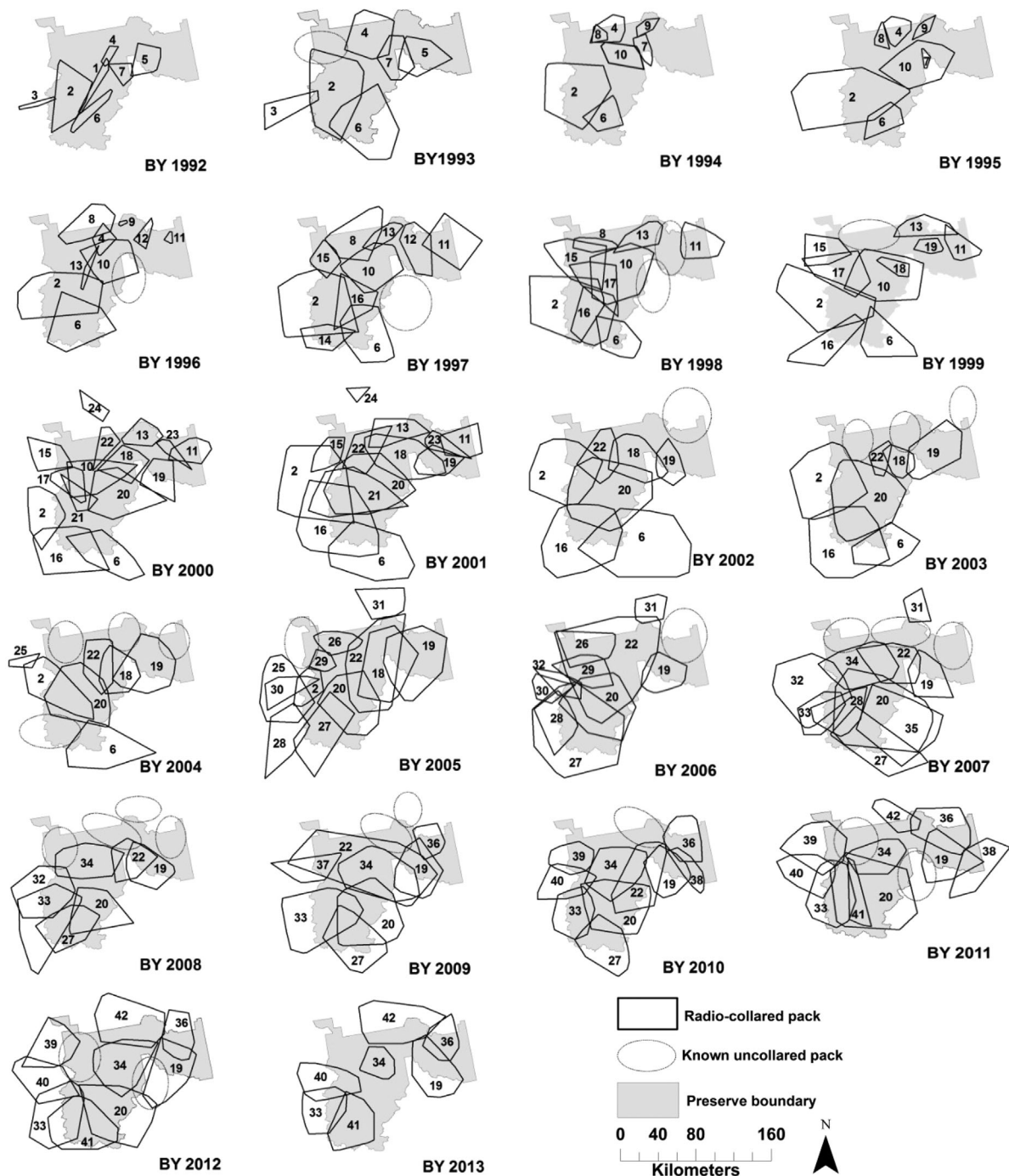
Several covariates explained important sources of variation in wolf vital rates. Monthly apparent survival probability was negatively associated with extraterritorial forays, indicating an increased risk of mortality or dispersal when packs traveled outside of their typical home range (Table 2, Fig. 11). Total snowfall in the previous winter (Fig. 12) was positively related to apparent survival probability as we predicted (Table 2, Fig. 11), indicating that fewer wolves were lost from the average pack in the year following winters with higher-than-average snow depths. Conversely, in years following winters with low snowfall, more wolves were lost from the average pack. Finally, apparent survival probability for wolves of unknown breeding status was reduced by approximately 15% on average during the lethal control period, indicating a direct additive effect of lethal control efforts on YUCH study packs (Table 2, Fig. 11).

Winter conditions and pack structure also influenced wolf natality. Total snowfall in the winter immediately preceding the denning season was negatively related to the number of individuals added to each pack (Table 2, Fig. 13). Natality was also positively related to the number of individuals in a pack at the end of the previous biological year (Table 2, Fig. 13). Conversely, the loss of a known breeder during the previous biological year was negatively related to productivity (Table 2, Fig. 13). Together, these factors suggest that smaller packs and those lacking experienced breeders produced fewer offspring (Table 2, Fig. 13), as we predicted.

The relative contribution of mortality and dispersal to overall apparent survival differed between known breeders and other wolves, with known breeders being much less likely to be lost from packs overall (Fig. 14A, B). In particular, known breeders were generally lost from packs because of mortality; dispersals were rare. Comparisons of estimates with inference to the collared sample (known-fate only), the YUCH population (integrated model), and the larger theoretical population (integrated model with heterogeneity) showed similar patterns in the relative importance of dispersal versus mortality to overall apparent survival (Fig. 14). However, loss rates for the theoretical population were estimated to be substantially lower.

Dispersal represented one of the major known causes of loss from the collared sample throughout our study despite the sample being biased towards breeding wolves that were much less likely to disperse (Table 3). In the entire collared sample, dispersals were the most common cause of loss for both yearlings and 2-year-old wolves, and were less frequently observed in older wolves (Table 3). Estimated dispersal rates indicated that known breeders had much lower dispersal rates than other wolves (Fig. 14), and this result was supported by the observed data (Table 3). However, although known-fate estimates suggested



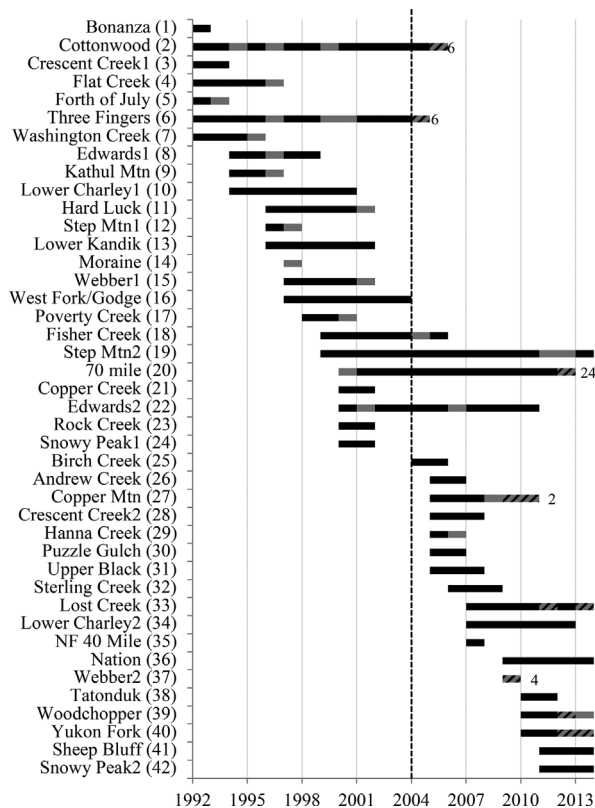


**Figure 4.** Polygons representing home ranges of studied wolf packs in and around Yukon-Charley Rivers National Preserve, Alaska, USA in each year of the study between biological years (BY) 1992–2013. Home ranges for monitored packs are based on minimum convex polygons using all locations from a given biological year. Approximate home ranges for packs that were observed but did not contain collared individuals are represented as dotted ovals for reference. Number of relocations for home range delineation varied widely among years and packs; therefore, relative home range sizes are not directly comparable. Numbers within each polygon correspond to the individual pack names in Figure 5.

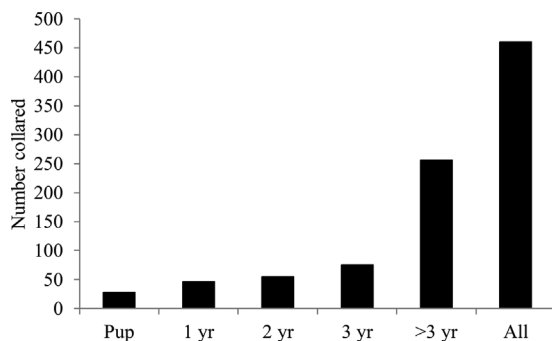
that yearlings dispersed at somewhat higher rates than other age classes, estimates were imprecise and 95% credible intervals overlapped extensively (Fig. 14C). The imprecision of these estimates was related to the relatively small number of collared dispersers in each age class.

We observed known dispersals in all years except BY 2001, 2012, and 2013, with the largest number of collared dispersers

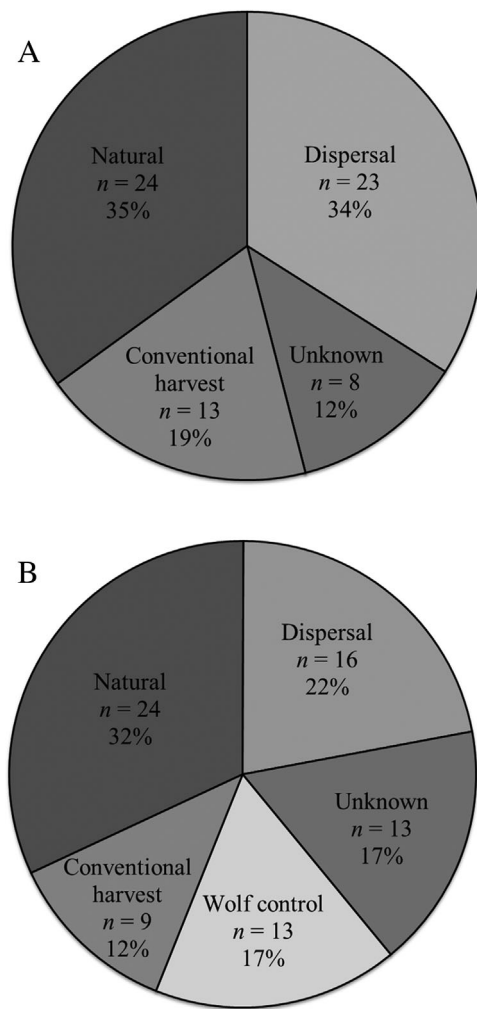
observed in 1997 and 2005 ( $n = 6/\text{yr}$ ). Known dispersers traveled up to 705 km (straight-line distance) from YUCH and contributed to harvest or other populations throughout much of the state and into Yukon Territory, Canada (Fig. 15). A majority of known dispersals resulted in death due to human harvest (Fig. 15), although the fate of harvested dispersers were more likely to be known because of reporting. In later years,



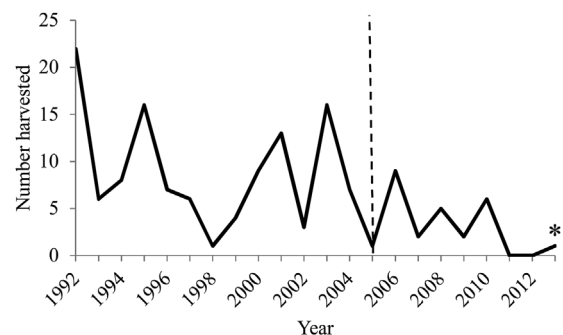
**Figure 5.** Horizontal bars represent the biological years (1 May–30 Apr) during which we monitored each pack with at least 1 radio-marked individual in Yukon-Charley Rivers National Preserve, Alaska, USA between biological years 1992–2013. Gray sections indicate years when wolves within a pack were known to have been harvested through conventional hunting and trapping. Hashed gray sections indicate when wolves from a pack were known to have been removed as part of the Alaska Department of Fish and Game predator control program, and the associated values at the end of the bars indicate the minimum number of individuals known to have been removed (total if from multiple years). The vertical dotted line indicates the start of the lethal predator control program (i.e., the winter of biological year 2004). Numbers in parentheses correspond to numbered home ranges in Figure 4.



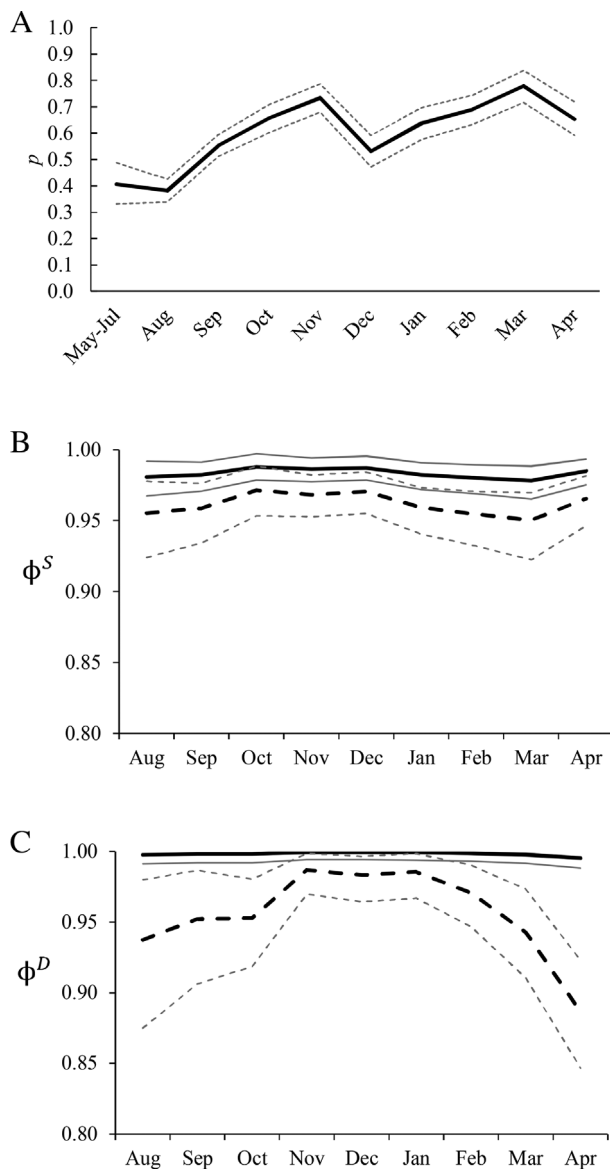
**Figure 6.** Number of monitored wolf-years by estimated age class in Yukon-Charley Rivers National Preserve, Alaska, USA between biological years 1992–2013. We monitored many of the 146 collared individuals for multiple years ( $\Sigma = 460$  wolf-years).



**Figure 7.** Number ( $n$ ) and percent of collared wolves lost to each of 4 fates in Yukon-Charley Rivers National Preserve, Alaska, USA during 1993–2004 before lethal control (A), and during 2005–2014 with lethal control (B). Natural indicates non-human caused mortalities, dispersal includes only known dispersals, unknown represents loss of contact with no known fate, conventional harvest includes hunting or trapping mortalities, and wolf control indicates the number of known mortalities due to control activities. The unknown category includes suspected dispersals that were not confirmed.



**Figure 8.** Reported conventional wolf harvest (i.e., hunting and trapping) from within the boundary of Yukon-Charley Rivers National Preserve, Alaska, USA during biological years 1992–2013. Vertical line indicates the onset of the lethal wolf control program. Numbers are based on annual sealing records provided by Alaska Department of Fish and Game staff. The asterisk for biological year 2013 indicates preliminary data.



**Figure 9.** Estimates of the average monthly probability of detecting an unmarked wolf ( $p$ ; panel A), survival ( $\phi^S$ ; panel B), and not dispersing ( $\phi^D$ ; panel C) for wolves in Yukon-Charley Rivers National Preserve, Alaska, USA between biological years 1992–2013. In panels B and C, estimates for known breeders are shown as a solid line and those for other wolves are shown as a dashed line. Estimates for survival and dispersal assume an average snow year and that wolves did not leave on a foray. Light lines represent 95% credible intervals.

dispersals of collared wolves and ultimate fates of those dispersers were more likely to be known because of the use of GPS collars. Individuals instrumented with VHF collars generally could not be tracked after they left the immediate study area.

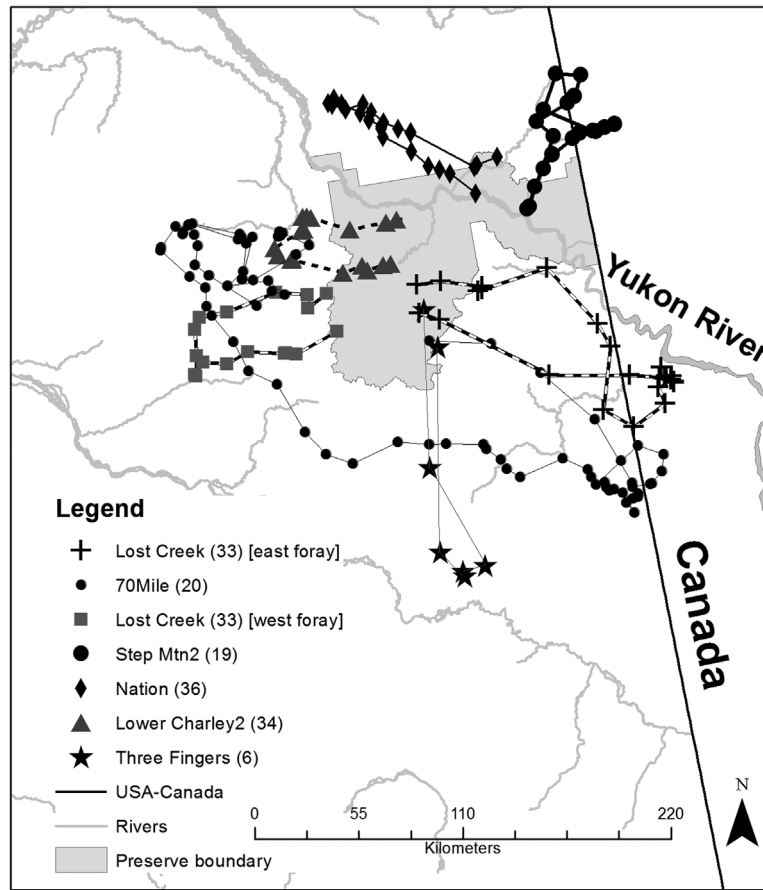
Known-fate estimates based on the collared subsample alone were highly biased when compared to estimates based on the integrated analysis (Fig. 16). A comparison of estimates of apparent survival for all marked wolves together versus separate estimates for marked known breeders and other marked wolves revealed the strong effect that targeted collaring of breeders can have on estimated vital rates (Fig. 16). The composite known-fate estimate (i.e., all wolves) was strongly influenced by the higher apparent survival probability for known breeders, meaning

the composite estimate was unlikely to be representative of the YUCH population. Known-fate analysis suggested that apparent survival of known breeders was 3 times higher than that of other wolves (Fig. 16). However, an analogous integrated model that included information on all unmarked wolves suggested the difference in apparent survival between groups was much smaller (Fig. 16). These findings provided strong empirical evidence that the collared sample was unrepresentative of the non-breeding segment of the population, as was expected because of the targeted collaring of breeders. When we added random effects to the integrated model, estimated apparent survival probability for both groups increased (Fig. 16), indicating that after accounting for heterogeneity in the sample, estimated apparent survival for a similar theoretically large population would be approximately 15% and 70% higher for known breeders and other wolves, respectively (Fig. 16). This result suggests that apparent survival for the YUCH population may be lower than would be expected compared to the theoretical population of wolves in interior Alaska.

Annual realized covariate values led to substantial variation in vital rates over the course of our study (Fig. 17). Despite this variation, apparent survival probabilities were approximately 25% lower during the lethal control period (0.34) as compared to earlier years (0.45) on average (Fig. 17A). This result indicated that the additive effects of lethal control contributed to a general reduction in survival in the YUCH population during the lethal control period during the average year. The relationship between control and natality was substantial, resulting in a near doubling of natality during the course of each wolf control program (Fig. 17B). Correspondingly, natality rates quickly returned to prior levels during the period between control programs (Fig. 17B), further suggesting such changes were related to control impacts, presumably through changes in overall wolf density. Together these results showed relatively large and opposing responses of apparent survival and natality rates to wolf control.

### Human-Caused Mortality and Population Trajectory

Our summarization of wolf population estimates, total reported harvest, and reported lethal removals presented by the ADF&G (2014b, 2015) suggested that human-caused mortality in the portion of the UYTPCA not including YUCH was  $\geq 28\%$  annually (Table 4, Fig. 18). This rate of human-caused mortality usually exceeded the 29% sustainability threshold proposed by Adams et al. (2008) and was always above the 22% and 25% thresholds suggested by Fuller et al. (2003) and Creel et al. (2015), respectively. The proportion of the population within YUCH that was removed each year was typically below these thresholds, except in the last 2 years of the study when several YUCH packs were largely or entirely removed as part of the lethal control program (Fig. 18). Proportions of mortalities due to natural and human causes were similar for known breeders (Table 3), although deaths of collared individuals due to lethal control efforts were mostly confined to known breeders (Table 3; 13 of 15 removals) and were often correlated (11 killed in 5 control events). However,  $\geq 75$  individuals from monitored YUCH study packs were killed during lethal control activities, suggesting a much larger proportion of removed individuals were



**Figure 10.** Examples of long-distance extraterritorial forays observed for monitored packs from Yukon-Charley Rivers National Preserve, Alaska, USA between biological years 1992 and 2013 showing extensive movements of individual packs well outside of their normal home ranges. Only a subset of observed extraterritorial forays are shown for clarity and to demonstrate that movements well outside of the study area occur in all directions. Numbers associated with pack names correspond to pack numbers in Figures 4 and 5 for reference.

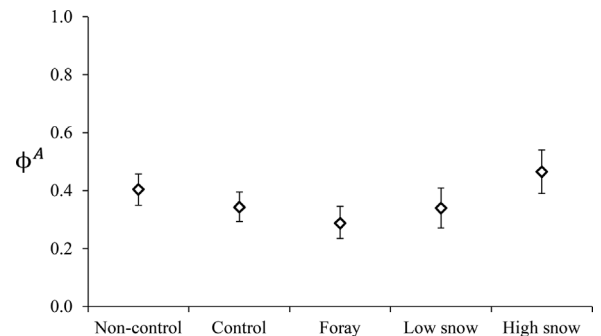
non-breeders than was evident in the collared sample. Anecdotal evidence also suggests that in some cases additional pack members were wounded during control efforts, suggesting additional control-related losses may have occurred.

**Table 2.** Parameter estimates and 95% credible intervals (CrI) from the integrated model for wolf apparent survival and natality with inference to the wolf population in Yukon-Charley Rivers National Preserve, Alaska, USA between biological years 1992 and 2013.

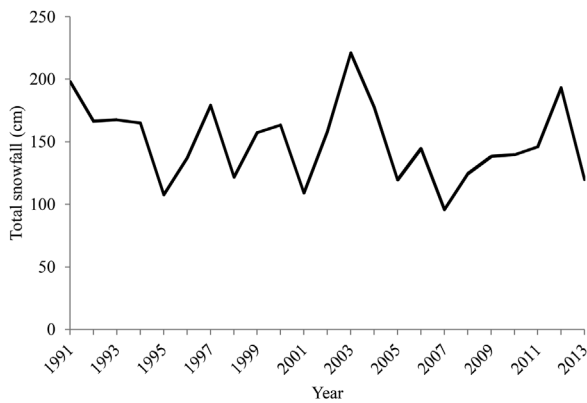
Parameter <sup>a</sup>	Mean	95% CrI
Survival		
$\beta_{\text{foray}}$	-0.80	-1.06, -0.54
$\beta_{\text{snow depth}}$	0.10	0.03, 0.19
$\beta_{\text{control}}$	-0.32	-0.52, -0.12
Natality		
$\beta_{\text{trend}}$	0.06	0.03, 0.10
$\beta_{\text{snow depth}}$	-0.12	-0.21, -0.02
$\beta_{\text{pack size}}$	0.08	0.05, 0.11
$\beta_{\text{breeder loss}}$	-0.48	-0.74, -0.24

<sup>a</sup> Parameters include the effect of going on an extraterritorial foray (foray), total snowfall the previous year (snow depth), the effect of lethal control (control), an annual trend in natality during the control periods (trend), pack size the previous year (pack size), and whether a breeder was lost the previous year (breeder loss).

Wolf density estimates based on either the subjective MCP or 95% MCP calculation method varied several-fold between years (Fig. 19A). Density and annual fluctuations in density appeared to decline over the course of the study. These declines

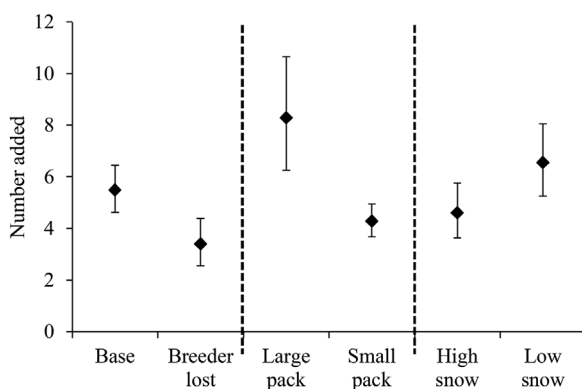


**Figure 11.** Estimated annual apparent survival probabilities ( $\phi^A$ ) for other pack-dwelling wolves (i.e., not known breeders) in Yukon-Charley Rivers National Preserve, Alaska, USA between biological years 1992 and 2013. Assumptions are average conditions without lethal control (non-control), average conditions with lethal control, a pack went on a 4-month foray from December to March in a non-control year (foray), lower than average snow in the previous year ( $-2$  SD), or a high snow year ( $+2$  SD). All estimates are based on the integrated model without heterogeneity. Error bars represent 95% credible intervals.

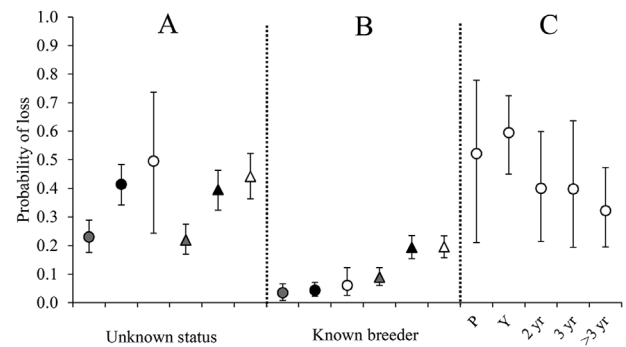


**Figure 12.** Total annual snowfall recorded in Eagle, Alaska, USA (adjacent to Yukon-Charley Rivers National Preserve) during wolf biological years 1991–2013.

corresponded with the dramatic increase in the mean number of locations acquired for each pack starting around 2003, when many more satellite and GPS collars were deployed (Fig. 19B). Density and annual variation in density were both negatively related to the mean number of locations per pack (Fig. 19C, D). Even at  $>1$  location per pack per day, the estimated curves did not reach an asymptote, indicating density estimates were influenced even at the highest sample sizes. The lack of stabilization is directly related to the continued increase in population area as the mean number of locations per pack increased (Fig. 19E). A steady increase in population area over time (Fig. 19F) indicated that trends and variation in density were largely confounded with effort. In short, all diagnostics indicated that density estimates and variation in density estimates



**Figure 13.** Estimated number of individual wolves added to each pack under a variety of hypothetical conditions for wolf packs in Yukon-Charley Rivers National Preserve, Alaska, USA between biological years 1992 and 2013. The conditions presented are average covariate values and a pack size of 5 (base), loss of a breeder during the previous year at a pack size of 5 (breeder lost), a pair of wolves (small pack) versus a pack containing 10 individuals (large pack), and greater-than-average snow in the previous year ( $+1.5$  SD; high snow) versus lesser-than-average snow in the previous year ( $-1.5$  SD; low snow) for a pack size of 5. Vertical dashed lines are included to visually separate scenarios. Estimates are based on the integrated model, and error bars represent 95% credible intervals.



**Figure 14.** Estimates of cause-specific annual probability of loss for wolves in Yukon-Charley Rivers National Preserve (YUCH), Alaska, USA for biological years 1992–2013. Average annual dispersal (circles) and mortality (triangles) probabilities based on the integrated model with random effects with inference to the larger theoretical population (gray), the integrated model without random effects with inference to the YUCH population (black), and a basic cause-specific known-fate model with inference to the collared sample only (open) are shown for wolves of unknown breeding status (A) and known-breeders (B). Panel C shows age-specific (pups [P], yearlings [Y], 2-year-olds [2 yr], 3-year-olds [3 yr],  $>3$ -year-olds [ $>3$  yr]) dispersal probabilities for collared wolves of unknown breeding status. All estimates based on the integrated model include collar and count data, whereas estimates from the known-fate model apply only to the collared sample. Error bars represent 95% credible intervals.

between years were confounded with sample size, even in years with the largest samples.

The dependency between density and effort also was reflected in estimates of  $\lambda$  between years (Fig. 19G). Annual variation in estimated densities suggested  $\lambda$  varied from 0.42 to 2.77 in the years before lethal control, whereas during the lethal control period  $\lambda$  varied from 0.77 to 1.23 (Fig. 19G). Reduced magnitude and apparent variation in  $\lambda$  paralleled changes in sampling effort (Fig. 19), indicating that a sampling effect rather than interpretable biological differences was likely responsible. Although numbers of relocations per pack increased in later years and density estimates became less volatile, density estimates were still clearly influenced by sample size, limiting their interpretability. The large differences in density estimates based on the subjective MCP versus 95% MCP methods (Fig. 19A) also indicates density estimates under either method were highly dependent on individual locations. The apparently greater stability of the subjective MCP approach was caused by a disproportionate increase in population area with the inclusion of relatively few peripheral locations. Simply removing 5% of the most extreme locations dramatically changed density estimates, more than doubling them in many cases. Combined, these results suggest that comparisons of densities based on relocations of radio-marked individuals were unlikely to be meaningful except on a very coarse scale (e.g., order of magnitude).

In contrast, estimates of  $\lambda^*$  were biologically interpretable and directly reflected variation in apparent survival and natality rates. Prior to lethal control (BY 1992–2004), estimates of  $\lambda^*$  were  $>1.0$  in 10 out of 13 years, indicating that the YUCH population was self-sustaining and acted as a population source to the surrounding area during that period (Fig. 20). In contrast, during the lethal control period (BY 2005–2013) estimates of  $\lambda^*$  were  $>1.0$  in only 3 out of 9 years, indicating YUCH acted largely as a sink supported by immigrants from the surrounding area during

**Table 3.** Number (*n*) and proportion (prop) of collared wolves for each fate type by age class and breeding status in Yukon-Charley Rivers National Preserve, USA between biological years 1992 and 2013.

Age	Dispersal		Natural		Harvest		Wolf control		Unknown		Survived		Total <i>n</i>
	<i>n</i>	prop	<i>n</i>	prop	<i>n</i>	prop	<i>n</i>	prop	<i>n</i>	prop	<i>n</i>	prop	
Pup	2	0.07	2	0.07	1	0.04	0	0.00	0	0.00	23	0.82	28
1 (non-breeder)	16	0.47	4	0.12	1	0.03	0	0.00	2	0.06	11	0.32	34
1 (breeder)	0	0.00	0	0.00	0	0.00	1	0.08	0	0.00	11	0.92	12
2 (non-breeder)	8	0.33	1	0.04	1	0.04	0	0.00	0	0.00	14	0.58	24
2 (breeder)	1	0.03	1	0.03	1	0.03	1	0.03	1	0.03	26	0.84	31
3 (non-breeder)	4	0.19	3	0.14	4	0.19	0	0.00	0	0.00	10	0.48	21
3 (breeder)	2	0.04	0	0.00	0	0.00	1	0.02	1	0.02	50	0.93	54
>3 (non-breeder)	7	0.21	9	0.27	4	0.12	2	0.06	4	0.12	7	0.21	33
>3 (breeder)	3	0.01	22	0.10	17	0.08	10	0.04	2	0.01	169	0.76	223
Total (non-breeder)	37	0.27	19	0.14	11	0.08	2	0.01	6	0.04	65	0.46	140
Total (breeder)	6	0.02	23	0.07	18	0.06	13	0.04	4	0.01	258	0.80	320
Grand total	43	0.09	42	0.09	29	0.06	15	0.03	10	0.02	321	0.70	460

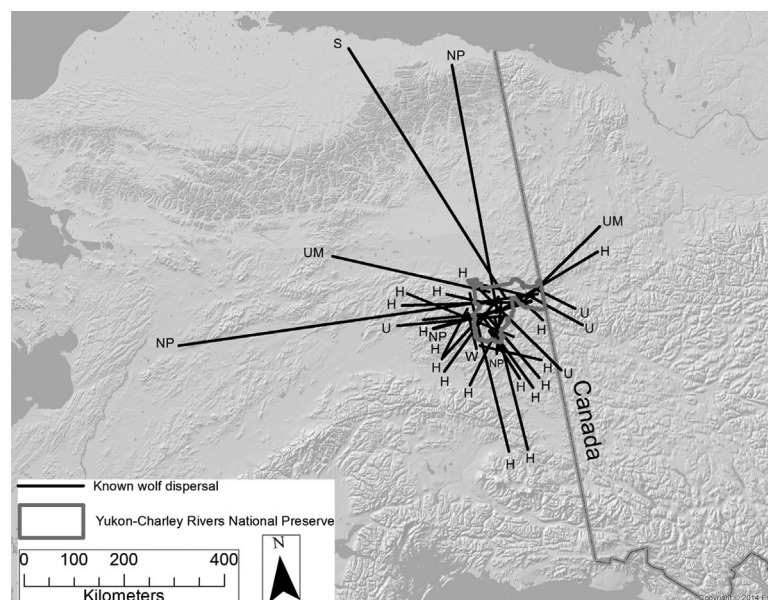
lethal control (Fig. 20). These findings correspond with our results showing that apparent survival was reduced during the lethal control period. Increasing natality rates during the lethal control period partially compensated for increased losses, but additions were insufficient in a majority of years.

## DISCUSSION

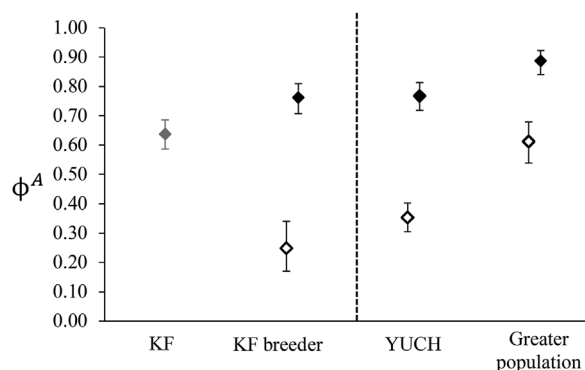
Our study was uniquely positioned to assess the broader impacts of a wolf control program on an adjacent protected population relative to several large projects that have investigated the direct effects of wolf control (Gasaway et al. 1983; Ballard et al. 1987; Boertje et al. 1996, 2017; Hayes et al. 2003). Although wolf control activities were prohibited within the boundaries of YUCH, the YUCH population was affected both directly and indirectly. The impact of the lethal control program shifted the status of YUCH from a population source providing dispersers to

the surrounding area to a periodic population sink sustained primarily by immigrants from other areas. Although YUCH is part of a largely continuous population of wolves that were therefore not at real risk of extirpation, control substantially altered the dynamics and vital rates of wolves within YUCH. Based on these findings, we suggest that simple prohibitions on harvest and control within a management boundary can be an insufficient management tool if conservation of a normally functioning wolf population is a primary goal.

There is a long history in the capture-recapture literature of using apparent survival rates (Lebreton et al. 1992), including studies of wolf population dynamics (Marucco et al. 2009), when particular vital rates such as emigration are not directly estimable. By modifying the integrated model of Schmidt et al. (2015), we could separately estimate mortality and dispersal rates for comparison with other studies, although we primarily restricted



**Figure 15.** Known dispersals of radio-collared wolves from packs in and around Yukon-Charley Rivers National Preserve, Alaska, USA during biological years 1992–2013. Some short distance dispersals are not depicted for clarity. Letters indicate observed fates of dispersers: H = human harvest, U = unknown (lost contact), UM = unknown mortality, NP = joined or formed a new pack, W = killed by wolves, S = starvation. Ultimate fates were biased toward human harvest because collars were much more likely to be recovered and reported when dispersers were harvested.

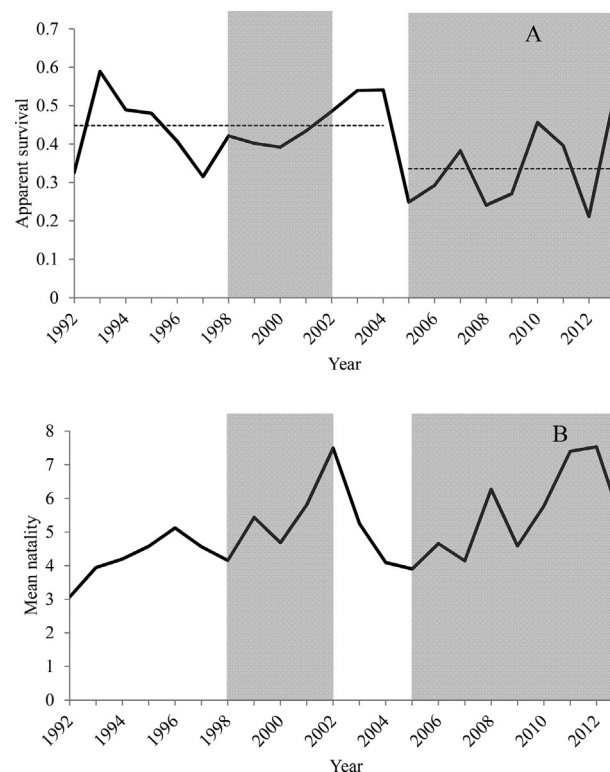


**Figure 16.** Apparent survival probability ( $\phi^A$ ) based on data collected on wolves in Yukon-Charley Rivers National Preserve (YUCH), Alaska, USA between biological years 1992–2013. Estimates are based on 4 models: apparent survival of all marked wolves (gray point; KF), apparent survival of marked known breeders and other marked wolves (KF breeder), apparent survival of marked known breeders and other wolves (both marked and unmarked) with no covariates or random effects accounting for heterogeneity with inference to the YUCH population (YUCH), and apparent survival of marked known breeders and all other wolves (both marked and unmarked) based on the integrated model accounting for heterogeneity with inference to a larger theoretical population (greater population). Solid black symbols indicate apparent survival probabilities for known breeders and open symbols indicate apparent survival probabilities for other wolves. The vertical dotted line indicates the division between estimates based on known-fate methods (left) and those based on the integrated model (right).

our analyses to apparent survival. We did so because the cause of loss (i.e., dispersal vs. mortality) from the large unmarked segment of the population could not be identified. The advantage, however, was that we leveraged the information contained in the marked and unmarked segments of the population to identify covariate relationships with inference to the entire population.

Known-fate approaches, as applied to wolf datasets, typically violate the assumption that marked individuals are a random selection from the population of interest (Pollock et al. 1989<sub>a,b</sub>; Williams et al. 2002), leading to bias. Less targeted sampling schemes and sophisticated analytical tools can help to address some of these issues (Smith et al. 2010, Cubaynes et al. 2014), although the integrated approach is more broadly applicable. Despite potential differences in sampling and inference between our study and past work, some broad comparisons with other populations are useful. Although apparent survival in the YUCH population was lower than losses to mortality and dispersal in the central Brooks Range of Alaska where harvest was considered to be compensatory (Adams et al. 2008), rates were similar to those observed in northwestern Alaska (Ballard et al. 1997) where the population was limited by human harvest. There is also some suggestive evidence that apparent survival in YUCH may be somewhat lower than would be expected for the larger theoretical population of wolves in interior Alaska.

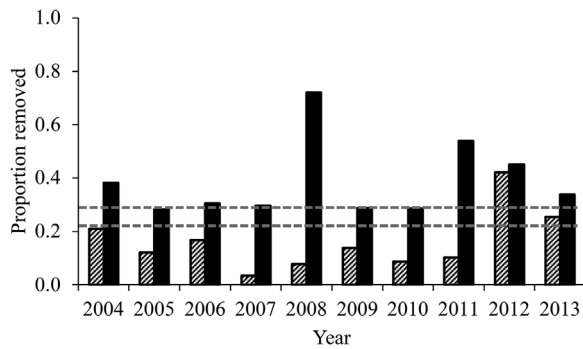
There is an extensive body of literature demonstrating the importance of addressing individual heterogeneity when estimating demographic parameters (Cam et al. 2002, 2013; Royle 2008; Marzolin et al. 2011; Lindberg et al. 2013; Guillemain et al. 2014); however, the topic has received relatively little attention in the wolf literature. Most analyses used in wolf studies



**Figure 17.** Annual realized apparent survival rates of wolves (a proportional combination of known breeders and wolves of unknown status) in and around Yukon-Charley Rivers National Preserve, Alaska, USA (YUCH) during biological years 1992–2013 through each April (A), and the average number of individuals added to each pack (mean natality) over the May–August interval of each biological year (B). All values are derived from the fixed-effects integrated model. Horizontal dotted lines in panel A indicate the mean apparent survival rates over the pre-lethal control period and during the control period. The gray sections indicate biological years (1-year lag) when active wolf control programs were in effect. During the first non-lethal control period, YUCH study packs were excluded from the sterilization treatments. During the second lethal control period, YUCH study packs were exposed to control efforts only when outside the preserve boundary.

**Table 4.** Annual number of wolves known to have been removed from the Upper Yukon-Tanana Predator Control Area in Interior Alaska, USA during biological years 2004–2013. Numbers include conventional harvest and control-related removals. Estimated total number of wolves in the lethal control area ( $\hat{N}_{\text{total}}$ ) and total reported removals are summarized in the 2015 report to the Alaska Board of Game (ADF&G 2015). The estimated number of wolves within the lethal control area that belonged to monitored packs ( $\hat{N}_{\text{YUCH}}$ ) represent minimum counts of wolves in monitored packs within Yukon-Charley Rivers National Preserve (YUCH; this study) adjusted to include 10% lone wolves. The YUCH removals represent the number from the total that were reported to have been harvested from within YUCH or wolves from monitored packs that were reported to have been shot during aerial control efforts.

Biological year	$\hat{N}_{\text{total}}$	Total removals	$\hat{N}_{\text{YUCH}}$	YUCH removals
2004–2005	380	135	57	12
2005–2006	335	85	58	7
2006–2007	362	103	54	9
2007–2008	382	98	58	2
2008–2009	372	226	65	5
2009–2010	235	60	51	7
2010–2011	274	62	81	7
2011–2012	329	145	78	8
2012–2013	386	171	88	37
2013–2014	356	116	55	14



**Figure 18.** Proportion of the fall population of wolves known to have been removed by humans each year from monitored wolf packs associated with Yukon-Charley Rivers National Preserve, Alaska, USA (hashed bars) and all other wolves within the Upper Yukon Tanana Predator Control Area (UYTPCA; black bars) during the lethal control period (biological years 2004–2013). The gray dotted lines represent the 0.22 and 0.29 human-caused mortality thresholds identified by Fuller et al. (2003) and Adams et al. (2008), respectively. Total reported human-caused mortality and population size for the entire UYTPCA were originally presented in the 2015 annual report to the Board of Game by the Alaska Department of Fish and Game (ADF&G 2015).

treat the fates of individuals as independent and implicitly assume there is no unmodeled individual heterogeneity (Heisey and Fuller 1985; Pollock et al. 1989<sub>a,b</sub>; Murray 2006; Smith et al. 2010). Such an approach may be appropriate in situations similar to ours where a majority of the individuals in the target population are included in the sample. However, if inference to some larger overall population is desired, failure to address heterogeneity generally results in negatively biased estimates (Link et al. 2002, Link and Barker 2009). Our estimates based on the heterogeneity model suggested that apparent survival rates would be higher for the greater theoretical population of wolves in interior Alaska (lethal control areas excluded). These values also could be considered to represent the average rates for wolves occurring in a collection of protected areas throughout interior Alaska (e.g., national parks). Specifically, our results suggest that apparent survival for YUCH wolves is generally lower than would be expected relative to the overall theoretical population. Additional work in other protected areas in Alaska could be used to confirm this interpretation and provide broader context for our findings.

In wolf populations, the breeding pair defines the pack and represents the most reproductively valuable population component. In general, breeders have low natural mortality and dispersal rates, consistent with the common assumption that breeders are lost from the population at lower rates than other wolves (Fuller et al. 2003, Smith et al. 2010). The loss of breeders can result in pack dissolution or decreased productivity (Brainerd et al. 2008, Sparkman et al. 2011, Borg et al. 2015), and the relationship between breeder loss and decreased natality highlights the importance of breeders to population trajectory. In YUCH, natality rates were indeed reduced following the loss of known breeders, and losses of breeders from multiple packs were associated with rather large reductions in natality. Similarly, smaller packs were also associated with reduced natality rates, leading us to speculate that pack size may influence the amount of indirect care (i.e., defense and provisioning) provided by pack

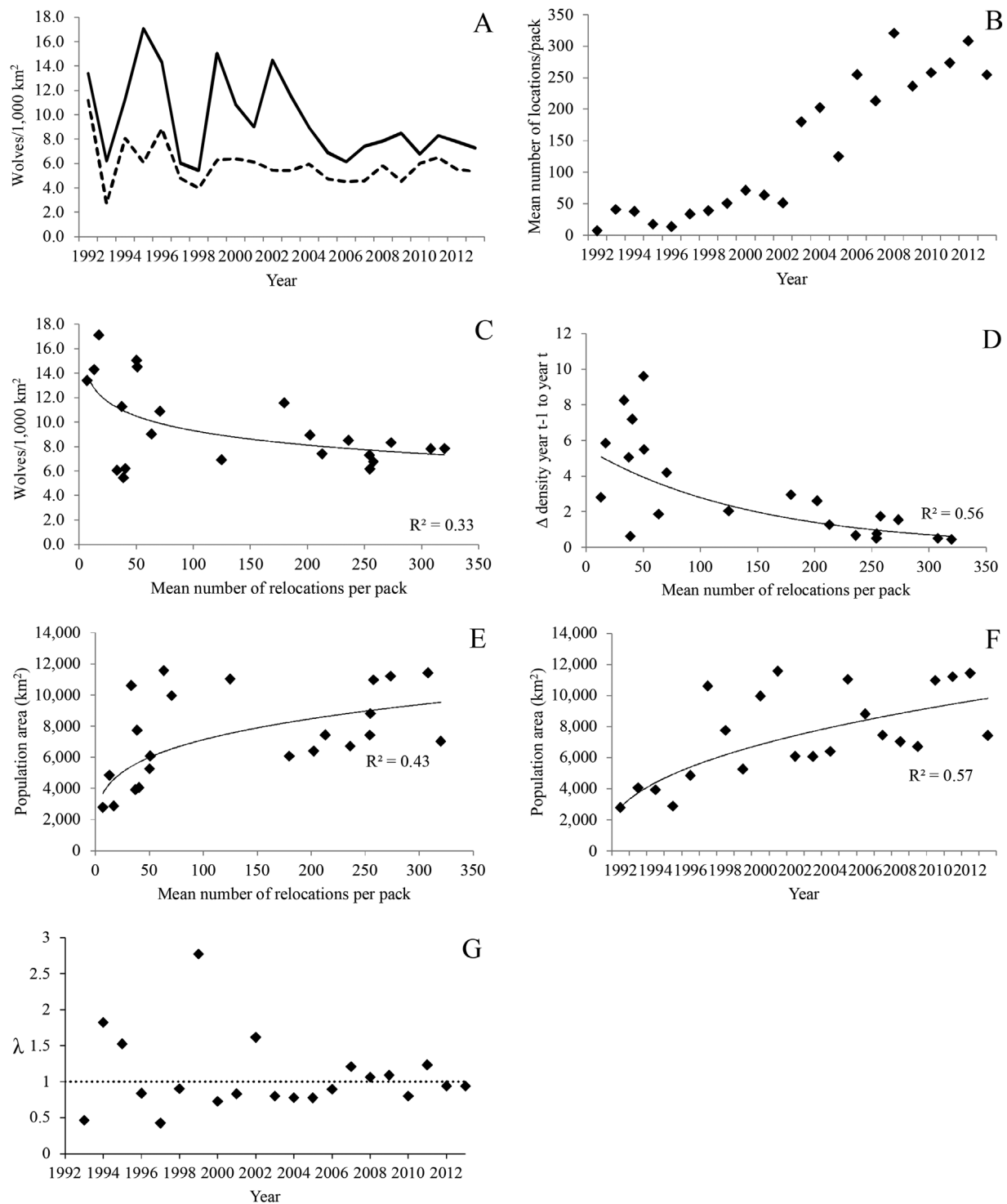
members (Mech et al. 1999, Mech 2000, Packard 2003), perhaps reducing pup survival or recruitment in smaller packs. Although breeders may be quickly replaced in many circumstances by immigrants or other pack members (Fuller et al. 2003), other pack members are primarily replaced through reproduction rather than dispersal (Mech et al. 1998). Therefore, we predict that targeted removals of breeders or multiple wolves from a single pack might have more additive effects on the population in the form of reduced natality than would occur under more typical conditions.

Wolf dispersal helps to mitigate localized losses of packs in relatively continuous populations (Fuller et al. 2003) and represents an important vital rate affecting wolf population dynamics (Mech et al. 1998, Adams et al. 2008). Dispersers from YUCH contributed to wolf populations throughout much of the state, sometimes hundreds of kilometers from their natal pack, at rates that are broadly similar to other regions in Alaska (Ballard et al. 1997, Mech et al. 1998) and the Yukon (Hayes and Harestad 2000). Many of the collared dispersers from YUCH were subsequently trapped, supporting the conclusion that dispersers are generally at higher risk of mortality and contribute significantly to human harvest (Peterson et al. 1984, Boyd and Pletscher 1999, Adams et al. 2008).

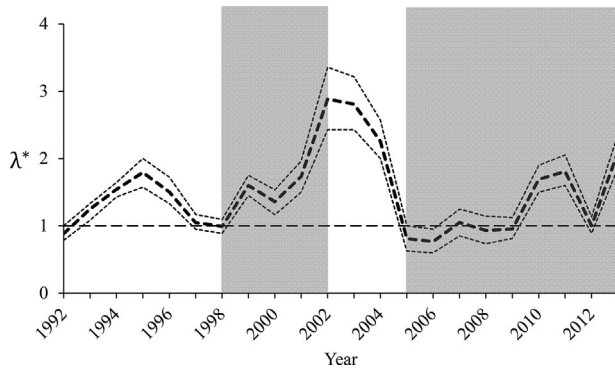
The role of dispersers in supporting sustainable harvest of wolves is important and suggests that large-scale wolf reduction efforts may have played a role in observed decreases in harvest in YUCH during our study. Although not actively managed to provide high yields of wolves to hunters and trappers, wolf harvest is considered an important use of wolves in YUCH. Therefore, decreases in legal harvest due to control efforts may represent a valid management concern. Apparent reductions in harvest also corresponded with estimates of  $\lambda^*$  indicating that YUCH acted as a population sink maintained primarily through dispersals of wolves from other regions during lethal control. Similar source-sink dynamics have been identified in areas where rates of human-caused mortality are high and populations are maintained primarily through dispersal (Mech 1989, Lariviere et al. 2000, Fuller et al. 2003), suggesting that sources of dispersers are critical for populations affected by or recovering from high rates of human-caused mortality (Smith et al. 2010). The trajectory of harvest and population status together point to similar impacts of control on the YUCH population.

The importance of source populations is more clearly identified in studies where immigration is limited. Such work has shown that wolf populations compensate for increased mortality through dispersals from surrounding areas to a greater extent than is often acknowledged (Vucetich and Peterson 2004, Creel et al. 2015). For example, the Kenai Peninsula (Peterson et al. 1984) and Prince of Wales Island (Person and Russell 2008) represent 2 areas in Alaska where dispersal is geographically limited, and human harvest was thought to be limiting populations. Similarly, the wolf population on Isle Royale went through a large decline in the early 1980s without any human-caused mortality and has not recovered (Vucetich and Peterson 2004), largely because immigration into the populations is effectively non-existent. These impacts may be particularly relevant for Alaska where multiple large-scale predator control programs are in various stages of consideration





**Figure 19.** Estimated wolf densities and diagnostic plots for the Yukon-Charley Rivers National Preserve, Alaska, USA during biological years 1992–2013. Density estimates based on 95% minimum convex polygon (MCP) methods (solid line) versus subjective MCP methods (dashed line) are shown in panel A. Panel B depicts the mean number of locations for each pack in each year of the study. Panel C represents the relationship between density and the mean number of relocations per pack. Panel D represents the change in density between years ( $t$ ) relative to the mean number of relocations per pack. Panels E and F represent the relationship between estimated population area and the mean number of locations per pack and by year, respectively. Panel G represents annual estimates of population growth rate ( $\lambda$ ) based on changes in density between years. Values in C–F are based on the 95% MCP method. Fitted lines and  $R^2$  values are shown to describe the basic pattern and strength of each relationship.



**Fig. 20.** Estimates of  $\lambda^*$ , the annual rate of population change due to additions (natality; immigration excluded) and losses (mortality and dispersal) for wolf packs in and around Yukon-Charley Rivers National Preserve, Alaska, USA in April for each biological year, 1992–2013. Fine dotted lines indicate 95% credible intervals. The thin horizontal dashed line represents the theoretical boundary between a primarily self-sustaining population and a population reliant on immigrants from the surrounding area. The gray sections indicate biological years (1-year lag) when active wolf control programs were in effect. During the first non-lethal control period, YUCH study packs were excluded from the sterilization treatments. During the second lethal control period, YUCH study packs were exposed to control efforts only when outside the preserve boundary.

and implementation. Evidence of direct and sustained impacts on an adjacent population such as YUCH indicates that the effects of widespread control could reduce the effectiveness of presumed source populations over a broad area.

Extraterritorial forays are an important but poorly understood component of wolf behavioral ecology that also play an important role in population dynamics. These forays were common and spatially and temporally extensive in YUCH study packs, suggesting they also could have important management implications for protected areas surrounded by lands with differing management goals. Although forays may be common, particularly in Alaska (Van Ballenberghe 1983, Ballard et al. 1997, Demma et al. 1997, Burch et al. 2005), little is known about the life-history trade-offs involved in the decision to leave an established territory for some period of time. Our finding that apparent survival was reduced while on an extraterritorial foray suggests that risk of loss is increased during these movements, possibly because of increased conflict with established territorial packs. Increased exposure to sources of human-caused mortality also may play a role, particularly in our study where movements outside the boundary of YUCH increased direct exposure to lethal control. Dispersal rates also may increase while on an extraterritorial foray in response to limited food resources. Ballard et al. (1997) speculated that large movements were related to low moose densities, resulting in packs following migratory caribou during portions of the year. We expect a similar dynamic operates in YUCH, where many territories sustain relatively low numbers of moose, possibly forcing packs to travel to find sufficient prey in some years, particularly when caribou are not available. However, the ability to follow migratory prey such as caribou may allow packs to maintain territories in areas with insufficient resources during some winters.

The dynamics of wolf populations are clearly linked with those of their prey. Unfortunately, data on prey abundance and

condition were not available for YUCH at temporal scales appropriate for analysis. However, harsh winters are known to be associated with increased prey vulnerability (Mech et al. 1987, 1998; Mech and Peterson 2003); therefore, it was not surprising that average snow depth had a positive effect on apparent survival in YUCH, at least suggesting that mortality or dispersal were reduced during periods of increased prey vulnerability. Although mean snow depth was an admittedly coarse metric related to prey vulnerability, its support implies that variation in prey vulnerability had a direct influence on wolf vital rates in YUCH. Unexpectedly, average snow depth was negatively related to natality rates in the following biological year. We speculate this relationship could have been due to the fact that breeding takes place during late winter before the realization of the impact of snow conditions, resulting in negative rather than positive effect. More work will need to be done in this area to assess the mechanism behind the relationship between average snow depth and natality.

Wolf control affected apparent survival and natality rates of YUCH study packs in opposing directions, suggesting direct and indirect effects on vital rates. Direct removals of individuals from YUCH study packs along with additional factors such as wounding loss or pack dissolution (Borg et al. 2015) resulted in lower annual apparent survival rates during the lethal control period. Although some compensation may have occurred, the approximately 15% reduction in apparent survival associated with lethal control indicated that the program represented an additive source of loss for wolves in YUCH study packs, although the effects on the population were partially counteracted by a large increase in average natality that occurred during both control periods. Reductions in wolf numbers increase the ungulate to wolf ratio, and higher ratios may be related to increased litter sizes (Boertje and Stephenson 1992, Fuller et al. 2003) and multiple litters (Mech et al. 1998). Correspondingly, sustained increases in YUCH natality rates during both control periods are consistent with a density-dependent response to reduced competition with other wolves from the surrounding area (Cariappa et al. 2011, Cubaynes et al. 2014). Early-season pup survival is generally high (Adams et al. 2008); therefore, we suspect that the increases in natality we observed represent increased pup production in response to decreased wolf densities, although we were unable to identify the mechanism directly. We did observe  $\geq 10$  pups in a single pack late during each of the 2 wolf control periods, at least suggesting that multiple litters may have been produced in some years. Increases in natality rates in response to reduced densities may explain the rapid recovery of wolf populations after the cessation of wolf control programs that has been observed in other areas (Ballard et al. 1987, Hayes and Harestad 2000) and suggests a mechanism for such recoveries. The interplay between wolf vital rates during periods of intensive harvest or lethal control operations have obvious implications for understanding their impacts over both short and long time horizons.

The relative additivity of human-caused mortality on wolf populations has received much discussion in the literature (Fuller et al. 2003, Adams et al. 2008, Creel and Rotella 2010, Murray et al. 2010, Gude et al. 2012). In most areas in Alaska and Canada, the primary sources of human-caused mortality are legal

harvest and lethal control, although in other regions poaching, livestock protection, and incidental causes (e.g., vehicle strikes) also play important roles. Reviews have suggested that rates of human-caused mortality  $\leq 22\text{--}29\%$  of the fall population may be compensatory (Fuller et al. 2003, Adams et al. 2008, Creel et al. 2015). However, threshold values imply consistent pack characteristics (e.g., size, structure) and harvest may have indirect impacts beyond kill rates (Ausband et al. 2015, Creel and Rotella 2010). Variation in natality, natural mortality, and dispersal rates could explain much of the observed variation among harvest rates and subsequent population trajectories (Fuller et al. 2003, Adams et al. 2008). Young or dispersing individuals are generally the most susceptible to conventional harvest techniques, particularly trapping (Adams et al. 2008, Person and Russell 2008, Webb et al. 2011) and represent a less reproductively valuable component of the population. In contrast, lethal control is less selective and breeders are more likely to be killed than they would be otherwise. As we and others have shown, breeder loss has a much greater impact on population dynamics than the loss of non-breeding wolves. In addition, a majority of the known removals due to lethal control occurred late in the season after most natural losses would have occurred, increasing the additive impacts of lethal control. We show that although natality rates quickly increased in an apparent density-dependent response to control efforts, other factors such as breeder loss and reduced apparent survival could still result in negative population trajectories.

Estimating  $\lambda$  is a basic objective of many studies of population dynamics, and those involving wolves are no exception. Changes in the estimated number of wolves between years is used to assess whether  $\lambda$  is  $>1.0$  or  $<1.0$ , indicating a population increase or decrease, respectively (Mech et al. 1998, Adams et al. 2008). Despite common usage, our results confirm and strengthen the assertion that density estimates based on home-range analyses are largely confounded with sampling effort (Bekoff and Mech 1984, Burch et al. 2005). Estimates of density and  $\lambda$  were influenced even at sample sizes  $>1$  location per pack per day; therefore, simply increasing sampling effort is not a valid solution. A simple comparison of our subjective MCP versus the 95% MCP density estimates revealed that the most extreme 5% of locations have an inordinately large effect on estimation. These few locations drive changes in apparent home range overlap of adjacent packs, size of the population area, and the edge to area ratio (length of the perimeter/total area) of the population area. Relatively few peripheral locations can have a large impact on any or all of these measures, resulting in artificial changes in density and subsequent estimates of  $\lambda$ . We concluded that such dependence is pervasive, unpredictable, and uncorrectable, thereby rendering density estimates unreliable for estimating  $\lambda$  in most cases.

We created a new metric,  $\lambda^*$ , that was a much more defensible and interpretable measure of population trajectory. Estimates of  $\lambda^*$  incorporate both production and losses (excluding immigration) at the level of the study population, thereby allowing direct assessment of whether a particular population is self-sustaining or reliant on immigrants from the surrounding area for maintenance. Although immigration rates are generally not estimable in collar-based wolf studies, the relative importance of immigration can be inferred directly from estimates of  $\lambda^*$ . Furthermore,

immigration in continuous populations may obscure important source-sink dynamics (Pulliam 1988) caused by ecosystem changes or harvest dynamics. Using  $\lambda^*$ , we showed that sustainable removal rates depend directly on the interplay of natality and apparent survival. Populations can sustain higher exploitation during periods of high natality and low natural loss rates, as one might expect. For example, the overall impact of the removal of 40% of the individuals from monitored packs in 2012 had a similar effect on population status as the removal of  $<10\%$  in 2005 because natality rates were much higher later in the lethal control period.

Reported removals in YUCH due to harvest and lethal control were generally  $<22\%$  of the fall population (except in 2012 and 2013), which is well below the levels of human-caused mortality expected to have an effect at the population level. However, the effects of lethal control and other factors (e.g., snow depth), combined to reduce annual apparent survival by approximately 25% on average (Fig. 17). Although natality increased and the decline in survival was not overly dramatic, the result was to shift YUCH from being a population source before lethal control to a population sink during lethal control. In effect, wolf control directly and indirectly altered the structure and function of the population of wolves using YUCH, leading to population-level impacts that are in direct conflict with current NPS management policies (NPS 2006).

## MANAGEMENT IMPLICATIONS

One of the primary purposes of protected areas, particularly for those managed by the NPS, is to preserve naturally functioning ecosystems. Removals or reductions of native predators to increase ungulate abundance is in conflict with NPS management policies that specifically require “minimizing human impacts on native plants, animals, populations, communities, and ecosystems, and the processes that sustain them” (NPS 2006:42). Additionally, it is well recognized that management actions and other activities that take place on lands outside park boundaries can affect park resources (NPS 2006). In our case, although wolf control actions occurred only outside the boundaries of YUCH, we demonstrated that such actions could have direct impacts on wolf population dynamics over broader areas. These findings suggest that managers of protected areas need to think more deeply to address the types of changes we observed in YUCH. The passive management approach often employed by managers in response to external threats may be insufficient to prevent a shift in ecosystem dynamics when management regimes differ in adjacent areas, particularly in the case of wolf control. This finding has direct and important consequences for management of protected areas going forward, particularly in the context of expanding wolf harvest and control efforts in Alaska and elsewhere.

Wolf harvest management decisions often rely implicitly on immigrants from surrounding areas to repopulate areas where harvest is high (Robichaud and Boyce 2010), effectively resulting in harvest over a much larger area. Using estimates of  $\lambda^*$ , we showed that the effects of control extend well beyond the borders of the control area itself. Similarly, a reduction in dispersers from the UYTPCA into YUCH may partially explain the decrease in reported harvest after the implementation of lethal control.

The implications of our work are broader than the effects of wolf control on the YUCH population in particular. In Alaska, most NPS units are adjacent to intensive management areas where wolf control programs are being considered or are already taking place. This situation is not unique to the NPS; managers of many other conservation units throughout the state face the same issue. In the continental United States where wolf populations are less contiguous and human access for hunting and trapping is greater, sustainable harvest levels may be lower than expected (Creel et al. 2015) because there are fewer areas from which dispersers can recolonize empty habitat. In Alaska and much of Canada where wolf populations remain largely continuous, harvest pressure is inconsistent, and high harvest rates in accessible areas are maintained by immigrants from less heavily harvested areas. However, if increased harvest or control programs were implemented at larger scales, the flow of immigrants to replenish vacant habitats would be expected to decrease, thereby reducing sustainable harvest rates over large areas. In light of our findings, managers should consider the potential geographical extent of impacts of wolf control on populations using protected areas both locally and regionally. We recommend collaboration to mitigate the effects of control on these management units. We expect a regional approach may be much more effective than individual efforts at the level of distinct conservation units because of the scale and frequency of control programs.

Human harvest represents a valuable use of wolves in Alaska where approximately 1,300 wolves are harvested annually (<http://www.adfg.alaska.gov>, accessed 10 Apr 2017). Wide-spread harvest of wolves is important to sport and subsistence users as a renewable resource. However, harvest has the potential to affect other user groups or alter wolf population dynamics as a whole. In Alaska, harvest is often considered to be compensatory in the absence of control efforts (Adams et al. 2008), and although population persistence is only one of many objectives for protected areas, the impact of harvest on other valid uses also must be considered. Harvest effects may play a more prominent role for protected areas in regions with discontinuous wolf populations, high user densities, and well-developed access. Under these conditions, harvest may need to be more carefully managed to meet population goals and avoid conflict between user groups. We encourage collaborative approaches incorporating the different goals and objectives of each management agency with a stake in wolf management (Smith et al. 2016), and we expect such approaches may represent the most productive path forward in managing wolf populations over large areas.

## SUMMARY

- 1) We studied the effects of 2 intensive wolf control programs on the population dynamics of wolves in an adjacent protected area (YUCH) in interior Alaska for >2 decades (BY 1992–2013).
- 2) Survival was demonstrably lower during the lethal control period for wolves in YUCH study packs even though wolf control efforts did not occur within the boundaries of YUCH, suggesting wolf control represented a source of additive mortality for wolves in YUCH study packs.

- 3) Estimated natality rates of YUCH packs nearly doubled during both wolf-control periods, suggesting a density-dependent response through increased reproductive output.
- 4) Despite the compensatory forces of increased natality rates, YUCH generally functioned as a population sink during the lethal control period, in contrast to the prior time period.
- 5) Extensive forays were common and were associated with lower apparent survival, suggesting additional risks were incurred during these movements. Conversely, apparent survival rates were higher following deeper snow winters, suggesting variation in prey vulnerability.
- 6) Density estimates based on the relocation of marked individuals were strongly confounded with sample sizes, even at high levels of effort, suggesting such measures are unreliable and of limited utility for assessing  $\lambda$ .
- 7) Our newly developed metric,  $\lambda^*$ , provided a biologically interpretable and defensible means to assess population trajectory and source-sink dynamics when  $\lambda$  is inestimable. This metric could provide a sensitive and useful tool for managers.
- 8) Wolf populations generally function over patchy landscapes consisting of a variety of management units with differing management goals and objectives. A deeper understanding of source-sink dynamics within this patchwork will help managers meet their respective goals.
- 9) Results from this study suggest that land managers must have clear objectives for the management of wolf populations to meet legislative mandates. These results also underscore the need for management agencies to cooperate to meet management responsibilities. Depending on objectives, managers of protected areas may need to consider whether the extensive effects of wolf control require more active and conservative management regimes than are typically applied.

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