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ARTICLE

Of wolves and bears: Seasonal drivers of interference and exploitation competition between apex predators

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Abstract

Competition between apex predators can alter the strength of top-down forcing, yet we know little about the behavioral mechanisms that drive competition in multipredator ecosystems. Interactions between predators can be synergistic (facilitative) or antagonistic (inhibitive), both of which are widespread in nature, vary in strength between species and across space and time, and affect predation patterns and predator–prey dynamics. Recent research has suggested that gray wolf (*Canis lupus*) kill rates decrease where they are sympatric with brown bears (*Ursus arctos*), however, the mechanisms behind this pattern remain unknown. We used data from two long-term research projects in Scandinavia (Europe) and Yellowstone National Park (North America) to test the role of interference and exploitation competition from bears on wolf predatory behavior, where altered wolf handling and search time of prey in the presence of bears are indicative of interference and exploitation competition, respectively. Our results suggest the mechanisms driving competition between bears and wolves were dependent on the season and study system. During spring in Scandinavia, interference competition was the primary mechanism driving decreased kill rates for wolves sympatric with bears; handling

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time increased, but search time did not. In summer, however, when both bear and wolf predation focused on neonate moose, the behavioral mechanism switched to exploitation competition; search time increased, but handling time did not. Alternartively, interference competition did affect wolf predation dynamics in Yellowstone during summer, where wolves prey more evenly on neonate and adult ungulates. Here, bear presence at a carcass increased the amount of time wolves spent at carcasses of all sizes and wolf handling time for small prey, but decreased handling time for the largest prey. Wolves facilitate scavenging opportunities for bears, however, bears alter wolf predatory behavior via multiple pathways and are primarily antagonistic to wolves. Our study helps to clarify the behavioral mechanisms driving competition between apex predators, illustrating how interspecific interactions can manifest into population-level predation patterns.

KEYWORDS
Canis lupus, exploitation competition, interference competition, interspecific interactions, Scandinavia, *Ursus arctos*, Yellowstone

INTRODUCTION

Competition is a fundamental concept in ecology, driving everything from long-term evolutionary processes and large-scale community structure to real-time individual behavior. Competition occurs within and between species via direct or indirect interactions that alter access to a shared resource (e.g., food, water, sunlight, or space; Case & Gilpin, 1974, Palomares & Caro, 1999). Competitive interactions between apex predators are important because they can alter the relative strength of top-down effects within an ecosystem (Bruno & Cardinale, 2008; Ives et al., 2005). Interactions between predators can be synergistic, resulting in facilitation of one predator by another, thereby increasing their combined impact on the prey population (Bruno et al., 2003; Losey & Denno, 1999), or antagonistic, where one predator inhibits another's foraging ability, thereby reducing predator fitness and diminishing their combined impact on the prey population (Finke & Denno, 2002). Both synergistic and antagonistic interactions are widespread, vary in strength between species and across space and time (Bruno & Cardinale, 2008), and affect ecological processes, including predation patterns and predator–prey dynamics (Kareiva, 1990). Clarifying the behavioral mechanisms that drive large-scale predation patterns is therefore crucial for understanding and predicting the consequences of multiple predators within an ecosystem (Bruno & Cardinale, 2008; Glen & Dickman, 2005; Périquet et al., 2015).

Kill rate, or the number of prey killed per predator per unit time, is an essential measure of predation, and is driven by how long it takes a predator to make a kill, that is, the time between consecutive kills, or the kill interval. In its simplest form, a kill interval is the sum of time a predator spends handling their first prey, and searching for and killing the second (Merrill et al., 2010; Tallian, Ordiz, et al., 2017). Prey handling time is commonly defined as the sum of time spent attacking and capturing a prey, and consuming and digesting the kill (Mukherjee & Heithaus, 2013), whereas search time is often simply defined as the total time spent actively searching for the next prey (Werner & Hall, 1974). The type of competition between predators may alter prey handling and search time in several ways. Interference competition includes direct and indirect, antagonistic interactions between individuals that result in resource exclusion for the subordinate competitor. Here, the theft of a kill may cause the subordinate predator to prematurely abandon their kill, thereby decreasing prey handling time (Elbroch et al., 2014; Krofel et al., 2012). Alternatively, handling time may increase if the presence of another predator causes the subordinate to dedicate additional time either defending the kill, or waiting for access to a stolen carcass (Tallian, Ordiz, et al., 2017). Exploitation competition occurs when an individual or species consumes a shared resource, indirectly resulting in resource limitation. Exploitation competition may lead to decreased encounter rates and increased search times for a second predator, if the first predator reduces the supply of a shared prey (Holt et al., 1994). Altered handling time and search time, which together comprise the kill interval, in the presence of another predator are therefore indicative of interference and exploitation competition, respectively (Figure 1).

Brown bears (*Ursus arctos*) and gray wolves (*Canis lupus*) are two of the most widespread apex predators in the Northern Hemisphere (Ordiz, Krofel, et al., 2020). Recent research has shown that wolf kill rates decrease (i.e., kill intervals are longer) where they are sympatric with bears (Tallian, Ordiz, et al., 2017), however, the mechanisms driving changes in wolf predation dynamics when bears are present remain unknown. Here, we used GPS-derived movement and predation data for wolves, and data describing brown bear presence, from two long-term research projects in Europe (Scandinavian Peninsula) and North America (Yellowstone National Park, USA) to test the role of interference and exploitation competition with brown bears on wolf predatory behavior. We evaluated how the presence of bears affected wolf search and handling time during two seasons when the potential for interspecific interactions differed: spring, which spanned the bear den emergence period, and early summer, which spanned the ungulate parturition period. In Scandinavia, we compared wolf search and handling time in regions of high and very low bear density (from this point forwards sympatric and allopatric areas) in those two seasons. In Yellowstone, where wolves and bears were sympatric throughout the system, we examined the effect of brown bear presence at a wolf kill on wolf handling time during early summer. Elk (*Cervus canadensis*) are the main ungulate prey for wolves and bears during summer in Yellowstone (Metz et al., 2012), however, both predators there use a broader range of prey species than in Scandinavia, where moose (*Alces alces*) are the dominant ungulate prey in both seasons and study areas (Sand et al., 2005, 2008).

Wolf kill intervals are longer where wolves are sympatric with bears (Tallian, Ordiz, et al., 2017). In sympatric areas in Scandinavia, we hypothesized that interference competition would occur mainly during spring when moose calves, wolves' main prey, are larger and approaching yearling status (Sand et al., 2005). Bears are adept scavengers, and, when not hibernating, regularly usurp kills from wolves (Ballard et al., 2003; Ordiz, Milleret, et al., 2020). Furthermore, the larger prey killed during this season (relative to neonate moose calves during summer) may allow more time for interference interactions as well as incite greater competition, or carcass defense, due to its greater resource value. In Scandinavia, we therefore predicted that wolf handling time in sympatric areas would increase during the spring den emergence period (March–May), as bears progressively emerged from hibernation, and that wolf handling time would remain constant in allopatric areas. We also expected that wolf search time would remain consistent through time for packs in sympatric and allopatric areas, as bears and wolves do not share the same prey resource during the spring den emergence period.

Alternatively, we hypothesized that exploitation competition would occur mainly during summer in sympatric areas in Scandinavia, because wolves and bears share the same prey base, neonate moose, during this season (Rauset et al., 2012; Sand et al., 2005; Tallian, Ordiz, et al., 2017). During summer in Scandinavia, we therefore predicted that wolf search time would increase through time in sympatric areas, as the supply of shared prey on the landscape successively diminished. Because neonate abundance also decreases via wolf predation in allopatric areas, and due to the rapid initial body growth of neonates (Sand et al., 2008), we expected wolf search time to

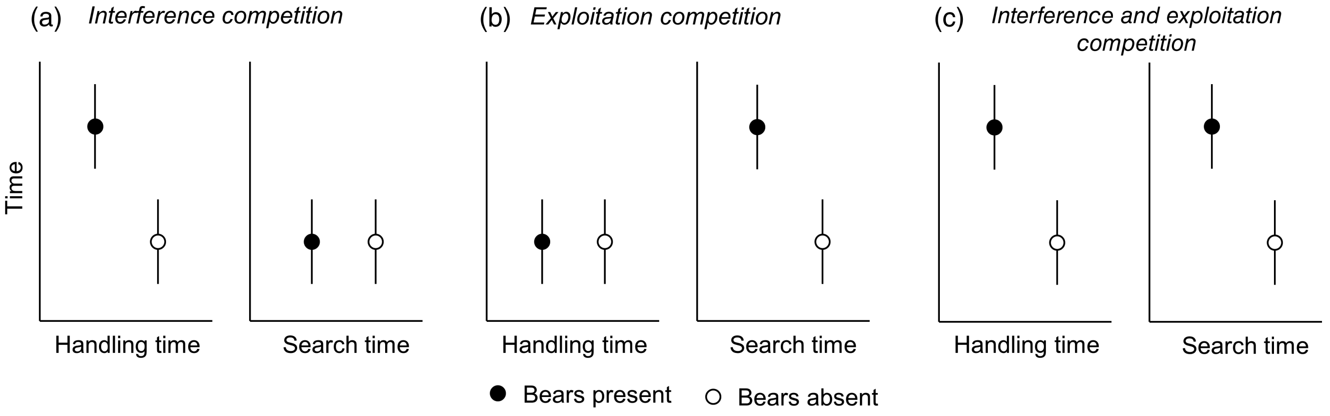

FIGURE 1 Visual representation of how (a) interference, (b) exploitation, and (c) both interference and exploitation might manifest within the predatory sequence. Where wolves are sympatric with bears (a) increased handling time is indicative of interference competition, (b) increased search time is indicative of exploitation competition, and (c) increased search and handling time indicate that both forms of competition occur

increase through time in allopatric areas as well, but at a slower rate. We expected handling time to be similar in sympatric and allopatric areas during summer, as wolves primarily prey on neonate moose that are small and consumed quickly (neonates comprise almost 90% of wolf-killed moose during summer; Tallian, Ordiz, et al., 2017).

In Yellowstone, we hypothesized that, if interference competition was occurring, it would be more acute at larger carcasses, where the extended duration and greater amount of available food biomass increases the potential for interference interactions and competition. Because wolves in Yellowstone prey more evenly on neonate and adult ungulates during summer (62% and 34% of all wolf-killed elk, respectively; Metz et al., 2012), we predicted that wolf handling time would increase when bears were present at wolf kills, with the greatest increase occurring with the largest prey. That is, wolves would spend more time at any kill when bears are present, but the increase would be disproportionally greater at larger carcasses. It is important to note that we also expected exploitation competition to occur simultaneously with interference competition during summer in Yellowstone, when wolves and bears both prey on neonate elk (Barber-Meyer et al., 2008). Unfortunately, we were unable to test this hypothesis directly as we would need to examine the effect of bear density on search time, rather than bear presence at a kill, and such data were unavailable.

MATERIALS AND METHODS

Study areas

Scandinavia

Our study was conducted in south-central Scandinavia (SCA; ~100,000 km^2, elevation 50–1000 m), which spans the border of Sweden and Norway. The landscape is mostly comprised of intensely managed boreal forest; for a detailed habitat description see Ordiz, Stoen, et al. (2013). The brown bear population in Scandinavia was estimated at ~3300 individuals in 2008 and ~2750 individuals in 2018, with densities reaching 3 bears per 100 km^2 (Bischof et al., 2020; Kindberg et al., 2011). Their population remained relatively stable between 2004 and 2012 (Kindberg & Swenson, 2018), showing a slight increase from 2012 to 2015 (Bischof et al., 2020). During the same time frame, the wolf population increased from ~100 to ~430 wolves (Bischof et al., 2020; Wabakken et al., 2002, 2016). Wolves and bears in Scandinavia mostly persist independently of one another, except for the northern portion of our study area where the two species overlap (Ordiz et al., 2015; Tallian, Ordiz, et al., 2017). Moose are the main ungulate prey for both predators in SCA (Rauset et al., 2012; Sand et al., 2005). Here, wolves predominantly prey on moose calves, switching from last years' juveniles to the newborn cohort during the parturition season (Sand et al., 2008). Alternative ungulate prey include European roe deer (*Capreolus capreolus*) (Sand et al., 2008, 2016) and, more recently and still rare, wild boar (*Sus scrofa*). Bears in Scandinavia use a wide variety of plant and animal foods throughout the year (Stenset et al., 2016) and prey heavily on neonate moose during early summer (i.e., May–June; Rauset et al., 2012), but rarely kill adult ungulates (Dahle et al., 2013).

Yellowstone

Our study was conducted on the Northern Range (995 km^2, elevation 1500–2000 m) of Yellowstone National Park (YNP; 8991 km^2) located in northwestern Wyoming, USA. The Northern Range wolf population ranged between 33 and 56 individuals from 2008–2017 (D. Smith et al., 2018). The Greater Yellowstone Ecosystem (which includes YNP) brown bear population was approximately 750 bears in 2014 (Haroldson et al., 2015), with densities of 5–13 bears per 100 km^2 on the Northern Range (Bjornlie et al., 2014). Elk are the main ungulate prey for both wolves and bears in YNP (Fortin et al., 2013; Metz et al., 2012). Secondary prey species available for wolves include American bison (*Bison bison*), deer (*Odocoileus* spp.), bighorn sheep (*Ovis canadensis*), moose, and pronghorn (*Antilocapra americana*). Similar to Scandinavia, bears in YNP rarely kill adult ungulates (Evans et al., 2006), but prey on neonate calves, particularly elk, from late May to early June (Barber-Meyer et al., 2008; Fortin et al., 2013). Brown bears in YNP also frequently scavenge ungulates, including usurping wolf-killed prey (Stahler et al., 2020), which results in a greater proportion of meat in the YNP bear diet compared with other systems (Fortin et al., 2013; Wilmers et al., 2003). American black bears (*Ursus americanus*) are present on the Northern Range and also prey on neonate elk (Barber-Meyer et al., 2008); however they rarely usurp wolf-killed ungulates.

Data collection

Scandinavia

Wolf predation studies were conducted in SCA between 2002 and 2015 during two distinct time periods, from this point forwards referred to as "spring" (1 March to

15 May) and "summer" (15 May to 30 June). Wolves were captured by immobilization from a helicopter according to accepted veterinary and ethical procedures (Arnemo & Fahlman, 2007; Sand et al., 2006). At least one of the breeding adults in a pack was marked with a GPS collar (Vectronic Aerospace, Germany) and followed during each study period (Appendix S1: Table S1a,b). Field crews searched for ungulate carcasses within a 100 m radius of all "clustered" GPS points and recorded cause of death, species, age (neonate, calf, yearling, or adult), and sex (Appendix S1: Table S2a,b; see Zimmermann et al. (2007) for further details). In SCA, we selected GPS data from one wolf per pack per study period, prioritizing males over females in spring. In summer, we excluded instances when only female wolves were followed ($N = 2$), to control for potential variation in sex-specific behavior near the denning period. The final data set for spring (2002–2015) and summer (2003–2015) included 11 male and 6 female wolves followed over 18 study periods, and 9 male wolves followed over 11 study periods, respectively (Appendix S1: Table S1a,b). Due to an early collar malfunction on the Gräsmark male in 2007, we used GPS data from both the female (up to 11 March) and male (after 11 March) wolf for the 2007 Gräsmark study period (Appendix S1: Table S1a). Wolf collars were programed to collect GPS locations at either 1-h ($\mathrm{N_{spring}} = 11$; $\mathrm{N_{summer}} = 3$) or 30-min intervals ($\mathrm{N_{spring}} = 7$; $\mathrm{N_{summer}} = 8$). To make the GPS data comparable, we subset the 30-min GPS data to a 1-h fix interval. Time of death (TOD) of wolf-killed prey was recorded as the first position of any radio-collared pack member within a cluster containing a killed prey (Tallian, Ordiz, et al., 2017). Time of first visit (TOFV) was estimated as the first position of the focal wolf within 200 m of the carcass site after the TOD occurred.

Edible prey biomass (kg) per kill during spring was estimated using the known mean body mass of prey species based on age and, for adult moose, sex, and corrected for the proportion of species-specific edible biomass (see Zimmermann et al., 2015; Zochowska et al., 2005). When age was unknown, body mass was estimated using the mean adult, yearling, and calf body mass (moose: $\mathrm{N_{spring}} = 5$; $\mathrm{N_{summer}} = 1$) or mean adult and calf body mass (roe deer: $\mathrm{N_{spring}} = 6$). For adult moose of unknown sex, we used the mean adult male and female body mass ($\mathrm{N_{spring}} = 3$; $\mathrm{N_{summer}} = 1$). For neonate and yearling moose kills made during summer, we estimated body mass using a linear growth curve assuming a starting mass of 13 kg on 1 June and 135 kg on 1 May, respectively (for further details see Sand et al., 2008, 2016). For neonates and yearlings that were killed prior to these dates, we assumed a fixed body mass of 13 kg and 135 kg, respectively. Double kills in SCA and YNP were defined as any wolf-killed prey for which the TOFV was <2 h and the distance between carcass sites was <1000 m, or TOFV was <8 h and the distance between carcass sites was <500 m, respectively. These time–space designations closely matched observer classifications of double kills in the field. The edible biomasses of carcasses classified as a double kill were added together.

In Scandinavia, the number and distribution of confirmed brown bear deaths are an established and tested index of brown bear distribution and density (Kindberg et al., 2009; Swenson et al., 1998). Therefore, following Ordiz et al. (2015), we generated a spatially explicit bear density index, derived from hunter harvest data, that spanned Scandinavia and ranged from 0 (i.e., no or sporadic bear presence) to 1 (i.e., highest bear density). We estimated the mean index within each wolf territory, defined as the 100% minimum convex polygon (MCP) of the GPS locations for each wolf study period. Most wolf territories were located in either very high or very low brown bear density areas (Appendix S1: Table S1a,b). Henceforth, we refer to wolves in SCA as either "sympatric" or "allopatric" with brown bears.

The acute nutritional status (from this point forwards nutritional status), or hunger, of a wolf may also affect its individual behavior between kills. For example, increased hunger (i.e., decreased nutritional status) may cause wolves to stay longer at a kill, whereas decreased hunger (i.e., increased nutritional status) may increase time spent resting and not searching for additional food. In SCA, wolf packs begin to dissolve during spring when most yearlings begin to make extraterritorial movements, ultimately dispersing by summer (Nordli, 2018). Wolf packs are much larger in YNP, where packs generally move together during winter, pack cohesion starts to decline during spring, and is lowest during summer when wolves regularly travel alone or in smaller groups (Metz et al., 2011). We therefore calculated nutritional status at the pack level for spring in SCA and at the individual level for summer in SCA and YNP, respectively, as winter pack sizes (when pack size was estimated) are likely to be an inaccurate estimate for summer pack sizes. Nutritional status was estimated as

$$NS = B - T \times FMR$$

where NS is the nutritional status of the pack or individual, B is the edible biomass (kg) of the previous kill(s), T is the number of days since the previous kill, and FMR is the daily metabolic field rate (i.e., the mean daily energy expenditure of an animal at average activity) of the pack or individual in kg biomass per day (Sand et al., 2016; Zimmermann et al., 2015). We used estimates of pack-size-specific and individual FMR based on mean wolf body mass in SCA and YNP (Zimmermann et al., 2015) to estimate the nutritional status at the start of each kill. Pack size in SCA was estimated by a combination of snow-tracking GPS-collared wolves during winter and sampling individual fecal DNA (Tallian, Ordiz, et al., 2017).

We calculated a proxy for moose density using annual hunter harvest statistics (number of moose harvested per km^2) from Norwegian municipalities and Swedish hunting districts. Moose density was estimated by calculating the average weighted mean harvest of all management units within a wolf territory, using a 1-year time lag, which has been shown to be a good predictor of moose density (Tallian, Ordiz, et al., 2017; Ueno et al., 2014). We also calculated the distance (m) to the nearest paved or gravel road from each carcass site for both SCA and YNP as a proxy for anthropogenic disturbance. For double kills, we used the minimum distance to either carcass site.

Yellowstone

Wolf predation studies were conducted during "summer" (1 May to 31 July) in YNP between 2008 and 2017 on 23 monitored wolves (10 females, 13 males) in 12 packs or pair groups (Appendix S1: Table S1c). Both breeding and non-breeding wolves were captured and immobilized by helicopter in winter and fitted with a GPS collar (Lotek, Newmarket, ON, Canada; Vectronic Aerospace, Germany) following animal handling guidelines of the American Society of Mammalogists (Sikes et al., 2011) and in accordance with National Park Service Institutional Animal Care and Use Committee approval. Collars were programed to collect GPS locations at 30-min intervals. Field crews searched for carcasses within a 400 m^2 area for all clustered GPS locations and recorded cause of death, species, age, and sex (Appendix S1: Table S2c; see Metz et al. (2011) for further details). TOD was recorded as the first location of any radio-collared pack member within the cluster. TOFV was estimated as the first location of the focal wolf within 100 m of the carcass site after the TOD occurred. Because we were only interested in handling time in YNP, we also included carcasses that were considered freshly scavenged, rather than killed, by wolves (i.e., cause of death as assigned by the field crew was not wolf and considerable biomass remained on the carcass upon site visit). Although these cases were infrequent (33 of 695 carcasses), adult bison represented the majority (58%) of all freshly scavenged carcasses (Appendix S1: Table S2c) and are an important food source for wolves in Yellowstone (Metz et al., 2012, 2020; Tallian, Smith, et al., 2017).

To control for wolves that visited kills made by other pack members when minimal edible biomass remained, we limited the YNP analysis to kills for which a wolf was located at least twice within 100 m of the carcass (killed by it or a pack member) and within 1 or 3 days after TOD, for a small ($\leq$130 kg) or large (>130 kg) ungulate, respectively (Metz et al., 2011). In addition, logistical constraints occasionally precluded site searches in YNP. We therefore limited the analysis to kills for which all clusters within the interceding kill interval were searched, except clusters $\leq$500 m of a wolf homesite (Tallian, Ordiz, et al., 2017).

Brown bears were classified as "present" at a wolf kill if field crews detected bear sign (brown bear or unknown species), or observed a brown bear, at a carcass site. Bear sign is often not diagnostic to species in YNP, however, brown bears are observed visiting wolf kills and interacting with wolves in YNP more often than black bears (Tallian, Ordiz, et al., 2017). Carcass biomass (kg) for deer and elk was estimated using age- and sex-specific growth curves for summer in YNP (Metz et al., 2011; Murphy et al., 1998). For other ungulate species (i.e., bison, moose, bighorn sheep, and pronghorn), carcass biomass was estimated using the known mean body mass of prey species based on age-class and sex (Feldhamer et al., 2003; Meagher, 1986; Metz et al., 2011), although we estimated bison neonate growth over summer by assuming a similar growth pattern as elk. The amount of edible prey biomass available per kill was estimated as 68% of live body mass for adult bison and elk, and 79% of live body mass for deer, bighorn sheep, mountain goat, pronghorn, and all neonates (Miller et al., 2013; Wilmers et al., 2003).

We also calculated nutritional status NS for individual wolves in YNP, but corrected FMR estimates (Zimmermann et al., 2015) using mean YNP wolf body mass. Sex-specific estimates of adult wolf body mass were based on multiple measurements of 155 adult male ($N = 84$) and female ($N = 71$) wolves (>2 years of age) caught during winter between 1995 and 2018. On average, adult males ($N = 109$) weighed 51.9 ± 0.6 kg (±2 SE) and adult females ($N = 93$) weighed 43.4 ± 0.6 kg (YNP *unpublished data*). Pack size was estimated from March observations, unless pack size was known to have declined via death or dispersal during the summer study period. Summer pack size estimates did not include newborn pups in either study system.

Defining wolf behavior

To evaluate how brown bears affected wolf foraging behavior, we used space–time cluster methodology to define proxies for handling and search time within each kill interval (e.g., Webb et al., 2008). We divided wolf GPS locations within each kill interval into two different categories: "space–time clusters" and "movement positions" (Figure 2). Space–time clusters were defined as a set of GPS positions where each location was ≤100 m or ≤200 m from the next sequential position for YNP (half-hour fix schedule) and SCA (1-h fix schedule), respectively. This generated a set of space–time clusters within each kill interval, interspersed with single "movement positions" with a step length >200 m/h (Figure 2).

Handling time

Studies often restrict the definition of handling time to time spent near killed prey (e.g., Merrill et al., 2010), thereby potentially missing some digesting time if predators bed away from kills between feeding bouts. We therefore defined handling time in two different ways. The first definition of handling time included all GPS positions within a space–time cluster where ≥1 position within the cluster was within 200 m and 100 m of the carcass site for SCA and YNP, respectively (Figure 2). This definition (from this point forwards time at carcass site, or T_c) serves as a proxy for time spent consuming prey, with the caveat that predators are not necessarily always actively feeding at carcass sites (e.g., Ebinger et al., 2016). The second handling time definition included T_c (i.e., all clustered positions near the carcass site), plus all space–time clusters where the first point within the cluster occurred within 12 h of a kill visit (Figure 2). We chose 12 h based on the gut retention times of domestic dogs (*Canis familiaris*) on a "large meat-particle" diet (mean = 10 h; Smeets-Peeters et al., 1998). This definition (from this point forwards handling time, or T_h) attempts to include both consumption and digestion time, and more closely represents prey handling time as it is commonly defined (Mukherjee & Heithaus, 2013).

The above methodology restricts T_c and T_h to the "kill interval" timeframe, as we were interested in the effect of bears on wolf kill intervals and wanted methods to be comparable between the two study systems. However, wolf movements were dynamic, and wolves preyed more evenly on small and large prey during summer in YNP than in SCA (Metz et al., 2012; Sand et al., 2008). It is possible that kill intervals in YNP, and subsequent handling times, for larger prey could be "prematurely cut off" by these definitions if wolves moved away from a large prey, killed a smaller prey, and returned afterward to the previous carcass. We therefore added a second definition for time spent at a carcass site (T_{c2}) for YNP only, which included all GPS positions within a space–time cluster where ≥1 position within the cluster was within 100 m of the carcass site within 21 days of the TOFV. Carcass depletion time varies widely between systems, prey species, and predator/scavenger composition and density (e.g., Kaczensky et al., 2005; Selva et al., 2016), and wolves are known to attend carcasses anywhere from <1 to >100 days, depending on the prey species (e.g., Eriksson, 2003; Hayes et al., 2000; Messier, 1984; Selva et al., 2016). The 21-day timeframe for T_{c2} was a compromise between maximizing subsample size (i.e., all carcasses with a TOFV <21 days before the end of the study period were excluded) and the potential for carcasses to remain active for extended time periods. The shorter study periods and overall smaller sample sizes precluded examining this second definition of T_c in SCA. We excluded a second definition for T_h, as the extended time frame resulted in space–time clusters that were assigned to more than one kill. To examine site fidelity, we also quantified the number of independent visits (N_v) wolves made to each carcass site (i.e., the total number of

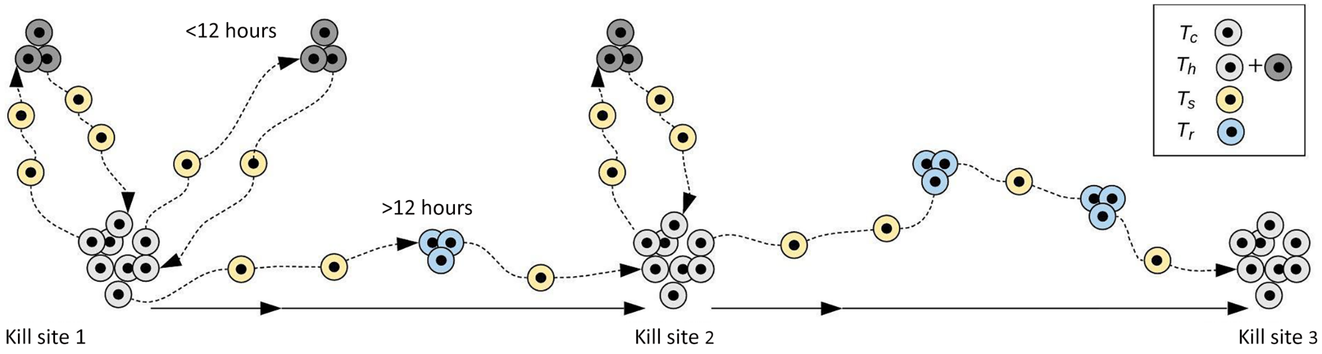

FIGURE 2 Illustration of the behavioral definitions used to quantify GPS location data from collared gray wolves in Scandinavia and Yellowstone. Clusters in light gray indicate time at a carcass site (T_c), all gray clusters (light and dark) indicate handling time (T_h), which includes clusters generated within 12 h of a carcass site visit, blue clusters (T_r) represent other resting sites between kills, that is, clusters generated outside the 12 h cutoff, and single yellow positions indicate time spent moving, or search time (T_s)

independent space–time clusters at each carcass site) within the kill interval and, for YNP, within 21 days of the TOFV.

Search time

Predator search times are often defined as the time period between the abandonment of the first prey and the start of the subsequent kill (Krofel et al., 2012; Merrill et al., 2010). However, this definition includes time when predators may not be actively searching for prey (e.g., they may be resting). Wolves are opportunistic predators and may attempt to kill prey at any time, regardless of time since the previous kill (Mech et al., 2015). Therefore, wolf search time is often subsequently defined as any time a wolf is moving (e.g., Hayes et al., 2000; Merrill et al., 2010). We therefore defined search time (T_s) as any positions within the kill interval that were not within a space–time cluster (i.e., all consecutive positions with a step length >200 m/h), that is, resting periods were excluded from our definition of T_s (Figure 2).

Data analysis

Behavioral mechanisms in Scandinavia

To determine the mechanism behind increased wolf kill intervals in areas where wolves were sympatric with bears, we evaluated the effect of bear density on time spent at carcass sites (T_c) and prey handling (T_h) and search (T_s) times during the den emergence period (March–May) and the moose parturition and immediate postparturition period (May–July). The number of bears on the landscape increased over the den emergence period; mean den emergence date was April 4 (March 6–April 25) for males and April 20 (March 6–June 14) for females (Friebe et al., 2001; Manchi & Swenson, 2005). Therefore, following Tallian, Ordiz, et al. (2017), we tested for an interactive effect of bear presence and Julian date of first visit on wolf behavior (T_c, T_h, and T_s) during spring. This interaction would indicate a change in wolf behavior as the number of bears increased on the landscape. Conversely, an additive effect would indicate a change in wolf behavior across the entire den emergence period. In summer, when all bears were active, we predicted that wolf search time would increase more sharply through time in sympatric areas, as the shared prey (neonate moose) abundance was successively depleted. We therefore also tested for an interactive effect of bear density and median Julian kill-interval date on T_s during summer.

The response variables T_s, T_c, and T_h were defined as the number of hourly positions. Variables in the candidate model sets for T_c and T_h during spring and summer in SCA were as follows (for ranges see Appendix S1: Table S3a,b): bear density, Julian date of first visit, nutritional status, moose density, edible prey biomass (kg), and distance to the nearest road (m). Variables in the candidate model sets for T_s during spring and summer included bear density, median kill interval Julian date, pack size, moose density, and edible prey biomass. We did not examine the effect of nutritional status on search time, as searching occurred over multiple days and nutritional status is a static measurement in time. Instead, we used the edible biomass of the most recent prey as a proxy for hunger. We limited the summer analysis to 15 May to 25 June, the timeframe when studies were conducted in both high and low bear density areas. Because 85% ($N = 66/78$) of summer kills were neonates, we used a categorical variable (neonate/non-neonate) for prey biomass during summer. To assess the relative importance of bear density and moose density on T_c, T_h, and T_s, we compared full models (i.e., including all variables) to models that included either bear or moose density, included neither bear nor moose density, and a null model. We also compared models within those frameworks that included hypothesized interaction terms between time and bear density (Appendix S1: Table S4a,b).

Behavioral mechanisms in Yellowstone

To determine the mechanism behind increased wolf kill intervals when bears were present at wolf-killed ungulates (Tallian, Ordiz, et al., 2017), we evaluated how bear presence at a wolf kill affected the amount of time wolves spent at a carcass site (T_c) and wolf handling time (T_h) during summer in YNP. We also evaluated how bear presence at a wolf kill affected the amount of time wolves spent at a carcass site within 21 days of the first visit (T_{c2}), using a subsample of data in which this information was known. We predicted that the effect of bear presence at a wolf kill would vary with respect to initial kill biomass, and therefore tested for an interactive effect of bear presence and kill biomass on wolf behavior (T_c, T_{c2}, and T_h) during summer.

Variables in the candidate model sets for T_c, T_{c2}, and T_h in YNP included bear presence, Julian date of first visit, nutritional status, pack size, edible prey biomass (kg), wolf sex, and distance to the nearest road (m) (for ranges see Appendix S1: Table S3c). The unit of analysis for the response variable was the number of GPS positions, which was at half-hour intervals in YNP. To test for an interaction between bear presence and kill biomass on T_c and T_h, we limited the analysis to kills with edible biomass <350 kg; bears were observed at all but two kills ($N = 20$) over 350 kg and 65% ($N = 13$) of those carcasses were considered scavenged. Similarly, we limited the T_{c2} analysis to kills with edible biomass <300 kg. To assess the relative importance of bear presence at a carcass site on wolf T_c and T_h, we compared models that included either bear presence, an interaction term with bear presence and prey biomass, or excluded bear presence, with a null model (Appendix S1: Table S4c).

Analyses were conducted in R version 3.6.1 with linear models (LMs) using the "glm" function with a Gaussian link in the *stats* package (R Core Team, 2018), and linear mixed models (LMMs) using the "lmer" function in the *lme4* package version 1.1-21 (Bates et al., 2015). Response variables were square root or log transformed to meet assumptions of normality. In SCA, year and wolf ID were included *a priori* as crossed random effects (one wolf per pack was followed each year), and YNP models included year and wolf ID nested within pack ID as random variables (multiple wolves within a pack were followed each year). We sequentially removed random effects that did not contribute to model fit, that is, the variance of the random effect was 0; note that this resulted in LMs for all SCA model sets. The sample size for the SCA summer dataset was relatively small ($N = 77$), and the null models generally outperformed the more complex *a priori* prediction models (Appendix S1: Table S4b). We therefore used backward stepwise regression using the "step" function in the *stats* package to select final models for the summer SCA dataset only. The correlation coefficients between variables in each model set were all less than 0.6. To control for the potential effect of collar failure on wolf behavior, we included kill-interval collar fix success ($\mathrm{N_{GPS\ positions}}/\mathrm{N_{programed\ locations}}$) as a variable in all models, including null models (Appendix S1: Tables S3, S4). All variables were centered and scaled. Population-averaged fitted values and 95% CIs for graphs were calculated from best-fit models, unless otherwise noted, using the "predict" and "bootMer" functions in *lme4*.

We used an Akaike information criterion (AIC) model selection framework (Burnham & Anderson, 2002) to test our main predictions; the best-fit model had the lowest AIC score, adjusted for small sample size ($\mathrm{AIC_c}$). To determine the relative importance of the effect of bear and interaction terms on wolf behavior, we examined whether they were retained in models that could be considered equivalent (models with a $\Delta\mathrm{AIC_c} < 2$; Burnham & Anderson, 2002). We examined whether 95% confidence intervals (95% CI) overlapped zero to determine whether included variables were "significant," and to interpret the direction of their effects on the respective response variables. We also examined 90% CI when the effect was near significant.

RESULTS

Spring in Scandinavia

Brown bears affected the amount of time wolves spent at a carcass site (T_c) and wolf handling time (T_h), but not search time (T_s) during spring, suggesting that interference competition was the primary competitive mechanism affecting wolf behavior during the bear den emergence period. LMs for spring included 143 observations from 17 wolves within 13 packs over 11 years (Appendix S1: Table S1a). Moose comprised 95% of the 148 kills (five double kills), including 103 juveniles born the previous year (Appendix S1: Table S2a).

Bear density was retained in the top two models for spring T_h (combined $W_i = 0.75$; Appendix S1: Table S4a), showing that T_h was greater in high bear density areas across the entire spring season (Figures 3a, 4a). On the median study date, 4 April, wolves spent an extra 27.2 h handling prey in sympatric areas ($\bar{x} = 54.3$; 95% CI = 45.9, 63.3), compared with allopatric areas ($\bar{x} = 27.1$; 95% CI = 22.4, 32.2). T_h also increased with prey biomass and fix success (Figure 3a; Appendix S1: Table S6a). We found no evidence that nutritional status, distance of the carcass site to the nearest road, or moose density affected T_h; the 95% CIs overlapped 0 (Appendix S1: Tables S4a, S6a). During spring in Scandinavia, wolves made independent visits to carcass sites in sympatric areas almost twice as often as wolves in allopatric areas (Welch's t test; $\bar{x} \pm$ SD: $\bar{x} = 5.0 \pm 2.3$; $\bar{x} = 3.2 \pm 2.4$; $t(115) = -4.7$; $p < 0.001$; Appendix S1: Figure S1a).

Bear density was retained in the two top models for T_c (combined $W_i = 0.76$; Appendix S1: Table S4a), indicating that T_c was also greater in high bear density areas across the entire spring season (Figures 3a, 4a). On the median study date, 4 April, wolves spent an extra 21.9 h at carcass sites in areas where they were sympatric with bears ($\bar{x} = 27.8$; 95% CI = 19.9, 38.9), compared with allopatric ($\bar{x} = 5.9$; 95% CI = 4.5, 7.7). An interaction between bear density and Julian date was retained in the second-best model (Appendix S1: Table S4a), but the 95% CI overlapped 0 (Appendix S1: Tables S4a, S6a), that is, the direction of its effect was not conclusive. T_c also increased with prey biomass, and was unaffected by nutritional status, distance to the nearest road, fix success, and moose density (Appendix S1: Tables S4a, S6a).

Bear density was not retained in the top model for T_s (Appendix S1: Table S4a), suggesting that wolf search

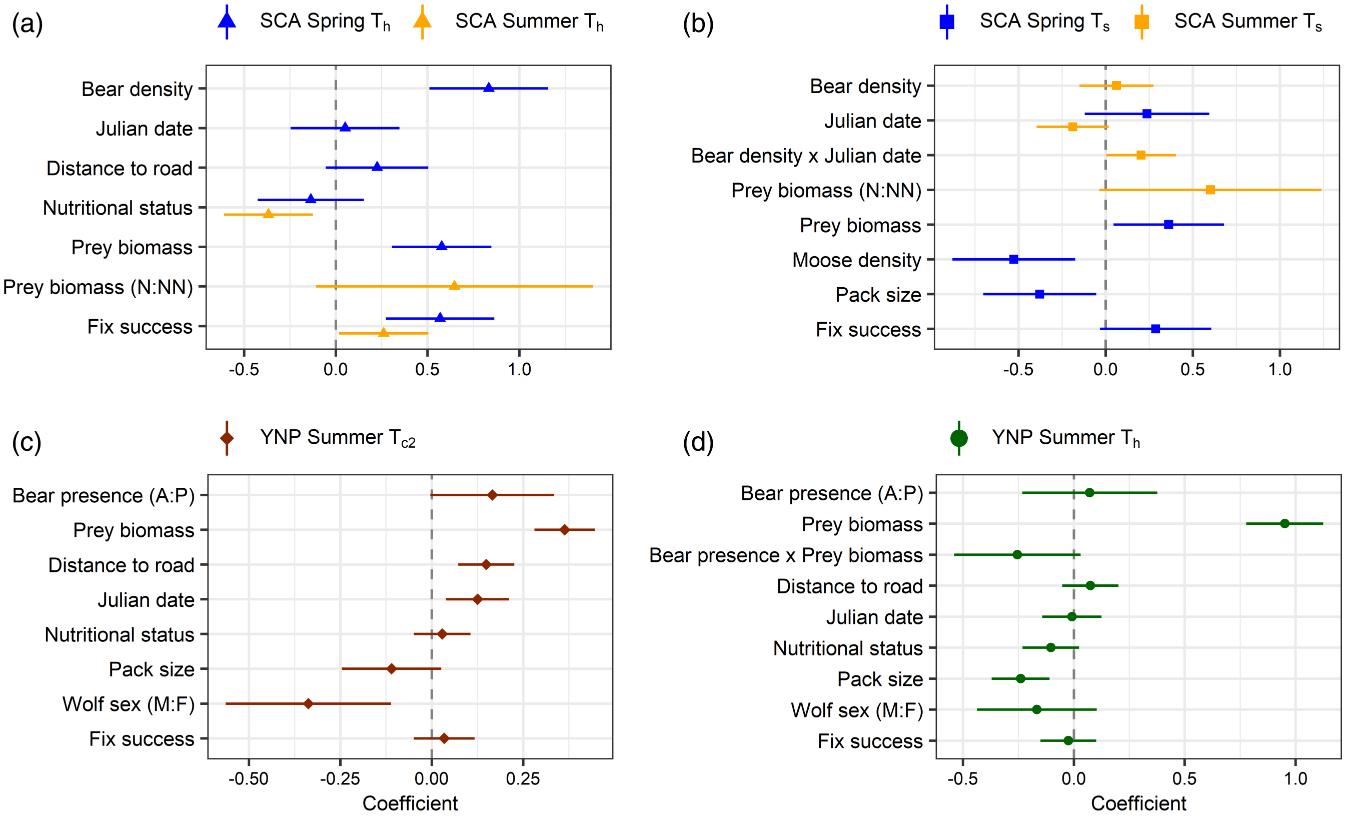

FIGURE 3 Parameter estimates and 95% CI from the top models (Appendix S1: Tables S4–S6) predicting gray wolf: (a) handling time (T_h); (b) search time (T_s) during spring (blue) and summer (orange) in Scandinavia; (c) time spent at a carcass (T_{c2}; brown); and (d) handling time (T_h; green) during summer in Yellowstone. Continuous variables were centered and scaled in all models. For the categorical variables, bear presence (A:P = absent:present) at a kill, prey biomass (N:NN = neonate:non-neonate), and wolf sex (M:F = male:female), the reference group is listed first in parentheses. Response variables for T_h and SCA spring T_s are on a square root scale, SCA summer T_s and YNP summer T_{c2} are on a log scale

time was unaffected by bears during spring (Figure 4b). In the top model, T_s increased with the size of the previous prey, and decreased with pack size and moose density (Figure 3b). There was moderate support that T_s increased with fix success during spring; that is, 90% CIs did not overlap 0 (90% CI = 0.02, 0.56). We found no evidence that median Julian date between kill visits affected T_s; the 95% CIs overlapped 0 (Figure 3b; Appendix S1: Table S6a).

Summer in Scandinavia

Bear density affected wolf search time (T_s), but not time spent at a carcass site (T_c) or handling time (T_h) during summer, suggesting that the primary competitive mechanism driving wolf behavior switched from interference to exploitation competition during the moose parturition period. LMs for spring included 77 observations for 9 wolves within 9 packs over 6 years (Appendix S1: Table S1b). Neonate moose represented 85% ($N = 66$) of the 78 wolf kills (1 double kill) during summer in SCA (Appendix S1: Table S2b). The null model was the top model in two of three model sets for summer (Appendix S1: Table S4b), suggesting that less complex models may be more suitable due to the relatively small sample size compared to spring. We therefore reported the results from the final model using backward stepwise regression. These models performed well ($\Delta\text{AIC}_c = 0$), when compared with the original null and next-best models from the original model sets in Appendix S1: Table S4b (all $\Delta\text{AIC}_c > 2$; Appendix S1: Table S5).

The final model for T_s included an interaction term between bear density and median Julian date between kill visits (Appendix S1: Table S6b), that is, T_s decreased over the summer season in low bear density areas, but stayed relatively constant through time in high bear density areas (Figures 3b, 4d). By 25 June, wolves searched for an additional 7.2 h per kill interval in the sympatric area ($\bar{x} = 12.4$; 95% CI = 5.9, 25.8), compared with the allopatric areas ($\bar{x} = 5.2$; 95% CI = 3.2, 8.6). There was moderate support that T_s increased with the size of the

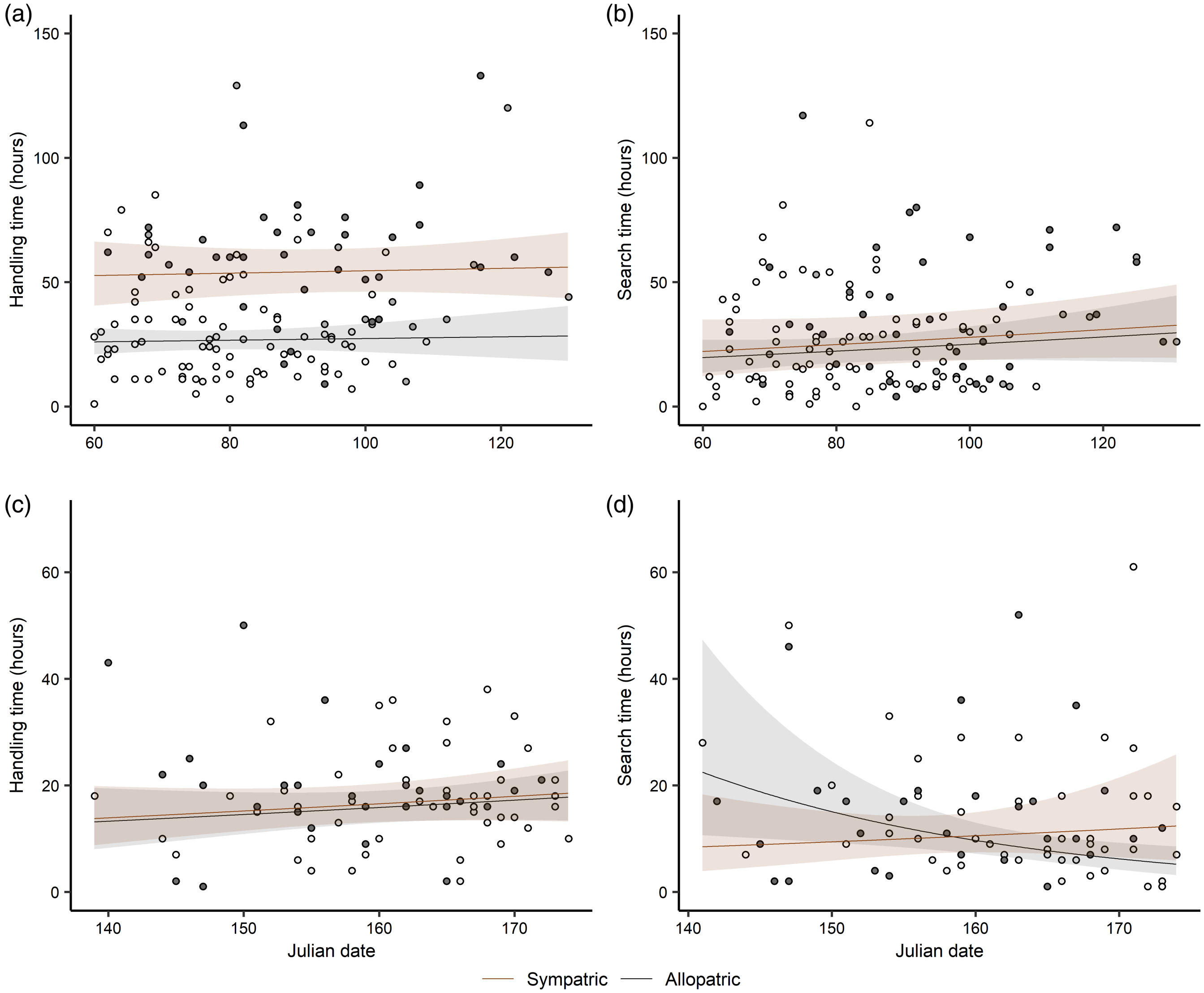

FIGURE 4 The effect of brown bear density during (a, b) spring and (c, d) summer on (a, c) handling time (T_h) and (b, d) search time (T_s) of gray wolves in Scandinavia. Brown and gray lines are population-averaged fitted values with associated 95% confidence intervals representing wolf packs sympatric and allopatric with brown bears, respectively (i.e., bear density was set at the minimum and maximum of the data range). Circles are observed frequencies across the low (white) to high (dark gray) bear density continuum. The top model from the AIC_c model set (a) and the model from the stepwise regression (d) were used to generate population-averaged fitted values, whereas (b) and (c) were generated using the best models that included bear density ($\Delta\text{AIC}_c = 2.08$ and $\Delta\text{AIC}_c = 2.18$, respectively), and are for illustrative purposes only (Appendix S1: Tables S4, S6)

previous prey during summer; the 90% CI did not overlap 0 (90% CI = 0.07, 1.14). We found no evidence that pack size, moose density, or fix success affected summer T_s, that is, they were not retained in the final model (Appendix S1: Table S6b).

Bear density was not retained in the final model for T_h (Appendix S1: Table S6b), suggesting that wolf handling time was unaffected by bears during summer. During summer, T_h decreased with nutritional status and increased with fix success (Figure 3a). There was moderate support that T_h increased with prey biomass (90% CI = 0.01, 1.28). Distance to the nearest road, moose density, and Julian date were not retained in the final model (Appendix S1: Table S6b). There was no difference in the number of carcass site visits made by wolves in allopatric versus sympatric areas ($\bar{x} = 1.8 \pm 1.4$; $\bar{x} = 1.6 \pm 0.8$; $t(83) = 1.0$; $p = 0.30$) during summer in Scandinavia (Appendix S1: Figure S1b).

Bear density was not retained in the final model for T_c (Appendix S1: Table S6b), suggesting that time spent at a carcass site was unaffected by bears during summer. T_c increased with the distance to the nearest road, and there was moderate support that T_c also increased with prey biomass (90% CI = 0.07, 0.99). We found no evidence that moose density affected summer T_c, and nutritional status, fix success, and Julian date were not retained in the final model (Appendix S1: Table S6b).

Summer in Yellowstone

Bear presence at a carcass site affected wolf time at a carcass within 21 days of the first visit (T_{c2}) and wolf handling time (T_h), but not time at a carcass within the kill interval (T_c). LMMs for T_c and T_h during summer in YNP included 808 observations across 23 wolves within 10 packs over 10 years (Appendix S1: Table S1c), and models for the subset of data for T_{c2} included 604 observations across 23 wolves within 10 packs over 10 years. For T_h, the random effect for "year" was removed from all models, because the variance of the random effect was 0. Wolf-killed prey ($N = 662$) comprised 95% of the 695 unique carcasses (23 unique double kills) visited by wolves during summer in YNP (Appendix S1: Table S2c). Elk comprised the majority (79%) of wolf-killed prey, and ungulate neonates (all species) represented approximately 52% of total wolf-killed prey (Appendix S1: Table S2c). The remaining 5% of carcasses visited were considered freshly scavenged ($N = 33$), which were mostly (58%) adult bison (Appendix S1: Table S2c). Bears were detected at 30% ($N = 198$) of the 672 unique carcass sites.

Bear presence at a carcass was included in the top two of three models for T_{c2}, or time spent near a carcass within 21 days of the first visit (combined $W_i = 0.79$; Appendix S1: Table S4c). Wolves spent an extra 0.6 h at the smallest carcasses (3 kg) when bears were present ($\bar{x} = 3.8$; 95% CI = 2.9, 4.8) versus absent ($\bar{x} = 3.2$; 95% CI = 2.6, 4.1), whereas they spent an extra 2 h at the largest carcasses (284 kg) when bears were present ($\bar{x} = 13.1$; 95% CI = 10.1, 17.9) versus absent ($\bar{x} = 11.1$; 95% CI = 7.9, 15.8). The second-best model included an interaction between bear presence and prey biomass (Appendix S1: Table S4c), however, the 90% CI and 95% CI overlapped 0 (Appendix S1: Table S6c). During summer in YNP, T_{c2} increased with prey biomass, Julian date, and the distance to the nearest road, and was lower for females compared with males, whereas the 95% CI for wolf nutritional status, pack size, and fix success overlapped 0 (Figure 3c; Appendix S1: Table S6c). However, for T_c, or time spent near a carcass within the kill interval, bear presence was not retained in the top model (Appendix S1: Table S4c).

The top model for T_h did not include a term for bear density, however, an interaction between bear presence and prey biomass was included in the second-best model ($\Delta AIC_c = 1.08$; Appendix S1: Table S4c) and there was moderate support for the interaction term, that is, the 90% CI did not overlap 0 (90% CI = −0.49, −0.1). T_h increased when bears were present at small kills (i.e., less

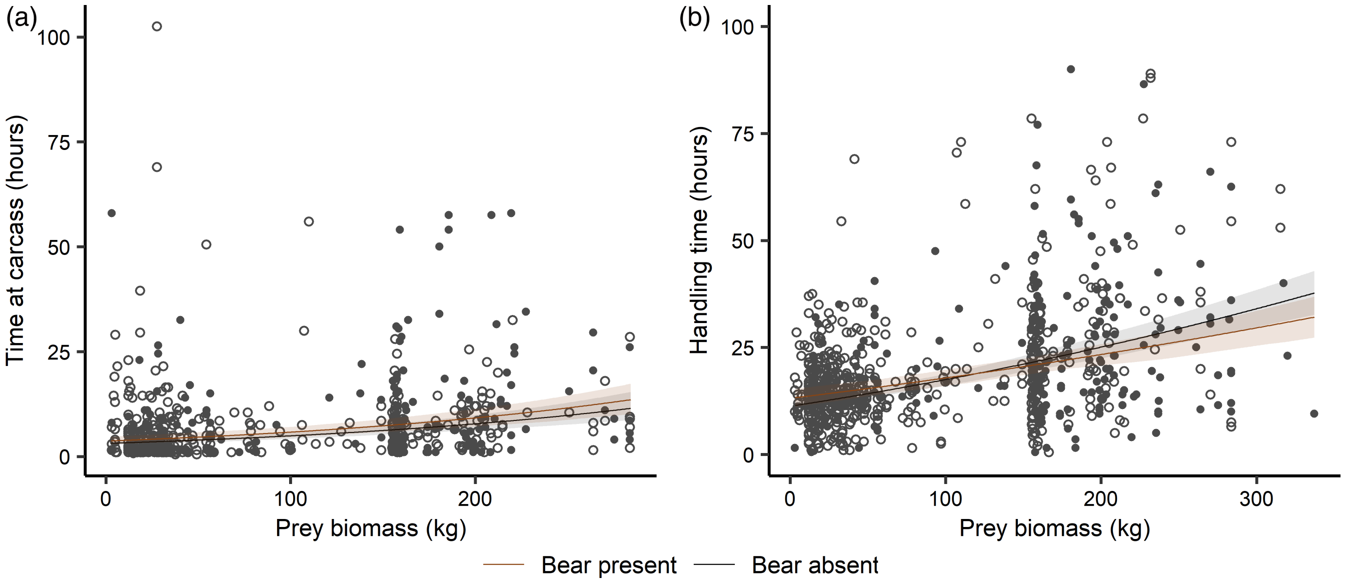

FIGURE 5 The effect of brown bear presence at a wolf kill during summer in Yellowstone with respect to initial edible carcass biomass (kg) on: (a) time spent at a carcass within 21 days of first visit (T_{c2}), and (b) handling time within the kill interval (T_h). Brown and gray lines are population-averaged fitted values with associated 95% confidence intervals representing bear presence or absence at a wolf kill, respectively. Open and closed circles are observed frequencies for bear absence and presence, respectively. Population-averaged fitted values were generated using the top models from the AIC$_c$ model set (Appendix S1: Table S4c) that included bear density (a: $\Delta AIC_c = 0$; b: $\Delta AIC_c = 1.08$)

than ~50 kg), was the same at medium-sized kills (i.e., >more than ~50 kg and <200 kg), and decreased when bears were present at large kills (i.e., more than ~200 kg; Figures 3d, 5). For neonate elk ($\bar{x} = 24.8$ kg), their main neonate prey, T_h increased by approximately 1.5 h when bears were present ($\bar{x} = 14.2$; 95% CI = 12.2, 16.3) versus absent ($\bar{x} = 12.7$; 95% CI = 11.5, 13.9) at the carcass site. For the largest prey (337.2 kg), bear presence ($\bar{x} = 32.1$; 95% CI = 27.3, 36.9) resulted in a 5.7 h lower T_h compared with when bears were absent ($\bar{x} = 37.8$; 95% CI = 32.7, 42.9). T_h also increased with prey biomass and decreased with pack size (Figure 3d). We found no evidence that wolf sex, fix success, Julian date, distance to the nearest road, or nutritional status affected T_h, as the 95% CI for the effects overlapped 0 (Figure 3d).

Within the kill interval in summer, wolves made fewer visits to large kills when bears were present versus absent ($\bar{x} = 4.4 \pm 4.0$ vs. $\bar{x} = 6.5 \pm 5.5$; $t(66) = 2.0$; $p = 0.05$) at the carcass, but there was no difference in the number of visits when bears were present versus absent at medium ($\bar{x} = 4.0 \pm 3.1$; $\bar{x} = 3.4 \pm 2.6$; $t(235) = -1.74$; $p = 0.08$) or small ($\bar{x} = 2.1 \pm 1.9$; $\bar{x} = 2.1 \pm 2.3$; $t(67) = 0.1$; $p = 0.92$) carcasses (Appendix S1: Figure S1c). However, within 21 days of the TOFV, wolves made more visits to medium kills when bears were present versus absent ($\bar{x} = 5.1 \pm 3.7$ vs. $\bar{x} = 4.3 \pm 2.9$; $t(194) = -1.99$; $p = 0.05$) at the carcass, but there was no difference for small ($\bar{x} = 3.2 \pm 4.3$ vs. $\bar{x} = 3.1 \pm 4.3$; $t(65) = -0.21$; $p = 0.84$) and large ($\bar{x} = 6.3 \pm 5.5$ vs. $\bar{x} = 7.3 \pm 4.5$; $t(66) = 0.88$; $p = 0.38$) kills (Appendix S1: Figure S1d).

DISCUSSION

Our results revealed that the competitive mechanisms through which brown bears altered wolf foraging behavior differed across seasons and study systems. During spring in Scandinavia, interference competition was the primary mechanism driving decreased kill rates (i.e., increased kill intervals) for wolves sympatric with bears (Figures 1, 4a,b). During summer in Scandinavia, however, the key behavioral mechanism switched to exploitation competition (i.e., increased search time; Figures 1, 4c,d). In Yellowstone, bear presence at a wolf kill increased the amount of time wolves spent at carcasses, increased handling time with smaller prey, and decreased handling time with larger prey, indicating that interference competition also affected wolf predation dynamics in this system (Figures 1, 5a,b). These results corroborate previous research showing wolf kill rates decrease when they are sympatric with brown bears in Europe and North America (Tallian, Ordiz, et al., 2017) and, more importantly, shed light on the underlying behavioral mechanisms driving interspecific interactions between apex predators.

During spring in Scandinavia, handling time was greater for wolves sympatric with bears (Figure 4a). Our results revealed that wolves spent an extra ~27 h handling prey in sympatric, compared with allopatric, areas, indicating interference competition was the key mechanism during this season. This corresponds with previous research suggesting that wolf kill intervals were approximately 2 days longer by 15 April in sympatric versus allopatric areas in Scandinavia (Tallian, Ordiz, et al., 2017). During late winter and early spring, wolves in Scandinavia primarily prey on juvenile moose born the previous year (Sand et al., 2008), which provide nearly 100 kg of edible biomass (Zimmermann et al., 2015). Accordingly, mean spring moose-calf handling time for wolves in Scandinavia was 50.1 (95% CI = 41.4, 59.7) h, allowing time for interference interactions, for example, time for bears to find, and potentially usurp, carcasses. Indeed, bears were recorded at over half of all wolf kills in sympatric areas, where they generally attended kills individually (Milleret et al., 2018; Ordiz, Milleret, et al., 2020). Extended wolf handling time during spring in sympatric areas may result from wolves lingering at a carcass site to actively defend the kill and/or spending more time attempting to gain access to the kill. Interestingly, wolves left and returned to their kills more often in sympatric areas during spring (Appendix S1: Figure S1a), suggesting that wolves possibly moved away to mitigate direct interactions, rather than defend their kill.

We did not find support for the predicted interactive effect between bear density and Julian date on the handing time of prey, suggesting that competition was relatively steady in sympatric areas over the spring season. This result was not surprising, even though it was opposite of our prediction. Bear den emergence in Scandinavia occurs between March 6 and April 25 ($\bar{x}$ = April 4) for males (Manchi & Swenson, 2005) and March 6 and June 14 ($\bar{x}$ = April 20) for females (Friebe et al., 2001). This implies that at least half of the bear population was already active during the first half of the spring study season (March 1–May 15). Large adult males, followed by lone adult females, emerge first (Manchi & Swenson, 2005), and are typically the most successful at usurping wolf kills (Ballard et al., 2003; Stahler et al., 2020). Less fierce, or less willing, competitors such as subadults and females with newborns (e.g., females with cubs rarely use wolf kills in Scandinavia; Ordiz, Milleret, et al., 2020), emerge later in the spring (Manchi & Swenson, 2005). Therefore, the strongest categories of bear competitors were likely to be active throughout the majority of the spring study season. Furthermore, competition for carcasses is likely to be highest just after den emergence, when bears are food limited (Mattson, 1997). Together, this helps to explain why competition remained steady, rather than increased, during spring in sympatric areas. As predicted, we found no evidence for exploitation competition during early spring (Figure 4b), as bears in Scandinavia rarely prey on moose during this time of year (Dahle et al., 2013).

During summer in Scandinavia, when both bears and wolves prey heavily on neonate moose calves (Ordiz, Milleret, et al., 2020), exploitation competition was the primary mechanism behind decreased wolf kill rates in sympatric areas. Search time decreased throughout summer for wolves allopatric with bears, but remained relatively constant through time for sympatric wolves (Figure 4d), whereas handling time remained unaffected (Figure 4c). Our results suggest that by June 25, wolves spent an extra ~7 h searching per kill interval for prey in the sympatric, compared with the allopatric, areas. Similarly, previous research showed that wolf kill intervals were, on average, 12.1 h longer in sympatric versus allopatric areas during summer in Scandinavia (Tallian, Ordiz, et al., 2017). As with most ungulates, the number of birth events for moose probably follows a normal distribution, for example, increasing until a mid-season peak and then tapering off (Barber-Meyer et al., 2008). Our results suggested that search time for wolves in allopatric areas decreased over the parturition period as the number of neonate moose available on the landscape progressively increased (Figure 4d). However, wolf search time in sympatric areas stayed relatively constant (Figure 4d), suggesting that bears and wolves together successively depleted the supply of shared neonate prey. Bears in Scandinavia prey heavily on neonate moose in their first few weeks of life (Ordiz, Milleret, et al., 2020; Rauset et al., 2012), and bear predation on neonates calves is expected to be additive to wolf predation (Griffin et al., 2011). It is possible that interference competition with bears occurs to some extent during summer in Scandinavia, particularly at larger kills, but we were unable to test for this, as wolves killed few large prey during our summer study periods. Nevertheless, exploitation competition was clearly a key mechanism driving interspecific competition in summer.

During summer in Yellowstone, wolves spent an extra ~0.5 to ~6 h at carcasses when bears were present, suggesting that interference competition also occurred in this system. Correspondingly, kill intervals during summer in Yellowstone increased an average of 7.5 h, or approximately 14% compared with the mean, when bears were present at the previous carcass site (Tallian, Ordiz, et al., 2017). Interestingly, we failed to detect variation in time spent near a kill with bear presence when time was limited to within the kill interval (T_c), which probably reflects the dynamic movement of wolves between carcass sites. For example, when bears were present, wolves in Yellowstone made more visits to medium-sized kills (Appendix S1: Figure S1d), suggesting that bears altered how wolves move between kills of different sizes, a pattern that could not be observed in Scandinavia, where most prey were neonates. This also suggests, unsurprisingly, that the interpretation of animal behavior is context dependent and sensitive to the way in which it is measured. In turn, our analyses, which involved necessarily coarse variables, may have failed to capture all variation in wolf and bear behavior (e.g., bear use of carcasses is also dynamic), particularly the outcome of direct interactions on wolf handling time. Furthermore, we were unable to directly test for exploitation competition during the summer in Yellowstone (i.e., there was no reason to expect bear presence at a kill would affect subsequent search time). However, this is likely to be an important mechanism driving competition in this system, in which both wolves and bears prey on neonate ungulates (Barber-Meyer et al., 2008; Fortin et al., 2013; Metz et al., 2012), and bear predation on neonates is generally additive to wolf predation (Griffin et al., 2011).

There was moderate evidence that bears affected wolf handling time in Yellowstone, with the direction of the effect opposite of our initial prediction. Wolf handling time increased with smaller prey (i.e., less than ~50 kg), but decreased with larger prey (i.e., more than ~200 kg), when bears were present at carcasses in Yellowstone (Figures 1, 5b). Almost 52% of wolf-killed prey during summer in Yellowstone weighed <50 kg, thus, increased handling time when bears were present at smaller prey may have contributed to observed extended kill intervals (Tallian, Ordiz, et al., 2017). Handling time remained constant at medium-sized carcasses and decreased with bear presence at larger carcasses (e.g., more than ~200 kg), which comprised a smaller proportion of total wolf kills (9%). Although this result is counterintuitive, several mechanisms might explain it. First, Yellowstone's Northern Range supports a relatively high density of brown bears (maximum ~13 bears per 100 km^2; Bjornlie et al., 2014). Bears have been observed at over half of all adult-ungulate wolf kills during summer in Yellowstone, where multiple bears often compete simultaneously for access (Stahler et al., 2020). Second, the number of brown bears present at a carcass increases with carcass size (van Manen et al., 2017), which may create a competitive tipping point for which it is advantageous for wolves to defend, or vie for access to, smaller kills, but not larger ones. In other words, multiple bears may be able to fully usurp a carcass from wolves, causing them to abandon their kill sooner than they would have otherwise. This could explain why handling time decreased within the kill interval for larger prey (Figure 5b) and why wolves made fewer visits to larger carcasses (Appendix S1: Figure S1c) when bears were present at a kill in Yellowstone.

Multiple other factors influenced wolf handling and search time in Scandinavia and handling time in Yellowstone. Consistent with results from other predator–prey systems (e.g., Cristescu et al., 2014; Elbroch et al., 2014), handling time increased with edible prey biomass across studies and seasons (Figure 3), suggesting that wolves remained longer at larger kills to exploit the resource. Handling time decreased when wolves were in better immediate nutritional condition, that is, less hungry, during summer in Scandinavia, but not during spring. This implies that wolves in worse immediate nutritional condition spent more time at kills during a potentially more food-limited time of year, summer (Metz et al., 2012). During summer in Yellowstone, handling time also decreased with pack size (Figure 3c), which is intuitive, as a greater number of animals consume prey more quickly. However, this result should be interpreted with caution, as packs are less cohesive during summer (Metz et al., 2011), and pack size may not necessarily represent pack use of kills.

In Scandinavia, search time decreased with increasing moose density during spring, but not summer, and moose density was not important for handling time in either season. The result related to spring search time is intuitive, as prey density alters encounter rates (Martin et al., 2018), subsequently affecting predator kill rate (Holling, 1966). It is possible that moose density affected search time during summer as well, but we were unable to detect this, possibly due to the small sample size. In both systems, handling time and/or time spent near a kill site increased as the distance of the carcass site to the closest road increased during summer (Appendix S1: Table S6), suggesting that human disturbance probably limits wolf foraging ability, particularly during this period. This is important, as anthropogenic disturbance may increase predation pressure if predators cannot efficiently use their kills (J. A. Smith et al., 2015, 2017), ultimately shaping the role of large carnivores on ecosystem function (Ordiz, Bischof, et al., 2013; Ordiz et al., 2021).

Search time during spring in Scandinavia was also affected by pack size. Larger packs spent less time searching for prey during spring (Figure 3b), possibly because they were better able to locate and/or take down large prey than could smaller packs (MacNulty et al., 2012, 2014). This result should also be interpreted with caution, however, as pack size could also affect an individual's moving time (our definition of search time) for reasons other than increased prey search and capture efficiency. Search time also increased with the amount of edible biomass available from their most recent kill in both seasons in Scandinavia (Figure 3b). This is likely to be indicative of immediate wolf nutritional status, which we were unable to include as a control variable here, as searching occurred over multiple days, whereas nutritional status was a static measurement in time.

It is well known that wolves facilitate feeding opportunities for scavengers, including bears (Ordiz, Krofel, et al., 2020; Stahler et al., 2020; Wikenros et al., 2013; Wilmers et al., 2003), although wolves may also be antagonistic to bears by decreasing prey availability (Barber-Meyer et al., 2008; Griffin et al., 2011). However, in wolf–bear–ungulate systems, bears are seemingly only antagonistic to wolves, as they decrease the abundance of shared neonate ungulate prey and usurp wolf-killed carcasses (Ballard et al., 2003; Griffin et al., 2011). Indeed, competition over food resources may help to explain why wolves took longer to establish in high bear density areas during recolonization in Scandinavia (Ordiz et al., 2015; Sanz-Perez et al., 2018), and the subsequent within-home range spatial segregation between the species once wolves established (Milleret et al., 2018). The antagonistic relationship of bears to wolves may partly explain why fatal interactions are seemingly unidirectional, that is, wolves are more likely to kill bears than vice versa (Stahler et al., 2020).

Historically, wolves and brown bears were sympatric across the majority of the Northern Hemisphere (Ordiz, Krofel, et al., 2020). As apex predators and obligate carnivores, wolves exert top-down pressure within ecosystems (Ordiz, Bischof, et al., 2013). Bears are typically considered an omnivore, yet they are also efficient predators and scavengers (Ordiz, Krofel, et al., 2020) that can alter wolf predatory behavior via multiple pathways. It is likely that a combination of interference and exploitation competition between these two species was once an important structuring force across northern latitudes, and the strength of these mechanisms was likely context dependent. For example, interference competition may be relaxed in systems, seasons, or years where high-quality alternative bear foods are more abundant (Stahler et al., 2020). Although still sympatric throughout much of their range today, both species have undergone range contractions, leaving wolf and bear populations that persist independently of one another (Ripple et al., 2014). Allopatry may result in a competitive release for wolves, a decrease in temporally stable high-protein food sources for bears, and altered predator–prey dynamics and top-down forcing.

Clarifying the mechanisms that drive broad patterns in predator foraging behavior is critical for understanding and predicting the consequences of multipredator effects on predator–prey dynamics and ecosystem function

(Glen & Dickman, 2005). Nevertheless, discerning underlying mechanisms driving large-scale ecological patterns often requires long-term, intensive research (e.g., Grace et al., 2016), which is particularly challenging for low-density, elusive species that are expensive to monitor, such as large carnivores. Although our study examined relatively coarse variables across large study areas, the uniquely long-term and large-scale monitoring of wolves and bears in two transcontinental study systems allowed us to uncover the behavioral mechanisms driving competition between two apex predators. Our study of competition between bears and wolves may be extrapolated to the large realm inhabited by both species across the Northern Hemisphere (Ordiz, Krofel, et al., 2020). It is also a case study of processes that probably occur elsewhere, that is, a combination of interference and exploitative competition between coexisting predators is likely to be a structuring force in many ecosystems.

Yet, the nature of competition between apex predators, and the corresponding top-down effect, is system and context dependent (Haswell et al., 2017). In general, the direction and magnitude of exploitation competition is driven by the type and abundance of prey species, as well as the relative abundance and comparative foraging efficiency of the competing predator (Caro & Stoner, 2003). Conversely, the mechanisms driving interference competition include the suite and abundance of predators in an ecosystem, and the array and density of available prey (Caro & Stoner, 2003; Rosenzweig, 1966). Variation in prey species type and availability is a particularly important driver of competition. Spotted hyena (*Crocuta crocuta*) in Ngorongoro Crater, for example, responded to changes in prey species availability, in part, by stealing kills from lions (*Panthera leo*) more often (Höner et al., 2002). Differences in prey guild composition can even lead to a reversal of "typical" competitive roles. For example, in coastal systems in Alaska where ungulate abundance is low, bears provide the subsidies and wolves are kleptoparasitic, that is, wolves steal salmon (*Oncorhynchus* spp.) from bears (T. S. Smith et al., 2004).

The outcome of interspecific interactions also depends on the relative rank of the predators within the "intraguild dominance hierarchy" (Groom et al., 2017), which is driven in part by competitors relative body size and social structure. In the African savannah, wild dog (*Lycaon pictus*), cheetah (*Acinonyx jubatus*), and leopard (*Panthera pardus*) prematurely abandon their kills when larger-bodied, social predators, such as lion and/or hyena, are present (Balme et al., 2017; Fanshawe & Fitzgibbon, 1993; Hunter et al., 2007). In northern systems, bear presence causes mountain lions (*Puma concolor*) and Eurasian lynx (*Lynx lynx*) to abandon their kills (Allen et al., 2021; Elbroch et al., 2014; Engebretsen et al., 2021; Krofel et al., 2012), and wolves similarly displace mountain lions from kill sites (Ruth et al., 2019). Premature abandonment, versus lingering at the site to defend or gain access to the kill, resulted in decreased handling time and increased kill rates for the above subordinate predators. However, competitors closer together in the dominance hierarchy may be more willing to linger and defend, or vie for access to, kills.

The probability a predator will compete for access is driven by the relative cost of carcass defense (e.g., energy expenditure and potential risk of injury or death) versus abandonment (e.g., energy expenditure and associated risk to successfully kill another prey), combined with the potential for reward (e.g., the likelihood of success and amount of food available). Social carnivores have a competitive advantage when defending kills, that is, larger groups mean increased potential for reward, or access to kill biomass (Carbone et al., 1997; Cooper, 1991; Stahler et al., 2020; Wilmers et al., 2003). Indeed, even smaller and generally subordinate wild dogs are better able to defend their kills from hyena when their relative group size is larger (Fanshawe & Fitzgibbon, 1993). Kleptoparasitism occurs in both directions between lions and hyenas, who are more equally matched; although lions are generally more successful at carcass defense, neither species consistently dominates the other (Périquet et al., 2015). Similarly, while brown bears are often able to dominate carcasses, the outcome of interactions between wolves and bears varies based on the demographics and number of individuals involved (Ballard et al., 2003; Stahler et al., 2020). Our results suggest that interactions at kills sites between more closely matched competitors are protracted, rather than cut short, probably because the potential for reward is greater. This is important for predator–prey dynamics, as the probability that predators will defend, or attempt to gain access to, their kill is a key driver of predator handling time and subsequent kill rates (Allen et al., 2021; Elbroch et al., 2014; Tallian, Ordiz, et al., 2017).

Our study illustrates how interspecific interactions can manifest at the population level with competing apex predators, influencing predation dynamics (Tallian, Ordiz, et al., 2017), species distribution (Ordiz et al., 2015), and habitat selection (Milleret et al., 2018). This has been observed across taxa and in a wide array of ecosystems. For example, interspecific interactions affect the space use and distribution of competing raptors (Martínez et al., 2008), sharks (Sabando et al., 2020), seals (Jones et al., 2015), and African savannah carnivores (Creel & Creel, 1996; Durant, 1998). In turn, competition among predators, and the resulting niche differentiation, affects both the population dynamics of their prey (Sinclair et al., 2003) and the demography and behavior of the subordinate competitor (Groom et al., 2017). Importantly, competition among predators, including interactions such as kleptoparasitism, can also stabilize ecosystem dynamics (Focardi et al., 2017). Complete assemblages of large carnivores and scavenger communities have been linked to ecological resilience and are therefore a conservation priority of global significance (Dalerum, 2013; Sebastian-Gonzalez et al., 2019). Therefore, a further understanding of the processes and mechanisms driving interactions between large carnivores in different ecosystems is important for facilitating their long-term management, conservation, and ecological function (Ordiz et al., 2021).

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CONFLICT OF INTEREST

We have no competing interests.

AUTHOR CONTRIBUTIONS

All authors helped conceived of the study and participated in data collection; Aimee Tallian carried out statistical analysis; Andrés Ordiz and Aimee Tallian wrote the manuscript; Barbara Zimmermann, Camilla Wikenros, Håkan Sand, Jonas Kindberg, Jon E. Swenson, and Petter Wabakken coordinated the long-term study in Scandinavia; Douglas W. Smith, Daniel R. Stahler, and Matthew C. Metz coordinated the long-term study in Yellowstone National Park. All authors helped draft the manuscript and gave final approval for publication.

DATA AVAILABILITY STATEMENT

Data (Tallian et al., 2021) are available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.dz08kprzb.

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SUPPORTING INFORMATION

Additional supporting information may be found in the online version of the article at the publisher’s website.

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