Prey size mediates interference competition and predation dynamics in a large carnivore community

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Direct competition for resources is especially fierce among predators, leading to disproportionately strong effects on fitness and functional roles. These competitive effects are exacerbated in complex predator guilds with dominance hierarchies that have clear winners and losers. The direct costs of losing these competitions are well understood, but the drivers of such interactions, and their indirect effects on prey, are not. We evaluate the drivers of interference competition for cougars, and how such competition affects cougar-prey dynamics, by leveraging 23 years of cougar predation data from Yellowstone National Park, USA. We show that the effect of prey size is context-dependent, negatively affecting how often cougars kill ungulate prey but positively affecting how often wolves/bears find and steal cougar kills. Further, cougars increasingly kill smaller prey as larger, primary prey density decreases. Handling time is shorter for smaller prey, leading to less kleptoparasitism by wolves and bears when primary prey density is lower. Our study counters the theory suggesting that interference competition should increase at kills when prey density declines, interspecific competitor density increases, or kill rates increase. We demonstrate that predator, competitor, and prey traits drive the strength of and even dampen interference competition, possibly increasing coexistence in complex communities.

Competition for resources fundamentally structures predator guilds. Interference competition (also referred to as "interference") should alter a predator's handling time of a carcass through kleptoparasitism (e.g. inter- and intraspecific food stealing)[1], while exploitation competition should alter the search time it takes a predator to find its next meal through reducing prey populations consumed by multiple predators[1,2]. Primary mediators of competition are the dietary overlap of competitors and the density of sympatric predator and prey species[3]. The effects of prey density on competition in predator guilds theoretically depend on the feeding strategies of competing predators[3].

If competition occurs primarily over live prey, then an increase in prey density should reduce both exploitation and interference competition because food becomes less limiting. However, if competition occurs primarily through kleptoparasitism of carcasses/carrion (common when prey are difficult and/or dangerous to hunt[3]), competition dynamics that are counterintuitive to traditional theory may arise. For example, subordinate African wild dogs (*Lycaon pictus*) experienced more severe interference competition from dominant lions (*Panthera leo*) and spotted hyenas (*Crocuta crocuta*) at higher rather than lower prey densities, even though exploitation competition expectedly declined[3]. Higher prey densities supported more lions and hyenas that subsequently found and stole more wild dog kills, leading to competitive exclusion and even local extinction of wild dog populations in areas of high prey density, but stable wild dog populations in areas of lower prey density[3]. As prey density increases, subordinate predator kill rates may also increase, resulting in more carcasses on the landscape and hence more opportunities for kleptoparasitism. In these cases, other factors like carcass size may drive interference competition more predictably than prey density. Finally, an increase in the dietary overlap or

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density of competing predators should lead to higher rates of interference competition. However, the costs and benefits of interference to competing predators and their prey are more nuanced.

Community outcomes from interference competition depend on a suite of factors, including the dominance status of involved predators[4]. A subordinate predator incurs greater kleptoparasitic costs from interference competition than does a dominant predator[3–5]. Costs may include increased energy expenditure, lower survival, and reduced fitness for subordinate predators, but potentially opposite effects for dominant predators[6–8]. Quantifying whether these interactions then lead to synergistic (i.e., greater combined)[9] or antagonistic (i.e., smaller combined)[10] effects on prey populations is central to the mechanistic understanding of predator-prey ecology and conservation of diverse ecological communities[11,12].

Synergistic or antagonistic effects on prey may arise through competition-induced shifts in predator densities and/or kill rates of prey (number of prey killed per predator per unit time), both key contributors to predation rate (proportion of prey population killed by predators). In asymmetrical competitive interactions, kleptoparasitism may reduce prey abundance by supporting dominant predators at higher densities through resource facilitation while simultaneously causing subordinate predators to abandon kills earlier and increase their kill rates of prey to compensate for lost food[13]. This outcome may be more likely if the subordinate predator has high hunting success and/or direct encounters with dominant predators pose a major safety risk. Alternatively, interference at kills may have little effect or even reduce predator impacts on prey if interference primarily occurs at scavenged carcasses, competition is more symmetrical between predators, direct interactions are often lethal for subordinate predators, or the involved predators hunt formidable prey or are relatively poor hunters[14].

We used 23 years of cougar (*Puma concolor*) predation data collected during three periods (1987–1994, 1998–2005, 2016–2022) in Yellowstone National Park, USA (YNP) to evaluate how interference competition by dominant predators (wolves and bears) shapes subordinate predator-prey dynamics. Large carnivore populations in northern Yellowstone have mostly increased since the mid-1980s. After wolf (*Canis lupus*) and cougar extirpation in the 1920s, cougars recolonized YNP in the early 1980s, and 41 wolves were reintroduced from 1995 to 1997[15]. Grizzly bears (*Ursus arctos horribilis*) and black bears (*Ursus americanus)* were never extirpated from YNP, but they experienced population declines in the mid-1900s followed by increases during our study[16–18]. YNP now has some of the highest densities (~32 individuals per 100 km²) and diversity of large carnivores in North America[19], which nonetheless vary in their densities across years. This carnivore community relies on multiple prey species; elk (*Cervus canadensis*) are historically the most common but their population has declined in recent decades, leading to increased use of alternative prey, such as deer [primarily mule deer (*Odocoileus hemionus*), but also white-tailed deer (*Odocoileus virginianus*)] and bison (*Bison bison*), by predators[20]. This diverse predator–prey community provides an exemplary system to test how interference competition via kleptoparasitism influences predator-prey dynamics for the subordinate, but most lethal, predator.

Our first aim was to estimate cougar predation metrics (see Fig. 1a) and the prevalence of interference by wolves/bears at cougar kills from 2016 to 2022 to examine how such dynamics have changed since 1987–1994 and 1998–2005. Our second aim was to determine how well prey/carcass size, dominant competitor density, and landscape characteristics predicted interference at cougar kills. Our final aim was to evaluate how prey size, interference competition, and a suite of landscape and biological factors influenced shorter-term (handling time, search time, and kill interval) and longer-term (kill rate and biomass acquisition rate) cougar predation dynamics. See Fig. 1b for a list of predictor and response variables included in each model, along with predicted effects.

We hypothesized that competitor presence at cougar kills would vary seasonally, with bears being the primary competitor detected at kills in summer[1], and wolves the primary competitor detected in winter. When dominant wolves/bears displaced subordinate cougars from their kills

(interference competition), we predicted that cougar handling times and immediate access to food would decline, leading to shorter inter-kill intervals (time between consecutive kills). This may lead to significant increases in long-term cougar kill rates and biomass acquisition rates (kg of prey acquired per predator per unit time) if displacement by wolves/bears is common. However, if displacement is uncommon, the short-term effects of interference competition may dissipate, and long-term effects on kill rate may be insignificant. Based on classic competition theory, interference and exploitation competition at cougar kills should increase from 1987–1994 to 2016–2022 as predator densities have largely increased and elk (the primary prey) densities have decreased through time. Yet, since interference competition is assumed to occur primarily over carcasses/carrion in this system, the typical negative relationship between prey density and interference may not hold. Instead, carcass size and predator densities may be more important in predicting interference competition and its associated costs. We predict that cougars are more likely to be displaced from larger, more conspicuous kills, which may produce counterintuitive rates of kleptoparasitism across research periods according to traditional theory centered on prey, and to a lesser degree, predator densities. For instance, if the size of cougar-killed prey were to decline through time, interference competition could similarly decline even as predator densities increase and prey densities decrease, contrary to current theory-driven expectations.

Our findings support this hypothesis. Carcass size was the most important predictor of not only wolf/bear interference at cougar kills, but also cougar kill rates and biomass acquisition rates of prey. This demonstrates how interspecific competition can manifest through complex mechanisms that in turn cause diverse effects on predator-prey dynamics. Although these dynamics are challenging to disentangle, especially in apex predator guilds, doing so is fundamental to understanding ecosystem structure and function[19,21–24].
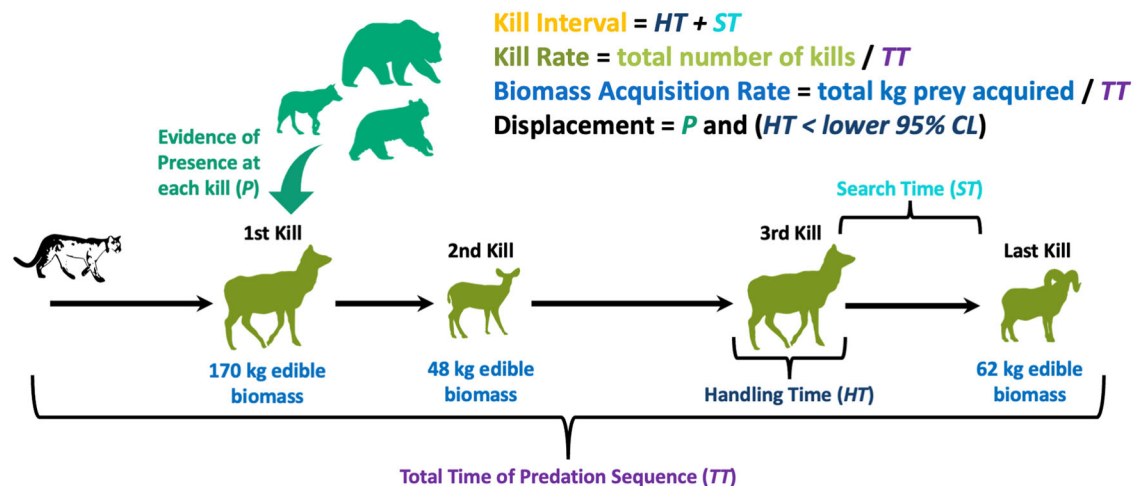
Results
Predation monitoring
From 2016 to 2022, we monitored cougar predation for 1888 days and searched 1393 GPS (Global Positioning System)-location clusters (hereafter, "clusters") from 46 predation sequences (see Fig. 1a) in three distinct seasons for 7 female and 6 male cougars. Early winter monitoring (EW, mid-November to mid-December, $n = 14$) averaged 31.9 (2.9 SD) days, late winter (LW, March, $n = 20$) averaged 34.1 (13.4 SD) days, and spring-summer (SS, early-May to mid-July, $n = 12$) averaged 63.4 (12.4 SD) days (Fig. S1). These periods indicated distinct shifts in predation ecology. Spring-summer overlapped with ungulate birth pulses, leading to an influx of vulnerable neonatal prey, while early winter and late winter typically represented periods of good and poor prey conditions, respectively[25]. We documented 403 feeding events: 380 were cougar kills (350 ungulates, 30 non-ungulates; Fig. S2), 14 were scavenges of other cougar kills, six were scavenges of non-predated ungulates, one was a scavenge of a bear kill, and one was unknown.

Prey killed during 2016–2022 were smaller on average than prey killed during 1987–1994 and 1998–2005. Of the 380 cougar kills documented during 2016–2022, 49.5% were elk; 37.6% were deer; 5% were other ungulates including pronghorn, bighorn sheep, and mountain goat; and 7.9% were non-ungulate prey including yellow-bellied marmot (*Marmota flaviventris*), coyote (*Canis latrans*), red fox (*Vulpes vulpes*), porcupine (*Erethizon dorsatum*), beaver (*Castor canadensis*), grouse (*Dendragapus obscurus* and *Bonasa umbellus*), and cougar (Fig. 2a). During 1987–1994 and 1998–2005, cougars killed more elk (60.3% and 74.2% respectively[26]) and fewer deer (18.3% and 13.8% respectively[26]) than during 2016–2022 (Fig. 2a). Cougars also killed proportionally more elk calves than adult elk during 2016–2022 than in 1987–1994 and 1998–2005 (Fig. 2b).

Components of predation
Handling time [mean (median) ± SE] of cougar-killed ungulates ($n = 350$) was 2.54 (2.0) ± 0.11 days, while search time ($n = 304$) was 2.94 (1.96) ± 0.17 days (Table 1). Ungulate kill interval ($n = 303$) was 5.37

a) Example predation sequence

Kill Interval = *HT* + *ST*
Kill Rate = total number of kills / *TT*
Biomass Acquisition Rate = total kg prey acquired / *TT*
Displacement = *P* and (*HT < lower 95% CL*)

Evidence of Presence at each kill (*P*)

1st Kill — 2nd Kill — 3rd Kill — Last Kill

Search Time (*ST*)

170 kg edible biomass
48 kg edible biomass
62 kg edible biomass

Handling Time (*HT*)

Total Time of Predation Sequence (*TT*)

b) Hypothesized effects of model covariates on each response

Handling Time	
Covariate	**Effect**
% Tree Cover	+
Roughness	+
Edible Prey Biomass	+
Wolf Use	–
Bear Density	–
Field Metabolic Rate	–
Wolf/Bear Presence	–
Displaced Prior Kill	–

Search Time	
Covariate	**Effect**
% Tree Cover	+
Roughness	+
Season (Early Winter)	++
Season (Late Winter)	+
Wolf Use	+
Bear Density	+
Field Metabolic Rate	–
Displaced Prior Kill	–

Kill Interval	
Covariate	**Effect**
% Tree Cover	+
Roughness	+
Edible Prey Biomass	+
Wolf Use	–
Bear Density	–
Field Metabolic Rate	–
Season (Early Winter)	++
Season (Late Winter)	+
Displaced	–

Kill Rate	
Covariate	**Effect**
Season (Early Winter)	– –
Season (Late Winter)	–
Average Prey Size	–
Field Metabolic Rate	+
Prop. Kills Displaced	+

Biomass Acquisition Rate	
Covariate	**Effect**
Season (Early Winter)	+
Season (Late Winter)	++
Average Prey Size	+
Field Metabolic Rate	+
Prop. Kills Displaced	–

Competitor Presence/ Displacement	
Covariate	**Effect**
% Tree Cover	–
Roughness	–
Live Prey Biomass	+
Wolf + Bear Density	+

Fig. 1 | Data collected while monitoring cougar predation and hypothesized effects of covariates on cougar predation and competition dynamics.
a Illustration of a predation sequence with estimated parameters for a GPS-collared cougar in Yellowstone, USA and **b** tables showing each model with the hypothesized effects of included covariates on response variables. Table headings represent the response variable of interest. Bear and wolf-specific presence/displacement models were also evaluated and included in Fig. S3, in which case "Wolf + Bear Density" was replaced with "Wolf Use" in wolf models and "Black Bear Density" and "Grizzly Bear Density" in bear models. For "Season," the reference category is Spring-Summer. "Field Metabolic Rate" refers to the monitored cougar. Cougar PhyloPic by @fblpalmeira (link to license), mule deer and bighorn sheep PhyloPics by *Gabriela Palomo-Munoz* (link to license).

(4.21) ± 0.23 days per ungulate kill during 2016–2022, significantly shorter than during 1987–1994 [7.9 (8.0) ± 0.8] or 1998–2005 [7.0 (6.0) ± 0.4], possibly due to cougars killing smaller, non-elk prey during 2016–2022[26]. Also, during 2016–2022, kill interval when cougars were displaced [4.08 (3.02) ± 0.46 days per ungulate kill] was significantly lower ($t_{79.04} = 2.91$, $P = 0.0046$) than when cougars were not displaced [5.61 (4.67) ± 0.25 days per ungulate kill]. From 2016–2022, cougars killed ungulates at a rate of 5.37 (5.1) ± 0.28 ungulates per 30 days, including elk at 2.75 (2.63) ± 0.23 per 30 days and deer at 2.39 (1.99) ± 0.24 per 30 days (Fig. 3a). Cougars acquired mostly ungulate prey, with elk as the dominant source of prey biomass acquisition across all seasons (Fig. 3b).

Competitor presence and displacements

We surveyed cougar kills for evidence (e.g. signs such as tracks, scat, hair) of competitors. Fifty (14.3%) cougar kills had only bear sign, 22 (6.3%) had only wolf sign, six (1.7%) had both wolf and bear sign, and 272 (77.7%) had no predator sign. Bears displaced cougars from their kills twice as often as wolves did (10.5% versus 5.1%; Table 1). Wolf/bear presence and displacements varied seasonally as predicted, with bears almost exclusively finding kills during spring-summer and wolves interfering at cougar kills year-round but peaking in winter (Table 1). Wolf/bear interference competition changed between the different phases of cougar research (Fig. 4b, Table 1). Bear presence at cougar kills was similar in 1987–1994 and

Fig. 2 | Variation in cougar prey composition by research phase. Barplots showing (**a**) the composition of cougar-killed prey and (**b**) the demographic composition of cougar-killed elk during 1987–1994 (n = 312 kills, n_{elk} = 188 kills), 1998–2005 (n = 465 kills, n_{elk} = 345 kills), and 2016–2022 (n = 380 kills, n_{elk} = 188 kills). "Deer" includes predominantly mule deer, but also white-tailed deer. "Other Ungulate" includes pronghorn, bighorn sheep, mountain goat, and moose. "Non-Ungulate" includes yellow-bellied marmot, coyote, red fox, porcupine, beaver, grouse, and cougar.
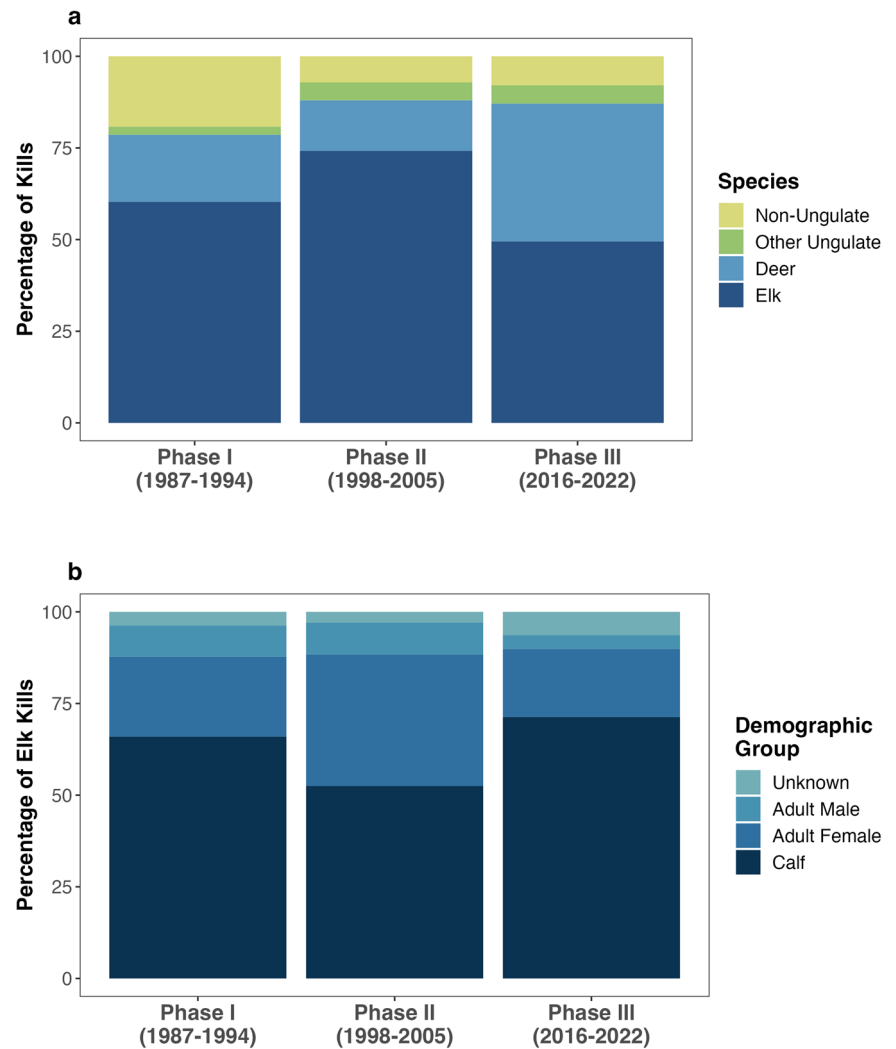
2016–2022 but was 48% higher in 1998–2005. Wolf interference competition was 47% higher in 1998–2005 than in 2016–2022. Due to the possibility that wolves/bears visited cougar kills without leaving behind evidence of their presence, these represent minimum estimates of competitor presence/displacement. Still, it is unlikely that wolves/bears that displaced a cougar or spent considerable time at a kill would have left no signs behind because of their distinct feeding behavior and propensity as dominant competitors to mark and defend resources from other competitors.

Based on handling time and carcass use, cougars lost access to a substantial amount of biomass to wolves/bears when a displacement occurred. For kills where no displacement occurred, cougars acquired an estimated 96.7 (100) ± 0.7% of edible biomass, leaving only 2.7 (0) ± 0.6 kg unacquired (n = 300). However, acquired biomass declined 2.62-fold when a cougar was displaced from a kill, as they only acquired an estimated 36.9 (28.8) ± 3.4% of edible biomass, leaving 43 (31.1) ± 5.5 kg unacquired on average (n = 50).

Factors affecting interference competition and predation dynamics

The odds of competitor (wolf/bear) presence at cougar kills increased significantly as live prey biomass (i.e., carcass size in kg) and competitor density increased (Table S3.1, Table S3.2, and Fig. S3). Percent tree cover (cover) had a near significant positive effect (β = 1.31, P = 0.052, CI: 0.99–1.73), while roughness had a negative effect (β = 0.57, P = 0.0004, CI: 0.42–0.77), on the odds of competitor presence. Live prey biomass and competitor density also had significant positive effects on the probability of displacement by wolves or bears (Fig. 5). For every 1 SD increase in prey biomass, the odds of

displacement by wolves or bears increased 1.67-fold (CI: 1.24–2.27). Competitor density led to a 2.37-fold (CI: 1.71–3.34) increase in the odds of displacement. Cover was not an important predictor of wolf/bear kleptoparasitism of cougar kills. Roughness decreased the odds of displacement by competitors (β = 0.66, CI: 0.46–0.93; Fig. 5). As we hypothesized, prey biomass increased the presence of both wolves and bears at cougar kills, as well as their odds of displacing cougars.

Responses for the handling-time, search-time, kill-interval, kill-rate, and biomass-acquisition-rate models were all log-transformed. The following β estimates are represented on the log scale. As hypothesized, edible prey biomass (i.e., kg of edible carcass) was the strongest predictor of cougar handling time of prey (β = 0.42, CI: 0.33–0.52, P < 0.00001; Fig. 6a). Aligning with predictions, both bear density (β = −0.16, CI: −0.26 to −0.06, P = 0.002) and cougar field metabolic rate (FMR; β = −0.1, CI: −0.19 to −0.003, P = 0.049) had significant negative effects on cougar handling time (Fig. 6a). The presence of wolves or bears at a cougar kill led to a near significant decline in handling time (β = −0.2, CI: −0.43–0.03, P = 0.09; Fig. 6a). Neither cover (β = 0.05, P = 0.31) nor roughness (β = 0.11, P = 0.12) were important predictors of handling time.

There was no effect of kill displacement on search time of the subsequent kill. Surprisingly, only wolf use (β = 0.2, CI: 0.04–0.35, P = 0.012) and FMR (β = -0.18, CI: −0.33 to −0.02, P = 0.027) explained any significant variation in search time (Fig. 6a). The full search-time model had a higher AIC than the null model (S2), demonstrating that included predictors could not explain any significant variation in cougar search time of kills. We therefore caution against making any inferences from the search-

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Table 1 | Summary statistics for cougar predation and competition metrics across research phases, and across seasons and prey-size classes during 2016–2022

Research Phase			
Metric	1987–1994	1998–2005	2016–2022
Handling Time (days)	2.5 (2.0)	2.9 (3.0)	2.54 (2.0) ± 0.11
Search Time (days)	5.6 (5.0)	4.1 (3.0)	2.94 (1.96) ± 0.17
Kill Interval (days/kill)	7.9 (8.0) ± 0.8	7.0 (6.0) ± 0.4	5.37 (4.21) ± 0.23
Kill Rate (kg/day)	22.3 (13.5) ± 3.7	24.6 (15.5) ± 2.1	17.21 (16.64) ± 0.99
Wolf Presence (% of kills)	NA	22.9%	8.0%
Wolf Displacement (% of kills)	NA	7.5%	5.1%
Bear Presence (% of spring-summer kills)	32.8%	48.6%	32.7%
Bear Displacement (% of spring-summer kills)	12.1%	22.7%	22.0%
Season (2016–2022)			
Metric	Spring-Summer	Early Winter	Late Winter
Search Time (days)	2.8 (1.9) ± 0.24	3.33 (2.81) ± 0.34	2.95 (2.13) ± 0.34
Ungulate Kill Rate (kills/30 days)	6.46 (6.75) ± 0.59	4.7 (4.48) ± 0.45	5.18 (5.46) ± 0.4
Biomass Acquisition Rate (kg/day)	5.75 (5.17) ± 0.74	10.76 (9.98) ± 1.06	11.41 (11.82) ± 0.79
Wolf Presence (% of kills)	6.5%	11.4%	8.0%
Wolf Displacement (% of kills)	5.4%	4.3%	5.4%
Bear Presence (% of kills)	32.7%	1.4%	0.0%
Bear Displacement (% of kills)	22.0%	0.0%	0.0%
Prey Size (2016–2022)			
Metric	Small (<40 kg)	Medium (40–105 kg)	Large (>105 kg)
Handling Time (days)	1.52 (1.23) ± 0.09	2.74 (2.46) ± 0.16	4.25 (3.69) ± 0.34
Wolf Presence (% of kills)	2.0%	11.1%	14.6%
Wolf Displacement (% of kills)	1.3%	5.1%	12.2%
Bear Presence (% of kills)	11.9%	14.5%	25.6%
Bear Displacement (% of kills)	9.1%	8.5%	18.3%

For non-percentage metrics, results are presented as mean (median) ± SE. Results from 1987–1994 and 1998–2005 are published in Ruth et al.[26].

time model. As hypothesized, edible prey biomass ($\beta = 0.3$, CI: 0.21–0.39, $P < 0.00001$; Fig. 6a) was once again the strongest predictor of kill-interval duration, followed by a negative effect of both displacement by wolves/bears ($\beta = -0.39$, CI: -0.62 to −0.16, $P = 0.001$; Fig. 6a) and FMR ($\beta = -0.12$, CI: −0.20 to −0.03, $P = 0.01$; Fig. 6a).

For both the kill-rate and biomass-acquisition-rate models, average prey size and FMR explained significant variation. As cougar energetic demands increased, so did kill rate on ungulates ($\beta = 0.14$, CI: 0.06–0.22, $P = 0.001$; Fig. 7) and biomass acquisition rate ($\beta = 0.17$, CI: 0.08–0.27, $P = 0.0005$; Fig. 7). As predicted, average prey size had an opposite effect on each response—an increase in prey size led to a decrease in kill rate ($\beta = -0.25$, CI: −0.34 to −0.16, $P < 0.00001$; Fig. 7) but an increase in biomass acquisition rate ($\beta = 0.2$, CI: 0.1–0.31, $P = 0.0004$; Fig. 7). Contrary to our predictions, there was no effect of the proportion of wolf/bear interference competition on cougar kill rate ($\beta = -0.33$, $P = 0.2$) or biomass acquisition rate ($\beta = -0.3$, $P = 0.32$). This was different from our kill-interval findings, in which interference competition led to decreases in the finer-scale kill interval. Finally, we found a significant increase in late winter biomass acquisition rate relative to spring-summer ($\beta = 0.32$, CI:0.02 to 0.61, $P = 0.04$; Fig. 6a). See Tables S3.1–S3.7 for model summaries.

Discussion

We show that cougars are competitively subordinate to bears and wolves in northern YNP, as evidenced by their frequent displacement from carcasses found by dominant competitors (Fig. 4b). Prey size was the dominant driver affecting interference of cougars at their kills by wolves and bears (Fig. 5). Moreover, prey size drove cougar predation dynamics, being the most important predictor of handling time, kill interval, kill rate, and biomass

acquisition rate from 2016–2022. Abundant large prey like elk and diverse medium-sized ungulates may also explain why cougars in Yellowstone acquired prey biomass at roughly double the average combined rate across all known cougar predation studies[27]. Finally, the size and availability of diverse prey in Yellowstone yielded unexpected competition dynamics compared to theory-driven hypotheses.

Competition theory predicts that as a resource declines, competition for that resource will increase as the same individuals vie for its more limited availability[28]. However, a decrease in the availability of a large, shared prey species may instead lead to declines in interference competition when carcasses are a more valuable or attainable resource compared to live prey[3]. Therefore, if elk were the only prey available in our system, the observed large (5-fold) decline in the elk population from 1998–2005 to 2016–2022 may explain the decline in kleptoparasitism by wolves and bears that was also observed during this time. However, with the elk decline, cougars compensated by killing more deer (13.8% to 37.6%, Fig. 2a), which contributed to increased cougar kill rates of ungulates from 1998–2005 to 2016–2022 (Table 1). Hence with more carcasses from cougar-killed prey available and predator densities remaining high, we expected a proportional increase in kleptoparasitism. But contrary to theory, rates of kleptoparasitism instead declined, demonstrating how interference competition was most affected by prey size, not resource availability.

Competitor densities also influenced interference competition, being positively correlated with the odds of kleptoparasitism (Fig. 5). Counter-intuitively, even as predator populations increased, the intensity of carcass displacement and the severity of its effects on cougar predation did not persist (Figs. 4, 6). Bear density increased from 1998–2005 to 2016–2022[16,17], yet bear presence at cougar kills declined (Fig. 4). Similarly, wolf presence at
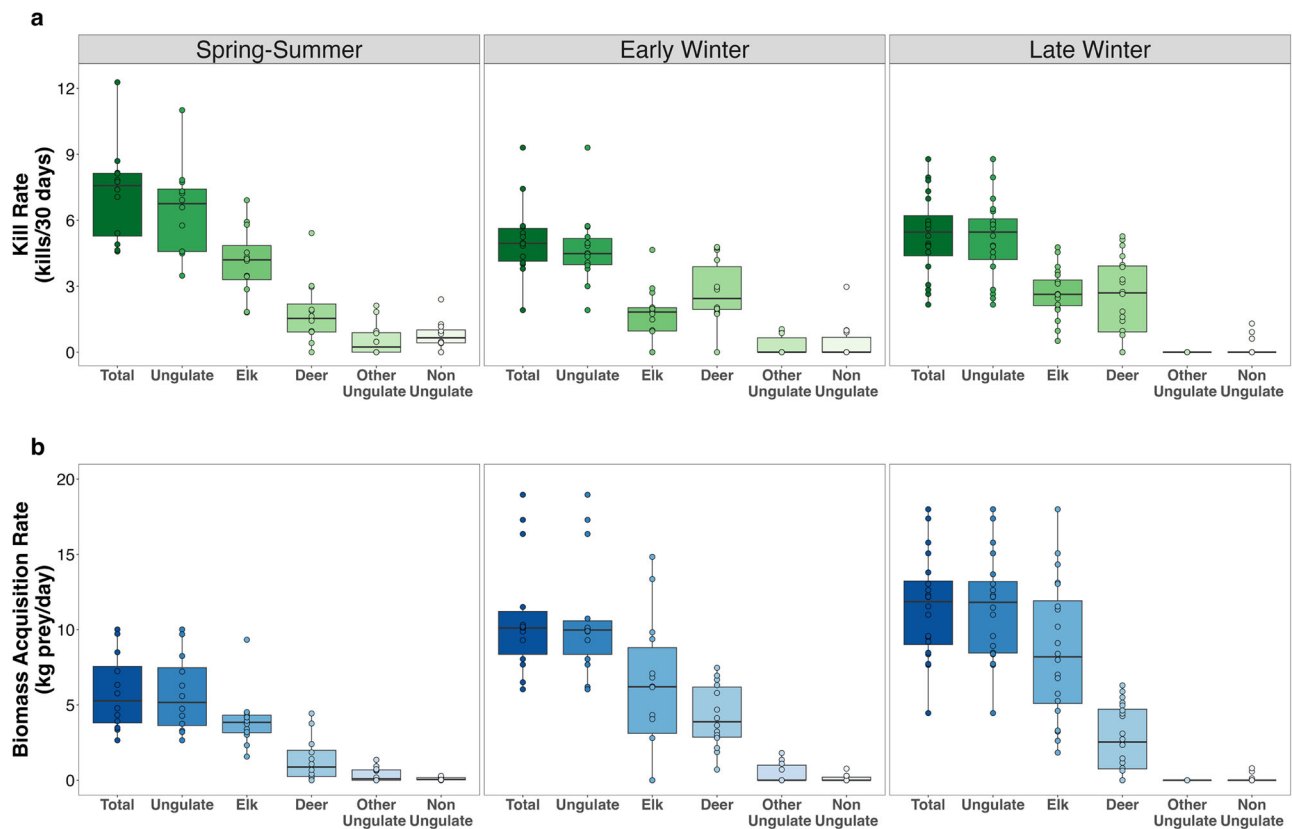
Fig. 3 | Distribution of cougar kill rates and biomass acquisition rates by season and prey species/groups. Seasonal variation in cougar (**a**) kill rates (kills per adult cougar per 30 days) and (**b**) biomass acquisition rates (kg per adult cougar per day) of different prey species/groups during 2016–2022 in Yellowstone National Park, USA. Each point represents an estimate for a single cougar predation sequence (*n* = 46) that occurred in the respective season. "Deer" includes predominantly mule deer, but also white-tailed deer. "Other Ungulate" includes pronghorn, bighorn sheep, and mountain goat. "Non-Ungulate" includes yellow-bellied marmot, coyote, red fox, porcupine, beaver, grouse, and cougar.

cougar kills declined 44% more than expected if predator densities were the factor mediating interference competition. The abundance of both cougar kills and wolves/bears appears less important in driving interference competition than carcass size. Instead, the shift to killing smaller ungulates from 1998–2005 to 2016–2022 (Fig. 2) contributed to fewer cougar kills being detected by wolves and bears (Fig. 4), alleviating negative effects of displacement on both cougar food acquisition and their kill rates on prey.

Our study, among others, indicates that carcass interference by wolves/bears also affects cougar predation metrics. Past work showed that cougar handling times of prey were significantly reduced at study sites in Colorado and California when bears were present at kills[13]. Considering bears were detected at over 47.8% and 77.2% of kills in these studies, respectively, this can have a major impact on cougar kill rates and both the cougar and prey populations. In Nevada during 2009–2012 and 2015–2017, feeding bout duration of cougars at kills significantly declined as bear density increased[29]. Similarly in Yellowstone, we showed that during 1998–2005, carcass displacement by wolves and bears increased cougar kill rates by 42% (CI: 18–65%)[26]. We also demonstrated that the effects of interference competition on both predator and prey can vary depending on the timescale of the predation metric. For instance, when a cougar was displaced, their shorter-term kill interval declined by 35% (CI: 16.2%–51.4%; Fig. 6), aligning with past findings[26]. However, we found no noticeable effect for how the proportion of displacements affected longer-term kill rates and biomass acquisition rates (Fig. 7), possibly indicating how long-term, cumulative effects of competition on the cougar population were dampened in this system. Such dampened effects caused by killing smaller prey could be a stabilizing mechanism for the coexistence of diverse predator-prey communities that may otherwise be destabilizing.

The importance of prey size likely extends to energy gains received by predators. That is, cougars could gain the same net energy killing smaller prey because cougars have a higher probability of getting displaced from larger kills. For example, in spring-summer, when 82% of displacements occurred, cougars acquired similar amounts of biomass from displaced kills as non-displaced kills, 22.5 (14.2) ± 4.1 kg and 28 (18.5) ± 2.5 kg, respectively. While acquired biomass was comparable, cougars were losing significant biomass from displaced kills that were significantly larger [65.5 (42.9) ± 8.2 kg] than non-displaced kills [28.7 (19.7) ± 2.6 kg], illustrating that prey size not only influences food acquisition of subordinate predators, but also the dominant, kleptoparasitic predators. Because little is known about how much food is lost to other scavengers that do not displace cougars, cougar-consumed biomass is likely much lower than the 98.9% estimated acquired biomass. Therefore, the impacts of displacement on biomass acquisition and kill rates of subordinate predators may be considerably less than predicted by effects of short-term metrics like kill interval. Nonetheless, interference competition poses lethal risks to subordinate competitors[6,10,23]. While no radio-collared cougars were killed by bears from 2016 to 2022, two were killed by wolves in 30.2 cougar-years, with both occurring in terrain with poor escape options for cougars. Still, since the majority of displacements are by bears, interference costs should mostly be short-term food and energetic losses rather than lethal interactions. Furthermore, because female cougars kill significantly smaller prey than male cougars (Fig. S4), interference competition and its associated costs are lower for female cougars, which are most important for population growth and stability, indicating how prey size can also influence subordinate predator population dynamics. Similarly, a shift in the prey size of subordinate predators should alter the food subsidies provided to dominant predators
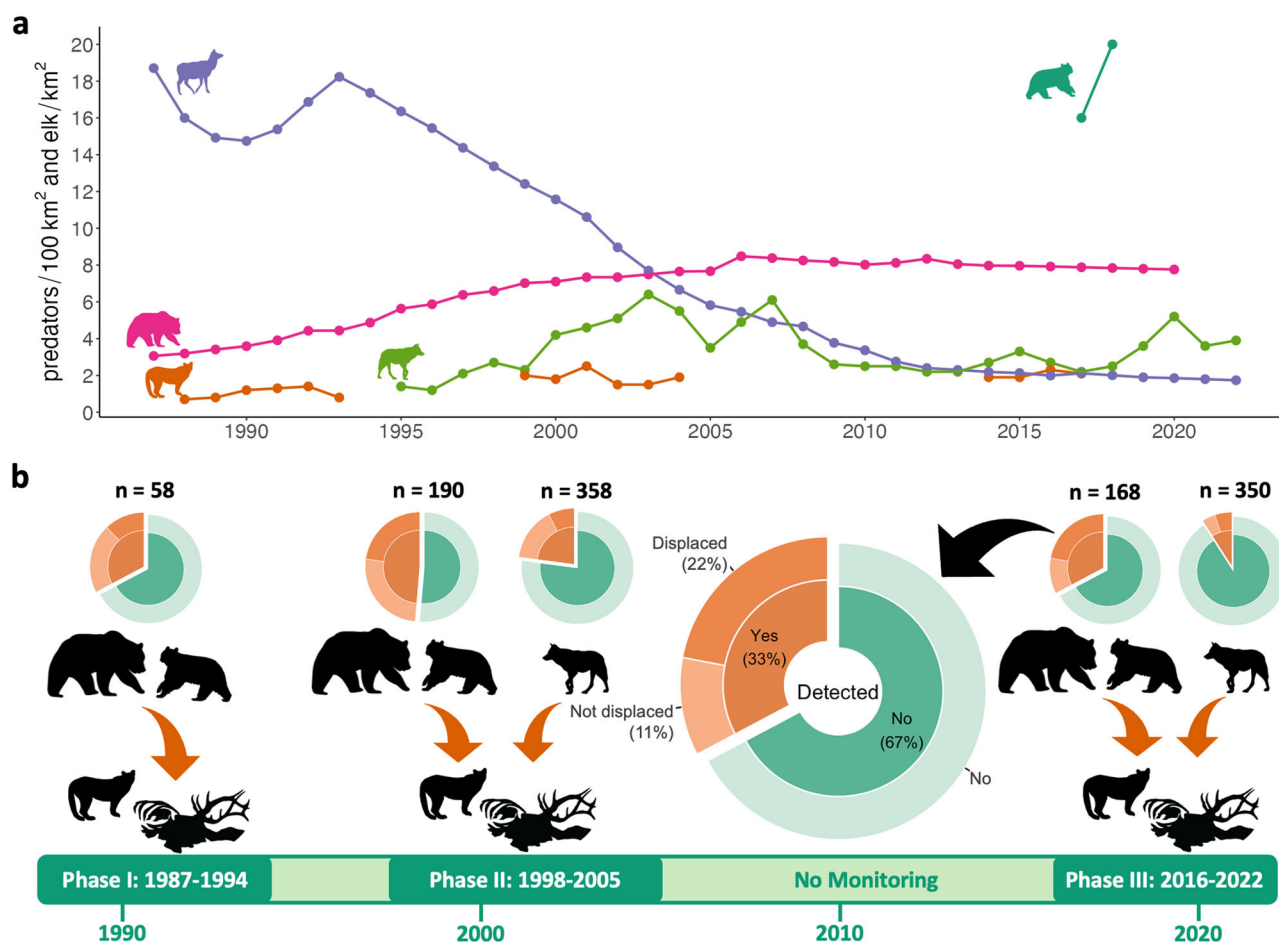
Fig. 4 | Densities of elk and large carnivores along with rates of interference competition at cougar kills through time. a Densities of wolf (green; 1995–2020)[71], cougar (orange; 1988–1993, 1999–2004, 2014–2017)[26,72], grizzly bear (pink; 1987–2020)[16,17], black bear (dark green; 2017–2018)[18], and elk (purple; 1987–2022)[73] on Yellowstone National Park's Northern Range, USA from 1987–2022. **b** Wolf/bear presence and displacement at cougar kills across each cougar monitoring phase (dark green sections of timeline). Above the year 2010 shows a reference key for interpreting each pie-donut chart. Inner pie slices represent the proportion of cougar kills detected by the wolf or bear, with dark green representing undetected kills and dark orange detected kills. The outer donut represents the proportion of kills a wolf/bear displaced a cougar from, with light green representing kills that were not interfering at kills, facilitating possible changes in the population dynamics of competing predators.

detected, light orange representing kills that were detected and possibly scavenged on by a wolf or bear, but likely after the cougar had left the kill, and dark orange representing kills that a wolf/bear actively stole and displaced a cougar from. Only spring-summer kills were included when estimating bear presence and displacement because of their winter hibernation. The number of cougar-kills included for evaluating presence/displacements by each competitor during each research phase are shown above each pie-donut chart. Cougar (by *Margot Michaud*), grizzly bear (by *@xgirouxb*), black bear (by *Margot Michaud*), and wolf (by *Margot Michaud*) PhyloPics are all dedicated as public domain under licenses CC0 1.0 or PDM 1.0. The bull elk carcass graphic was created and provided by Kira Cassidy.

Interference by dominant competitors also changes the behavior of subordinate competitors by shifting space use and/or diet. After wolves were reintroduced (1998–2005), cougars used rougher, more covered terrain in winter than prior to reintroduction (1987–1994). While we do not know if cougars continued to increase their spatial separation from wolves in 2016–2022, competition refuges may have contributed to the observed decline in wolf/bear interference at cougar kills since an increase in roughness led to a decrease in wolves/bears finding and stealing cougar kills (Fig. 5)[26]. Subordinate competitors may avoid immediate risks of interference competition by shifting fine-scale movements, such as cheetahs maintaining distance from dominant hyenas and lions[30]. Predators may also mitigate competition by changing diet[29]. While deer were increasingly used by Yellowstone cougars, the increase was not disproportionately larger than the decline in elk abundance, so it is unlikely that cougars shifted to killing smaller prey as a widespread strategy to mitigate interference competition, as has been seen in other species and systems[31].

Similar to cougars consuming more deer, wolves fed more on bison in winter over this same period (from ~10% during 1998–2005 to ~50% during 2016–2022)[32], as the Northern Range bison population increased 5-fold. This increased bison use likely facilitated a shift to wolves spending more time away from areas of high cougar density because bison generally use open grassland habitat in lower-elevation valleys and high-elevation plateaus that cougars avoid (see Ruth et al., 2019 for cougar habitat selection and White et al., 2015 for seasonal distributions and movements of bison)[26,33]. More bison in wolf diets would contribute to the observed decline in interference by wolves, thereby making bison a secondary factor affecting wolf-cougar interference competition. The increase in bison may also affect grizzly bear interference competition at cougar kills because grizzly bears are common scavengers of both bison carcasses and wolf kills[1,32]. With this analysis, we identified that the availability of alternative sources of prey/carrion for both subordinate and dominant competitors played an important role in reducing interference competition and its negative effects on subordinate competitors. This finding illuminates how species diversity at one trophic level may promote coexistence and diversity at other trophic levels, contributing to ecosystem diversity, stability, and resiliency.

Cougars are the most widespread native terrestrial mammal in the western hemisphere, ranging from the Yukon to the southern-Andes[34,35]. Their expansive range and role as an apex predator means cougars may have

Fig. 5 | Predicted probability of cougar displacement by competitors given prey size, competitor density, and roughness. Effect of prey size, and 1 SD marginal effects of competitor density and topographic roughness on the probability of wolf or bear displacement of cougars from their kills (n = 350). Models use predation data collected from 2016–2022 in Yellowstone National Park, USA. Cougar PhyloPic by *Jody Taylor* is dedicated as universal public domain under CC0 1.0.
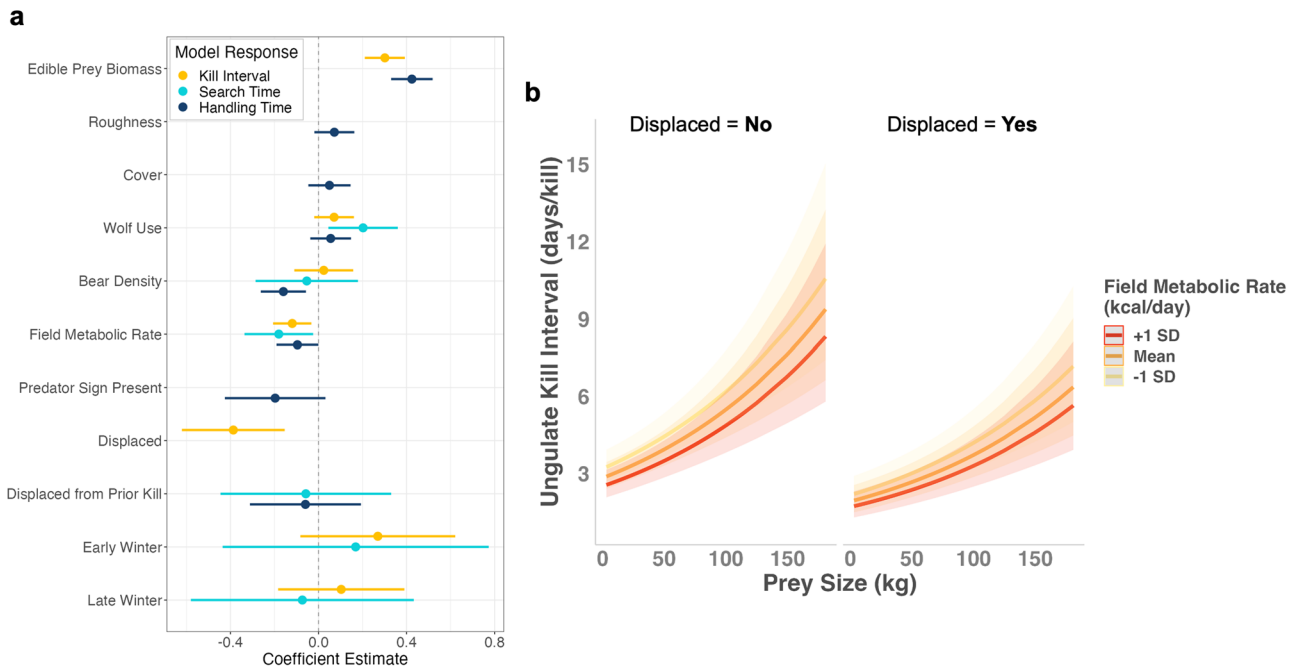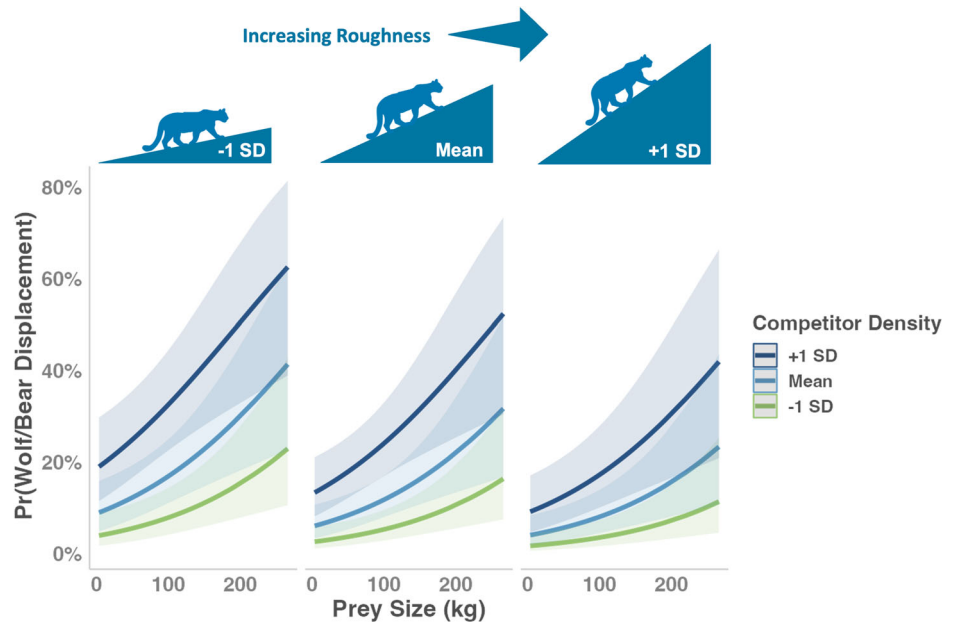

Fig. 6 | Effects of predictors on log cougar kill interval of ungulates. a Fitted model coefficient estimates (points) with 95% confidence intervals (lines) of covariate effects on log-cougar kill interval (orange, n = 303), log-search time (light blue, n = 304), and log-handling time (dark blue, n = 350) of ungulate prey. **b** Effect of prey size, and 1 SD marginal effects of field metabolic rate (energetic needs of study cougar and dependent young, if present) and displacement on the cougar kill interval of ungulates. Models use cougar predation data collected from 2016 to 2022 in Yellowstone National Park, USA.

a heightened functional role in shaping community structure across many ecosystems[19,36]. Yet, due to their size and solitary nature, their broad geographical extent means cougars are subordinate competitors to several apex predators (e.g. gray wolf, grizzly bear, black bear, and jaguar (*Panthera onca*)) across roughly half their range[4]. Given the variation in competition dynamics that we observed with changes in predator-prey community structure through time, such a broad geographic range implies that cougars and their prey may experience vastly different consequences from intraguild competition depending on both the dominance status of cougars as competitors and the size, diversity, and abundance of available prey. The same can be said for carnivore competition more broadly; variation in community structure undoubtedly shapes the outcomes of competitive interactions across systems and taxa.

Our work demonstrates the key importance of understanding prey size and diversity, dominance status, and hunting/feeding strategies in the context of ecological communities and its broader implications for predicting how predator-prey and competition dynamics unfold. For instance, while much is known about the dominance hierarchies and behavioral ecology of multi-apex predator systems on other continents, e.g. Africa[3,30,31,37,38], studies have generally lacked the requisite predation data to address these competition dynamics and link them to impacts on prey. While wolves have lower hunting success than cougars[39,40], we show that
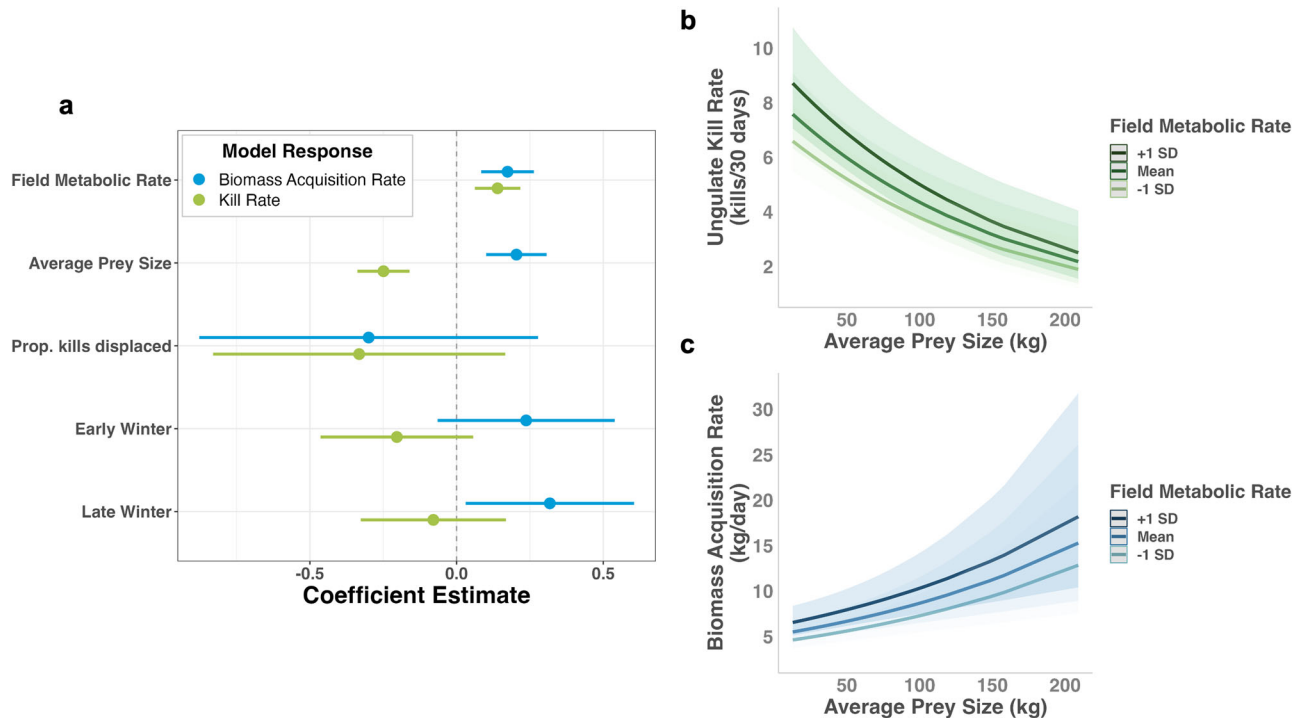
Fig. 7 | Effects of predictors on log cougar kill rate and biomass acquisition rate. **a** Fitted model coefficient estimates (points) with 95% confidence intervals (lines) of covariate effects on log-cougar kill rate (green) and log-biomass acquisition rate (blue) of ungulate prey for predation sequences. Effect of field metabolic rate (energetic needs of cougar that serves as a proxy for demographic group), and 1 SD marginal effects of average prey size on (**b**) cougar kill rate of ungulates (kills per 30 days) and (**c**) biomass acquisition rate of prey (kg per day). Models use cougar predation data (*n* = 46 predation sequences) collected from 2016 to 2022 in Yellowstone National Park, USA.

they compensate for this by being dominant competitors and scavengers. These differences in hunting success and competitive dominance alters the impact of interference competition on wolf kill rates. When grizzly bears interfere with wolf kills and scavenged carcasses, there are likely fewer physical risks and energetic costs to wolves competing with grizzly bears over feeding opportunities than to abandon those carcasses and start hunting prey again. As a result, kleptoparasitic grizzly bears unconventionally reduce wolf kill rates in both Scandinavia and Yellowstone[14]. We found the opposite in subordinate cougars[1,14], demonstrating that as interference competition becomes more asymmetrical, disparities between the costs to subordinate competitors and their prey, and the benefits to dominant competitors, should grow. Yet, we also show that these consequences are mediated by factors like prey size and competitor density.

Quantifying how sympatric predators affect each other, and their impacts on prey populations, is required for developing a mechanistic understanding of the functional role of predators in multi-predator, multi-prey communities. How these costs subsequently influence individual and population-level fitness, coexistence, resilience, and biodiversity of both predators and their prey can be challenging to tease apart but are, nonetheless, necessary for understanding ecosystems. With the recovery of large carnivore populations in some areas and further declines in others across the globe, disentangling these complex community interactions between competing predators and their prey is essential.

Methods
Study area
The Greater Yellowstone Ecosystem (58,026 km²) is a matrix of public and private wildland occupying parts of Wyoming, Montana and Idaho, USA. Within the heart of the Greater Yellowstone Ecosystem lies Yellowstone National Park, an 8,991 km² protected area often divided into two ecological subsystems due to geographic and biological differences, the Northern Range and the Non-Northern Range[41]. The Northern Range is delineated by the wintering range of Yellowstone's most prominent elk herd[42]. Our study

was primarily conducted on the Northern Range, which is 1530 km², with 995 km² inside Yellowstone National Park and the remainder located north of the park boundary. It is predominantly characterized by shrub steppe and grasslands with interspersions of large coniferous and small deciduous forests[42,43]. Cougars mostly frequent the Black Canyon of the Yellowstone River, as well as the surrounding tributaries, which all generally have steep, rough terrain and dense mixed Douglas-fir (*Psuedotsuga menziesii*) and juniper (*Juniperus* spp.) forests. During summers, our study area periodically extended into the Non-Northern Range due to cougars following ungulate prey that migrate into the higher elevations of Yellowstone[44].

Data collection
We studied cougar predation on the Northern Range of YNP from 2016-2022 during three distinct seasons: spring-summer, early winter, and late winter. To monitor cougars, we immobilized and captured individuals during winter using trained hounds following National Park Service's Institutional Animal Care and Use Committee's approved animal handling protocols (IMR_YELL_Stahler_Cougar_2018), and fitted them with GPS radio-collars (Vectronic Aerospace, Germany). During each predation sequence (Fig. S1), we searched clusters identified through use of ArcGIS (2016–2020) and the *GPSeqClus* package[45] in R (2020–2022). Using 3-h GPS fix rates, clusters required ≥2 GPS locations within 200 meters and six days of one another to form[46,47]. When carcasses were detected at clusters, we performed necropsies to record the prey's geographic location of death, cause of death, species, sex, age, and carcass use (% biomass consumed). Wolf, bear, and other scavenger presence at kills were recorded through sign identification (e.g. tracks, scat, hair).

Components of predation
Handling time of carcasses was defined as the total time between a cougar's first visit to the carcass within a cluster (midpoint in time between last GPS location prior to cluster and first GPS location of cluster), to the time a cougar left the carcass site and began searching again after acquiring all

significant edible biomass (midpoint in time between last GPS location of cluster and first GPS location after cluster). We characterized significant biomass as no longer being acquired if cougars left a carcass for ≥24 h and returned for ≤3 h, unless this was followed by longer visits.

Search time for each kill was defined as the duration between when a cougar left a previous kill (midpoint in time between last GPS location of prior kill cluster and first GPS location after prior kill cluster) until the estimated time the next kill was made (midpoint in time between last GPS location prior to kill cluster and first GPS location of kill cluster). Search time could not be calculated for the first kill in each predation sequence. Cougars rarely made double-kills (11 of 380 kills). For these events, search time between kills was zero and handling time was divided proportional to the edible biomass of each carcass.

Kill interval (time in days between successive cougar kills of ungulate prey) was estimated as the handling time of the current kill plus the search time of the following kill. The kill interval between double-kills at clusters would simply be the handling time of the first kill. Kill interval was estimated for each kill in a predation sequence with the exception of the first kill because the search time was unknown. Hence, kill interval represents a shorter-term metric of predation because each kill is the sampling unit. See Tables S1.1–S1.3 for more details on each predation metric.

Competitor presence and displacements

We identified carcass displacement at ungulate kills as when a bear and/or wolf was detected at a cougar kill and the cougar's handling time fell below the lower limit of the CI for the respective prey size (Fig. S5). We first binned prey into three size classes according to live weights: small (<40 kg), medium (40–105 kg), and large (>105 kg). We then calculated the mean handling time and 95% confidence interval (CI) for cougar kills of each prey size where bears and wolves were not detected. To calculate CIs for each prey size category, we generated $n = 100,000$ bootstrap samples and used a bias-corrected and accelerated (BCa) bootstrap CI to account for bias and skewness in handling time data distributions.

Kill rate and biomass acquisition rate

We used ratio estimation[48] to calculate cougar kill rates of prey. Kill rates were estimated as y_i/x_i, where y_i was the number of kills detected during predation sequence i, and x_i was the number of days in predation sequence i. Because the kill rate mainly provides a "prey's perspective" of predation, we also estimated the amount of biomass that cougars acquired daily to evaluate the effects of competition on the "cougar's perspective."

We calculated biomass acquisition rates (kg per cougar per day) by first identifying all carcasses (killed or scavenged) acquired by a cougar during predation sequence i. Amounts of live, edible, and acquired biomass (in kg) were estimated for each cougar-killed prey. Live weights for elk and deer carcasses were assigned according to seasonal Gompertz-growth curves accounting for species, sex, and age of prey[25,49] while estimates for other ungulate and non-ungulate prey came from the literature[50–54]. We then assumed that edible biomass constituted 68% of live weight for non-neonatal elk and 79% for all other carcasses consumed by cougars[55]. Lastly, we applied a final correction factor from edible biomass to acquired biomass depending on carcass use recorded at field necropsy and evidence of displacement. Each predation sequence is an individual sample. Kill rate and biomass acquisition rate represent longer-term metrics of predation because the entire predation sequence is the sampling unit. See Table S1.1, Table S1.2, and Fig. S6 for more details regarding biomass calculations.

Statistics and reproducibility

Model structure. We limited our dataset to only ungulate kills because small, non-ungulate prey are consumed quickly and therefore under-detected using cluster methods[56–59]. More so, these kills provide little biomass to cougars, with ungulate prey being the dominant food source (see *Results*).

Analyses were conducted in R version 4.3.1[60] through either the "glmer" or "lmer" function from the *lme4* package version 1.1-34[61] if the model was a generalized linear mixed effects model (GLMM) or a linear

mixed effects model (LMM), respectively. Cougar ID was included a priori as a nested random intercept in all models unless the variance was estimated near zero (suggesting that fixed effects accounted for any among-individual variability), in which cases the random intercept was dropped and models were simplified to generalized linear models (GLMs) or linear models (LMs) using the "glm" or "lm" function, respectively, from the *stats* package[60].

For each response variable, we developed one full model that included all predictor variables of interest for a particular response (see Fig. 1b for list of included covariates) and one null model to avoid known concerns of multiple comparisons associated with developing many competing models and performing model selection[62–64]. Predictor variables for each model were carefully selected based on a priori hypotheses. The number of predictors included (k) was determined using $n/k \geq 10$, where n was the effective sample size of the response being considered[62,63,65].

Model fixed-effect variables. Our first interest was quantifying which factors (see Fig. S3) influenced the probability that a wolf or bear discovered and displaced a cougar from their kill, hereafter referred to as the predator-presence and predator-displacement models, respectively. For each kill, we used the estimated live biomass of the carcass, the mean percent tree cover (cover) and topographic ruggedness index (roughness) values within a 250-m circular buffer, and temporally-explicit estimates of mean wolf use and bear density within a 1-km circular buffer to quantify variation in the probability of predator presence and predator displacement. Wolf use was calculated as the summed 99% utilization distributions of GPS and VHF (Very High Frequency)-collared wolves from all monitored wolf packs, with values for each pack weighted by pack size, such that values represented the average number of wolves within the 1-km buffer during the time period of interest. Bear density was the sum of black bear average density (1-km spatial resolution) and grizzly bear density indices (14-km spatial resolution). Black bear data is based on a SECR model using baited hair snare and rub tree data from 2017 to 2018[18]. The same values were used for black bears across all years. Grizzly bear density indices are based on VHF and capture locations, along with life-history data to reconstruct lifetime activity ranges. Values for each 14-km grid cell represent the sum of all activity ranges found in the cell during a given year (e.g., if 2 bears each had 50% of their activity range in a given cell, the cell would receive a value of 1 activity range in the cell). Grizzly bear density data was available from 1983 to 2020[16,17]. Black bear densities were assumed to be zero during winter sampling periods, while grizzly bear density indices for each cougar kill were corrected based on the estimated proportion of grizzly bears not hibernating during the week the kill was made according to data from Haroldson et al.[66].

We were also interested in assessing if drivers of presence and displacement differed between wolves and bears due to unique behavior or ecology. For example, because bears hibernate during the majority of winter, bear presence/displacement at cougar kills would be far greater in spring-summer than winter. However, to reduce analytical redundancy and issues of multiple comparisons that would arise from including results from multiple subsets of the same data, we excluded species/season-specific models of competitor presence and displacement, and focused on drivers of overall competitor presence and displacement at cougar kills. Species/season-specific model results are included in Fig. S3, but model performance was further limited by small effective sample sizes, particularly with wolf presence/displacement rates.

Our second interest was quantifying which factors (see Tables S1.1–S1.3) best explained variation in cougar handling time and search time of prey, shorter-term kill interval, and longer-term kill rate and biomass acquisition rate. For the handling-time model, we used the estimated edible biomass of each kill instead of the live biomass, as it is a more biologically meaningful predictor of handling time. We also used cover, roughness, wolf use, bear density, if predator sign was detected at a kill, if a cougar was displaced from the prior kill, and the field metabolic rate (FMR)[67] of the cougar that made the kill. FMR represented the estimated daily energetic demands of an individual sub-adult or adult cougar. If the

individual was a maternal female, the energetic demands associated with supporting young were included[54]. When calculating FMR using formulas from Laundré, we accounted for the average capture weight of the collared cougar, average daily movement distances according to different cougar demographic classes from monitoring of collared individuals by Laundré, and both the age and number of dependent young when present[67]. For the search-time model, we again included cover, roughness, FMR, wolf use, bear density, displacement from prior kill, and season to quantify changes in prey availability and exploitation competition predicted to influence search time[1]. We excluded double kills from models to reduce bias and eliminate search times having a zero duration, which allowed log-transforming the response to better satisfy assumptions of linearity. Lastly, we ran kill-rate and biomass-acquisition-rate models at the predation-sequence rather than kill level. For both models, we included the average edible weight of kills made, FMR, proportion of kills a cougar was displaced from, and season.

See Tables S1.1–S1.3 for descriptions of how each response and predictor variable was acquired and estimated.

Model fitting and evaluation. Predictor variables for all models were centered and scaled when appropriate to improve model fitting and interpretation. For the predator-presence and predator-displacement models, we used binomial logistic regression (GLM for presence and GLMM for displacement) with a Bernoulli distribution and logit-link function. For handling time (LMM), search time (LLM), kill interval (LMM), kill rate (LM), and biomass acquisition rate (LM), responses were log-transformed to better satisfy linear model assumptions.

Correlation coefficients and variance inflation factors (VIFs) of predictors for all models except search time did not exceed 0.5 and 2, respectively. In the search-time model, bear density and season were highly correlated (~0.7) due to the majority of bears hibernating in winter, leading to VIFs of 3–3.5 for both variables. We retained both in the model, however, because 1) both variables were predicted a priori to have biologically meaningful and unique effects on search time, and 2) one was a continuous and the other a categorical variable. We acknowledge the increased SEs that may result from such collinearity.

We evaluated model goodness-of-fit for GLMs using pseudo-R^2 values computed with the "pR2" function from the *pscl* package[68]. Pseudo-R^2 was calculated by comparing the likelihood of the data under the fitted model with that of a null model[69], with values running from 0 to 1 as the model fit improves.

Reporting summary
Further information on research design is available in the Nature Portfolio Reporting Summary linked to this article.

Data availability
All relevant cougar predation and competition data (from 2016 to 2022) used in statistical analyses is available on Data Dryad[70] at https://doi.org/10.5061/dryad.sxksn03c5. Summary statistics presented for data from 1987–1994 and 1998–2005 are published in Ruth et al.[26].

Code availability
The code used for analyses is available from the corresponding author upon request. Details regarding the use of statistical programming software for analyses are outlined in "Statistics and reproducibility."

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Author contributions

J.W.R., C.B.A., and D.R.S. conceived of the 2016–2022 study, while K.M.M. and T.K.R. under the vision of Dr. Maurice Hornocker conducted the 1987–1994 and 1998–2005 studies, respectively. J.W.R., W.J.B., C.B.A., C.J.M., and D.R.S. collected the data and coordinated the study for 2016–2022, while K.M.M. and T.K.R. collected the data and coordinated the 1987–1994 and 1998–2005 studies, respectively. J.W.R. developed the methods and analyzed the data. M.C.M. and B.J.S. helped develop covariates that were essential to analyses. J.W.R. and J.K.B. wrote the manuscript with substantial input from all authors. J.K.B., D.W.S., and D.R.S. oversaw project logistics and completion.

Competing interests

The authors declare no competing interests.

Additional information