

Article

Individual Variation in Predatory Behavior, Scavenging and Seasonal Prey Availability as Potential Drivers of Coexistence between Wolves and Bears

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Received: 11 August 2020; Accepted: 12 September 2020; Published: 15 September 2020



Abstract: Several large carnivore populations are recovering former ranges, and it is important to understand interspecific interactions between overlapping species. In Scandinavia, recent research has reported that brown bear presence influences gray wolf habitat selection and kill rates. Here, we characterized the temporal use of a common prey resource by sympatric wolves and bears and described individual and seasonal variation in their direct and/or indirect interactions. Most bear–wolf interactions were indirect, via bear scavenging of wolf kills. Bears used >50% of wolf kills, whereas we did not record any wolf visit at bear kills. Adult and subadult bears visited wolf kills, but female bears with cubs of the year, the most vulnerable age class to conspecifics and other predators, did not. Wolf and bear kill rates peaked in early summer, when both targeted neonate moose calves, which coincided with a reduction in bear scavenging rate. Some bears were highly predatory and some did not kill any calf. Individual and age-class variation (in bear predation and scavenging patterns) and seasonality (in bear scavenging patterns and main prey availability of both wolves and bears) could mediate coexistence of these apex predators. Similar processes likely occur in other ecosystems with varying carnivore assemblages.

Keywords: apex predators; bear; interspecific interactions; moose; predation; scavenging; wolf

1. Introduction

During the last two centuries, large carnivores have suffered drastic population declines, range contractions, and habitat fragmentation [1]. Although carnivores have adapted to almost every habitat, barely ~5% of the Earth's terrestrial land area contains five or more overlapping species of

large carnivores [2]. Despite rarity and typically low population densities, large carnivores influence ecosystems in multiple ways through predator-prey interactions, i.e., carnivores are keystone species [3]. They affect prey and mesopredators in both demographic and behavioral terms, which can ultimately drive trophic cascades [4].

Although many large carnivore populations remain threatened [2], others are expanding nowadays in different continents [5,6], increasing the chances for different species to overlap. At the worldwide scale, northern Eurasia is the region with the greatest expansion range of a four-species guild (gray wolves *Canis lupus*, Eurasian lynx *Lynx lynx*, brown bear *Ursus arctos*, and wolverines *Gulo gulo*) [2,6]. Natural recolonization by large carnivores provides opportunities to study interspecific interactions among them, which is crucial to understanding how they can affect each other and lower trophic levels.

Several empirical studies on interspecific interactions among large carnivores have been conducted in northern Europe. Research has focused on habitat and resource use by different species in the large carnivore guild [7]; competition between species, such as wolf and lynx [8] and wolverine and lynx [9]; interference competition between trophic levels [10]; and on the demographic impact of coexisting predators on prey [11]. Interspecific interactions between the two largest carnivores (brown bears and wolves) that roam over large areas of the Northern Hemisphere have been studied in North-America (e.g., [12–14]) and in Scandinavia (Norway and Sweden) in recent years [15]. In Scandinavia, research has focused on wolf habitat selection at different spatial scales [16–19] and on the wolves' kill rates in areas sympatric and allopatric with bears [20]. In moose *Alces alces*—bear—wolf systems, predation is a major driver of moose population dynamics [21], so research has also informed management to optimize ungulate harvest yield where wolves and bears coexist [22].

The body of literature on large carnivores in northern Europe has highlighted the existence of individual variation in habitat selection and kill rates. For instance, wolverines display high individual variation when selecting home ranges [23] and lynx show individual variation in home-range size [8]. Large individual variation has also been shown in wolf home range size [24], bear habitat selection [25], and bear kill rates [26]. The latter implies different levels of specialization reflecting individual foraging behavior [27]; in turn, individual differences in predator behavior may help explain the large individual variation in bear habitat selection [17].

Intraspecific variation in habitat selection may be an adaptation for wolves and bears to reduce intra- and interspecific competition, i.e., individual variation may promote coexistence between these large predators [17]. The role of individual variation in habitat selection, activity patterns [28], and foraging behavior [27] at higher levels of biological organization is indeed gaining increasing recognition [29,30]. Individual variation can have consequences for population and community ecology [31], favoring coexistence of sympatric species [32].

Besides individual variation, seasonality is another important factor that may have implications for coexistence between large carnivores [33]. Seasonal and daily spatio-temporal patterns may influence the intensity of interspecific interactions and the resulting distribution of sympatric species [34]. In a Scandinavian context, wolves prey on moose all year round, bears often scavenge wolf kills, and both predators largely rely on neonate moose during spring [20]. Thus, individual and seasonal variation in predation and scavenging rates may help understand the patterns of wolf habitat selection and kill rates in relation to brown bear presence reported earlier. Namely, bear density has had a negative effect on the probability of wolf territory establishment in Scandinavia during the wolf recolonization process [16,18], and wolf kill rates are lower in areas sympatric with bears, despite wolves losing food to bears via scavenging [20].

In this study, we characterized the temporal use of a common prey resource by sympatric wolves and bears in Sweden, describing individual and seasonal variation in wolf–bear interactions. The latter can be direct, if individual wolves and bears meet at the same time, or indirect, if they use the same place or resource, but not simultaneously, which can provide evidence of exploitation competition, e.g., via scavenging. Describing individual variation and seasonal trends in kill and scavenger rates of competing carnivores can reveal underlying mechanisms behind the observed effects of bears on wolf

habitat selection and kill rates at higher spatial and temporal scales. Ecological theory is improving the forecast of changes in species interactions and coexistence in a scenario of global change, but more specific empirical data are needed to understand the mechanisms driving interactions and thus species coexistence (e.g., [29]). Our study contributes empirical data to document the role of individual variation and seasonality as drivers of interspecific interactions between apex predators via predation rates and scavenging, which in turn can also reflect on predator-prey interactions.

2. Material and Methods

2.1. Study Area and Study Species

The study area in central Sweden (in Dalarna, Jämtland, and Gävleborg counties) is a rolling landscape mainly covered by boreal, coniferous forests dominated by Scots pine *Pinus sylvestris* and Norway spruce *Picea abies*. Altitudes range between 100–830 m. Human density is low, 1–7 inhabitants/km², but the landscape is crisscrossed by many gravel roads (1 ± 0.5 km/km²), because logging is a major activity [35]. Snow typically covers the ground from December to March. Wolves became functionally extinct in Scandinavia in the 1960s, but wolf recolonization and recovery started by the late 1970s [36] and continued until 2015, when the general increasing population trend stabilized [16,37]. The first wolf territories reestablished in our bear-wolf sympatric study area in 2000/2001, and afterwards between one and eight wolf territories have been detected annually [17], with a pack size of 4 ± 2 wolves (mean \pm sd) for the packs included in our study. For brown bears, as few as about 130 were left in Sweden about a century ago [38], but human attitudes and legislation changed, the population recovered, and currently bear density reaches ~ 30 bears/1000 km² in our study area [39]. As of winter 2019–2020, there were ~ 450 wolves in Scandinavia, ~ 365 of them in Sweden [37]. The Scandinavian brown bear population consists of ~ 3000 bears, most of them (~ 2800) in Sweden [40]. Lynx and wolverines are also present, yet in low densities, in the study area. Moose is the most abundant ungulate (0.7 – 1.6 /km²) and very low densities of roe deer *Capreolus capreolus* (0.05 – 0.08 /km²) also occur [41].

2.2. GPS and Predation Data from Bears and Wolves

Studies of predation by wolves and bears on moose in the study area were conducted during two time periods; late winter and early spring (hereafter, “late winter”; from mid-February to the end of April) and early summer (hereafter, “early summer”; from the beginning of May to early July). For this study, we conducted predation studies of wolves in 2010–2015, and of bears overlapping with wolf territories in 2014 and 2015. Both wolves and bears were darted and immobilized from helicopters, according to accepted veterinary and ethical procedures [42], as determined by an ethical committee (Djurförsöksetisk nämnd) and the wildlife management authorities (Naturvårdsverket). The breeding pair in each wolf pack (6 wolves in total) was equipped with a GPS collar (Vectronic Aerospace, Berlin, Germany) and was monitored during each study period. In 2014, we monitored the predatory behavior of two wolf packs and 11 radio-collared bears with overlapping territories, and in 2015 we monitored one of the packs and nine collared bears (Tables 1 and 2; see also Figure 2 in [17]). There are more bears in the study area, but up to 80% of the adult female bears and 50% of the adult males have been radio-collared [43].

We searched for carcasses of killed prey at clusters of GPS locations [20,26] and recorded cause of death and age of the dead animal. We built clusters independently for bears and wolves, and we used the time of first bear or wolf location within each cluster of GPS locations as the time of death of each killed prey. We downloaded and plotted the GPS locations in ArcView GIS (Environmental Systems Research Institute, Inc., Redlands, CA, USA). We created a buffer around each location with a radius of 100 m and overlapping buffers generated clusters of ≥ 2 locations [44]. We uploaded them into handheld GPS receivers (Garmin, Olathe, KS, USA) and we visited all the generated clusters of GPS locations of wolves and bears within the study periods in the field. As in previous studies [20,26,45],

we generally visited the clusters of locations after 3 days, trading off carcass detection and avoidance of disturbance of study animals. Kills were relatively easy to find; even the predation of a neonate moose removed the understory vegetation, as previously reported [26] and typically the jaws and other small pieces of bones and skin were present. As additional sign, within each cluster of GPS locations we also recorded if there were tracks, scats, and hair of wolves or bears in the ground and lying vegetation, at the sites where prey were consumed and/or at surrounding daybeds within the clusters.

Table 1. Individual variation in the number of neonate moose calves killed by brown bears in central Sweden in early summer, during the moose calving season, according to bear sex and age categories, including the specific period in which each bear killed moose calves.

Bear	Year	Predation Period		Predation Period (# Days)	# Killed Calves	Bear Sex and Age Class
Galju	2014	16.05.2014	17.06.2014	32	10	Single adult female
Ruta	2014	18.05.2014	18.06.2014	31	5	Single adult female
Spjuta	2014	21.05.2014	12.06.2014	22	10	Single adult female
Strandas	2014	03.06.2014	09.06.2014	6	2	Single adult female
Klummy	2014	15.06.2014	15.06.2014	1	1	Subadult female
	2015	08.05.2015	18.06.2015	41	4	Single adult female
Klumpa	2014	10.06.2014	25.06.2014	15	4	Subadult female
	2015	06.05.2015	19.05.2015	13	1	Single adult female
Jarpa	2014	–	–	0	0	Subadult female
	2015	–	–	0	0	Subadult female
Lafmamack	2014	23.05.2014	24.06.2014	32	3	Adult male
Risslo	2014	13.05.2014	06.06.2014	24	7	Adult male
	2015	20.05.2015	21.06.2015	32	4	Adult male
Tappele	2014	22.05.2014	01.06.2014	10	10	Adult male
	2015	11.05.2015	17.06.2015	37	4	Adult male
Kil-kalle	2014	28.05.2014	09.06.2014	12	3	Subadult male
	2015	28.05.2015	10.06.2015	13	3	Adult male
Lutane	2015	18.05.2015	21.06.2015	34	2	Adult male
Abborrgina	2015	23.05.2015	19.06.2015	27	8	Adult female + 2 year-old cubs
Gymasa	2015	18.05.2015	20.06.2015	33	4	Single adult female

Table 2. Wolf territories for which GPS clusters were visited in 2010–2015. Start date and end date columns denote the time during which clusters were checked. Fieldwork in 2014 and 2015 was extended during the moose calving season, thus two fieldwork seasons are differentiated (a and b) for the wolf territories tracked during those years. Number and age class of killed moose per wolf territory and study period is also reported.

Wolf Territory	Year	Start Date	End Date	Killed prey (# per Moose Age Class)
Tenskog	2010	2/13/2010	4/11/2010	5 juveniles
	2011	3/14/2011	5/16/2011	8 juveniles
Tandsjön	2012	2/20/2012	5/14/2012	1 neonate calf, 5 juveniles, 7 adults, 1 unknown (juvenile or adult)
	2014a	3/19/2014	4/28/2014	3 juveniles
Kukumäki	2014b	5/21/2014	6/21/2014	11 neonate calves, 3 juveniles
	2013	2/25/2013	4/28/2013	2 juveniles, 2 adults
	2014a	3/3/2014	4/27/2014	3 juveniles
	2014b	5/19/2014	6/22/2014	7 neonate calves, 6 juveniles
	2015a	3/4/2015	4/24/2015	11 juveniles, 1 unknown (juvenile or adult)
	2015b	5/18/2015	6/29/2015	16 neonate calves, 2 juveniles, 1 adult

2.3. Monitoring of Scavenging with Camera Traps

To record visits of wolves and bears at kills made by any of the predators, in 2014–2015 we placed camera traps (Reconyx, Holmen, WI, USA and Scoutguard, Santa Clara, CA, USA) targeting the carcasses and immediate surroundings. We placed cameras at all kill sites with some remaining biomass. Cameras were triggered by movement sensors from passing animals and were programmed to record three pictures at a time, with a 1-min time lapse until the next three-picture set. We left the cameras in the field for at least 2 weeks or until the kill had been completely consumed (typically, no leftovers at all or only the jaws and/or some skin and hair of the moose were left).

2.4. Data Analyses

2.4.1. Kill Rates

We calculated average daily kill rates of moose by wolves (at the pack level) and bears during the study period. We estimated the variation in wolf and bear kill rates over time by calculating the average number of moose killed/day within a 7-day moving window. We then used bootstrapping to derive 95% confidence intervals. Wolves are obligate carnivores and mostly prey on moose in the study area [41], whereas bears are omnivores that use multiple food items, including moose calves in early summer [46]. Thus, we also checked for individual variation in the predation pattern of bears. In the early summer study period, i.e., the peak of the moose calving season, we summed the number of moose calves killed by each bear and calculated the average number of moose calves killed by the different sex and age categories of bears (<4 years old were considered as subadults [17]), to test for sex- and/or age-related differences in kill rates by using nonparametric Kruskal–Wallis and Mann–Whitney U-tests. The moose calving season overlaps the bear mating season (see Figure 3 in [17] for a graphical description of the seasonal phenology of bears, wolves, and moose). At that time, female bears with cubs of the year have small home ranges and limited movements to avoid conspecifics [47]. Therefore, we did not visit GPS clusters of females with cubs of the year in this study to prevent their displacement. However, we visited the clusters of one female with yearling cubs in 2015 (it was included as an “adult female” in the tests, i.e., we did not have a specific “female with yearlings” category because it was only one family group).

2.4.2. Scavenging Events

We defined a scavenging event as ≥ 1 picture of one of the large carnivores per day at a kill. We calculated the average number of scavenging events per day across all active cameras within a 7-day moving window and used bootstrapping to derive 95% confidence intervals.

3. Results

We visited a total of 1051 clusters of GPS locations of bears (530 clusters in 2014 and 521 in 2015) and 891 clusters of wolf GPS locations (97 in 2010, 169 in 2011, 179 in 2012, 76 in 2013, 218 in two territories in 2014, and 152 in 2015).

3.1. Direct Interactions Derived from GPS-Data and Field Visits

The only direct interaction (i.e., recorded GPS locations of both wolf and bear meeting simultaneously at the same place) that we could confirm occurred in 2012 at a yearling moose carcass killed by wolves in late March. The male wolf of the pair approached the carcass (25 days later) and stayed nearby for a day, but did not access it, likely due to the presence of a 9-year old male bear that was feeding at the carcass. There was likely another direct interaction in late June 2014, but the incomplete success of wolf GPS locations that day prevented confirmation. In the latter case, both bear and wolf locations overlapped on the remains of a neonate moose, which had presumably been killed

by the bear, based on sign (a bear daybed and hair) found at the spot. Therefore, direct interactions with bears and wolves meeting simultaneously at the same place seem to be very rare in our study area.

3.2. Temporal Patterns in Bear and Wolf Kill Rates

In total, we found 85 moose neonate calves killed by 14 different bears during a total of 19 different bear-years (for 1 bear, we did not find any killed moose) (Tables 1 and A1), and 95 moose killed by wolves, including 35 neonate calves, 48 juvenile moose (<12 months old), 10 \geq 1-year old, and 2 moose for which it could not be determined if they were yearlings or older individuals, in 7 different wolf territory-years, some of them with two predation studies (spring and summer) per year (Table 2). During the annual study periods between late February and early July, wolf pack kill rate averaged \sim 0.21 moose killed per day, yet it showed much variation and peaked at 0.65 moose killed per day in late May (Figure 1). Bears, with a shorter predation season, started to kill neonate moose calves around mid-May and stopped around the end of June, i.e., bear predation was limited to the moose calving season. Bear kill rates also peaked in late May, reaching a maximum of 0.4 moose killed per day and an average of 0.08 moose killed per day during the predatory period (Figure 1).

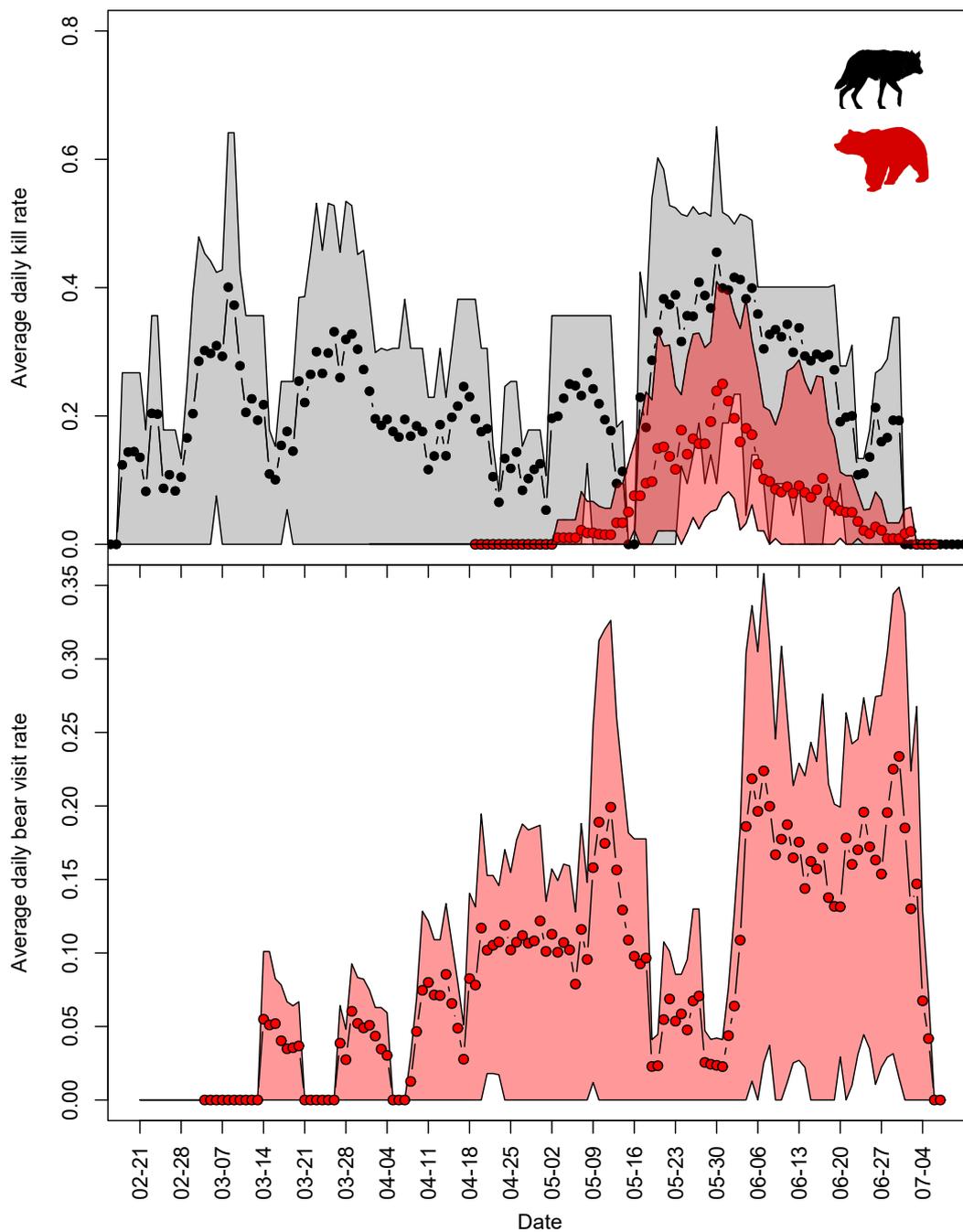


Figure 1. Average brown bear (red dots) and gray wolf (black dots) kill rates and 95% confidence intervals (gray and red shades) in 2014–2015 in central Sweden, calculated with a 7-day moving window (top panel). Daily average bear visits to wolf-killed moose carcasses and 95% confidence intervals in 2014–2015 in central Sweden, calculated with a 7-day moving window (bottom panel). In both panels, the x-axis displays the date.

On average, a bear killed 4.25 moose calves per season ($sd = 3$), but there was large individual variation. Whereas some bears killed up to 10 calves during an early-summer period, one did not kill any (Table 1). On average, an adult female bear killed 5.5 calves ($sd = 3.46, n = 8$), a subadult female killed 1.25 calves ($sd = 1.9, n = 4$), an adult male killed 4.71 calves ($sd = 2.81, n = 7$), and one subadult male killed three calves during the early-summer period overlapping the moose calving season. Adult bears killed significantly more moose calves than subadults (Mann-Whitney $U = 63.5$,

$p = 0.02$), with no significant differences in kills rates between male and female bears (Mann-Whitney $U = 43.5$, $p = 0.75$) or when combining sex and age classes (Kruskal–Wallis chi-squared = 5.74, $p = 0.12$; Figure 2). The bear predatory period in early summer, i.e., the time span between the first and last kill of neonate calves by bears in a given year, showed much individual variation; e.g., the average predatory period for bears that killed at least two calves in a season was 25 days (sd = 11, range 6–41; Table 1).

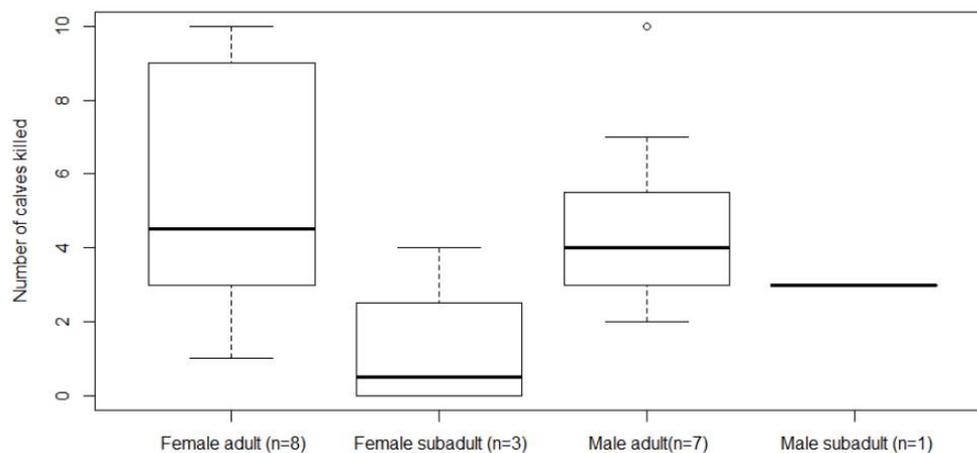


Figure 2. Adult brown bears killed significantly more moose calves in central Sweden than subadult bears, but there were no significant differences in kill rates between male and female bears or when combining sex and age classes, during the early summer period overlapping the moose calving season.

Bear predation focused exclusively on moose neonate calves, and wolves also preyed mostly upon neonate moose in the early-summer period. From mid-May onwards, 81% of the wolf kills were neonate calves and 16% were juvenile (~12 month old) moose, whereas earlier in the year, from late February until the moose calving period started in May, 81% of the wolf kills were juvenile moose <12 months and the rest, older individuals. Therefore, the moose calving period was the time when bears and wolves shared the same resource, with both species relying on neonate moose calves as main prey.

3.3. Scavenging Events

We placed cameras at 62 different kill sites in 2014–2015 (40 at wolf-killed carcasses, most of them yearling and adult moose, and 22 at bear-killed carcasses of neonate moose). Bears were seen on 58% of all cameras, which resulted in 3572 pictures and 122 different events. Wolves were detected on 27% of all cameras, which resulted in 366 pictures of wolves in 31 different events. Bear pictures (of both collared and uncollared bears) were taken at 50% (in 2014) and 60% (in 2015) of the wolf kills, but no wolf picture was taken at bear kills. Occurrence of bears at a carcass varied over time, with a lower average number of bear visits from mid-May to early June, the period when bear kill rates were highest (Figure 1). Adult and subadult bears visited wolf kills, as confirmed by photos of our collared bears, but we did not record any visit of a female bear with cubs of the year at wolf kills, and only two wolf kills were visited by uncollared bear females with 2-year-old cubs. Bears were photo-trapped at kill sites throughout the 24 h, with a peak in the number of bear pictures taken during the evening, whereas wolves were most often photographed at kills during late evening and, especially, at nighttime (Figure A1).

4. Discussion

Our study shows that indirect, nonsimultaneous interactions between wolves and bears at wolf kill sites are the norm, with direct interactions being rare. Bears used wolf kills very often, whereas wolves did not visit, potentially with one exception, bear kills. All neonate moose calves that bears

killed were completely consumed shortly after the kill. However, two thirds of the moose killed by wolves (60 of 95) were ≥ 9 –10 months old; thus, the large carcasses provided feeding opportunities to scavengers. Some individual bears were efficient predators, but preyed exclusively on neonate moose, as described earlier in our study system [26,48] and elsewhere [15]. Bears are also efficient scavengers of other predators' kills [49], as confirmed in our study, with $\geq 50\%$ of the wolf kills visited and thus presumably scavenged by brown bears each study year.

The start of the moose calving period, around mid-May, triggered a clear change in the behavior of some individual bears, which became predatory, but not all did. The average number of neonate moose calves killed by bears during the early-summer study period (4.25) seemed lower than estimated in earlier studies in the same area (6.8 calves for bears ≥ 4 year old in Swenson et al. 2007 [48], and 7.6 calves for 3–13 year old female bears in Rauset et al. 2012 [26]). However, moose densities have declined there (and elsewhere in Sweden) from the 1990s, possibly resulting in a functional response by bears, and in any case preventing direct comparisons [26]. Furthermore, the number of wolf territories in the study area increased substantially after the earlier studies on bear predation were carried out [16], likely causing further changes in the moose population and increasing the number of wolf-killed prey to be eventually scavenged by bears. Most importantly, earlier studies on bears also reported large individual variation in per capita kill rates, 2 to 15 calves per season, which was attributed to a large individual variation in hunting skills and maybe effort [26]. In our study, several single female and male adult bears were the most predatory, preying upon calves in a period up to 4–5 weeks, whereas younger bears killed fewer or even no calves (Table 1). Thus, it seems that some bears actively searched for moose neonates during the calving season, whereas others killed fewer or none moose calves, denoting a more opportunistic predatory behavior and/or different levels of hunting experience and ability. Individual- and age-class differences may reduce intraspecific competition among bears and, most important in the context of this study, may promote interspecific coexistence between wolves and bears [17]. Individual foraging specialization, i.e., different predatory levels among individual bears and bear age classes, could be one of the mechanisms involved reducing competition with the (obligate carnivorous) wolves.

Besides the fact that direct wolf–bear interactions were very rare, no wolves were photographed at bear kills, no females bears with cubs of the year were photographed at wolf kills, and only two females with 2-year-old cubs were photographed at two wolf kills. However, visits of single bears (adults and subadults) at wolf kills were common. Photo-trapped bears at kills were typically smelling and/or biting and moving the carcasses, either standing or lying on top of them, thus reflecting that they were scavenging on them. Wolf absence at bear kills (neonate moose) is likely explained by the fact that little or no biomass is left by the bear. We could not quantify the relative frequency of bear use of wolf kills by bear age and sex class, because assigning bear sex and age class to uncollared bears, which often visited kills based on photos taken by camera traps, is not reliable. However, an interesting result was that females with cubs of the year did not use wolf kills, despite a minimum of 19 collared females with offspring partially overlapped the wolf territories included in our study in 2014 and 2015 (Scandinavian Brown Bear Research Project monitoring data). Bear females with cubs avoid conspecifics spatially and temporally [47,50] and both bears and wolves can kill the offspring of each other [12]. Single bears were photographed at kills throughout the day (Figure A1), likely explaining why we did not record any visit of females with cubs at wolf-killed carcasses. Altogether, different levels of trophic specialization and fine-scale spatial avoidance, with virtually no bear-wolf direct interactions and no use of wolf kills by the most vulnerable bear classes, are mechanisms reducing predation risk and favoring coexistence between sympatric large carnivores.

Fine-scale spatial segregation among large carnivores can be achieved via fine-scale movement patterns, with neighboring individuals avoiding each other when they use shared resources at kill sites [51]. In turn, fine-scale spatial segregation may be a mechanism reflecting on individual habitat selection at larger scales. We have earlier shown that bear density has had a negative effect on the probability of wolf territory establishment during the wolf recolonization of central Scandinavia [16,18]

and that overlapping wolves and bears use different habitat types to a larger extent than expected [17]. Wolves seem to avoid bears at different spatial scales, yet wolf habitat selection within home ranges is not different in areas sympatric and allopatric with bears [19]. The results of our present study show that bears, except females with offspring, take advantage of wolf predation; i.e., indirect interactions at wolf kills sites where bears feed, are hotspots mediating coexistence between these species.

We visited carcasses typically 3 days after a prey was killed to avoid disturbance; human scent may influence the frequency and timing of subsequent visits by the predators, and individual bears and wolves may display different levels of reaction to such disturbance. Most often, >80–90% of the wolf kills (and ~100% of the bear kills) had been already consumed at our first visit. If the wolves returned to a previous kill to resume feeding and it had been partially depleted by bears and/or other scavengers, kleptoparasitism is the ongoing process. If, however, bears and other scavengers use already-abandoned wolf kills, facilitation would be the dominant mechanism. We recorded 31 visits of wolves at ~one third (27%) of their kills, i.e., wolves returned to their kills presumably to resume feeding. The level of consumption of wolf kills, as visually determined at our first visit, is a rough proxy of available biomass at the carcass and it is very similar in bear and non-bear areas (authors' unpublished data). Thus, bear consumption of wolf kills may not necessarily impact wolves in terms of food loss, because wolf kill rates are not higher in bear areas than in non-bear areas [20]. Both kleptoparasitism by bears, which are able to remove substantial amounts of the carcass, and facilitation seem to occur in our system, and these mechanisms likely occur elsewhere, over the vast range where these species overlap.

Direct interactions between wolves and bears might occur at sites other than carcasses, such as breeding dens, where consequences could be most dramatic, e.g., in terms of offspring survival. Nevertheless, all clusters of GPS-locations we have identified and visited in the field ($n = 1942$ clusters), were either daily resting sites (daybeds) and places with no observable sign (90% of the clusters) or sites with predated moose (10%). Even though our predation studies in spring overlapped the breeding season of wolves (and the monitored wolf packs reproduced during the study period) and the season when female bears are coming out of winter dens with their newly born cubs, we did not record any wolf or bear predatory attempt on offspring of the other species. These results reinforce that the vast majority of interactions between wolves and bears occur at kill sites [12], and help discuss mechanisms regulating coexistence of these apex predators.

In Scandinavia, as in other boreal ecosystems, bears rely mainly on berries during summer and autumn, before winter denning [46], and they are also efficient scavengers [49]. Our study documents that during early summer, bears reduce scavenging and actively start to prey on the very same resource that wolves exploit. This defines a seasonal gradient of interspecific competition that peaks in early summer, when wolves also switched from predation on juvenile moose (~80% of wolf kills in late winter) to neonate moose (~80% of wolf kills in early summer). These seasonal prey age preferences by Scandinavian wolves reinforce previous findings [45], and our study documents the importance of both individual variation (in bear predation) and seasonality (in bear diet, predation and scavenging patterns, and in wolf predation on varying prey age classes) for understanding interspecific interactions [33,34].

The role of individual variation, sometimes referred to as personality, at the population level is increasingly recognized in ecology [31,52,53]. Some bears use specific food items, e.g., of anthropogenic origin, that other bears do not use and that reflects on individual differences in movements patterns and habitat selection [54]. The variation in bear predatory behavior at individual and age-class levels documented in our study builds upon this topic. The predatory behavior of a bear may depend on social learning during the ≥ 1.5 year spent with its mother, as suggested for sea otters (*Enhydra lutris*). Consistent individual variation in sea otters' diet could be related to the matrilineal transmission of foraging preferences and/or skills [55]. Matrilines have been documented in Scandinavian brown bears [56], which makes this species suitable for further studies on the topic of individual variation, cultural transmission across generations, and the implications it can have in different grounds. For instance, removal of bears and other large carnivores is a management tool to reduce depredation on livestock, in Scandinavia [15] and elsewhere [4], thus the individual identification and

eventual removal of most predatory individuals, rather than indiscriminate removals, could increase management efficiency. Individual variation in large carnivore behavior is indeed gaining recognition in conservation-oriented research [57]. We suggest that individual variation is also important to understand the outcome of interspecific interactions at higher levels of biological organization, i.e., at the population level of involved species.

Interspecific interactions between species of different size (e.g., larger predators controlling mesopredators and prey numbers [4,58]) and interactions in carnivore assemblages that have been coexisting for a long time, such of those in some African ecosystems (e.g., [59,60]), are better documented than interspecific interactions between top predators, especially in recolonizing scenarios in the northern hemisphere. The recent recovery of some large carnivore populations in North America and Europe allow for overlapping distribution of competing species, and for studies on interspecific interactions and their effects on predation and scavenging patterns [20,61]. Long-term monitoring of bears and wolves combined with intensive fieldwork help understand the mechanisms involved in the coexistence of these apex predators. Therefore, we suggest that this approach can shed light to similar processes elsewhere, in ecosystems holding the same and/or alternative species assemblages.

Author Contributions: Conceptualization, C.M. and A.O.; Methodology, C.M., A.O., and A.U.; Formal Analysis, C.M., A.O., and A.U.; Investigation and Data Curation, A.O. and C.M.; Resources, B.Z., P.W., C.W., H.S., J.E.S., and J.K.; Writing—Original Draft Preparation, A.O. and C.M.; Writing—Review & Editing, all authors; Visualization, C.M. and A.O.; Supervision and Project Administration, B.Z., P.W., C.W., H.S., J.E.S., and J.K.; Funding Acquisition, A.U., B.Z., P.W., C.W., H.S., J.E.S., and J.K. All authors have read and agreed to the submission of the manuscript. All authors have read and agreed to the published version of the manuscript.

Funding: The Scandinavian wolf and bear research projects (SKANDULV and SBBRP, respectively) have been funded by the Norwegian Environment Agency, Swedish Environmental Protection Agency, Norwegian Research Council, Swedish Research Council Formas, Austrian Science Fund, Norwegian Institute for Nature Research, Inland Norway University of Applied Sciences, Swedish University of Agricultural Sciences, Office of Environmental Affairs in Hedmark County, Swedish Association for Hunting and Wildlife Management, WWF (Sweden), Swedish Carnivore Association, Olle and Signhild Engkvists Foundations, Carl Tryggers Foundation, and Marie-Claire Cronstedts Foundation. A.O. and C.M. received QR funding from Nottingham Trent University.

Acknowledgments: We are grateful to everyone monitoring wolves and bears in Scandinavia, including the teams that captured and handled the animals. E.R. Dahl, F. Holen, K. Nordli, J. Romairone, M. Rostad, D. Roviani, and A. Tallian helped us in the field in 2014–2015. GPS data was collected into the Wireless Remote Animal Monitoring database system for data validation and management [62]. We acknowledge the editor and reviewers for constructive comments during the review process.

Conflicts of Interest: The authors declare no conflict of interest. The funders had no role in the design of the study; in the collection, analyses, or interpretation of data; in the writing of the manuscript, or in the decision to publish the results.

Appendix A

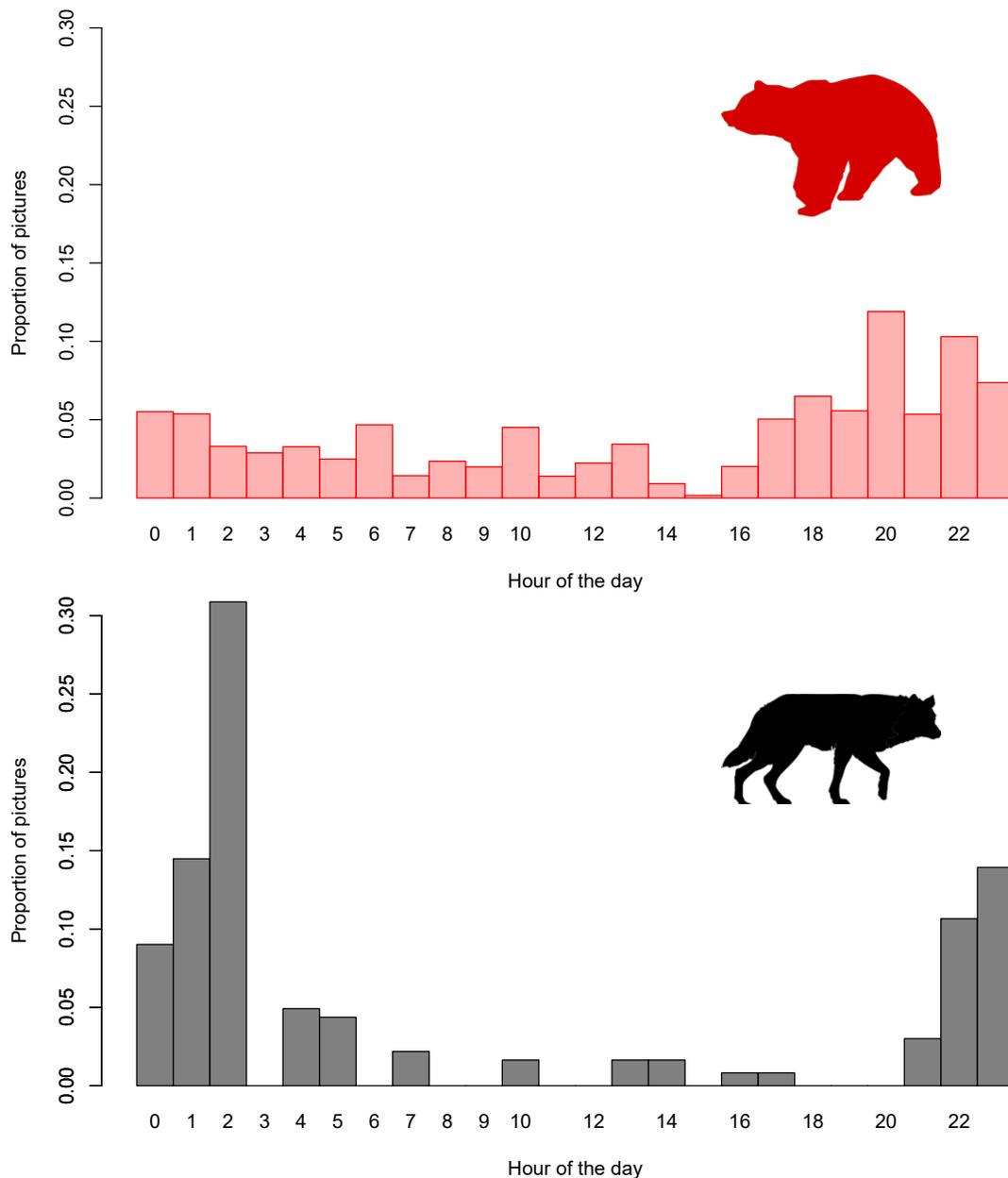


Figure A1. Proportion of bear and wolf pictures photo-trapped per time of day at kill sites (mostly, at wolf kill sites) in central Sweden.

Table A1. Brown bears for which GPS-clusters were visited. Start date and end date columns denote the time during which clusters were checked, i.e., when bears were inside the study area overlapping wolf territories. The study period overlapped the bear mating season, so some males occasionally left the study area and returned. We visited their clusters when they were inside the study area.

Bear and Year of Study	Start Date	End Date
Lafmamack 2014	5/14/2014	5/14/2014
Lafmamack 2014	5/22/2014	5/27/2014
Lafmamack 2014	6/3/2014	6/9/2014

Table A1. Cont.

Bear and Year of Study	Start Date	End Date
Lafmamack 2014	6/12/2014	6/27/2014
Galju 2014	4/28/2014	7/1/2014
Klummy 2014	4/30/2014	5/9/2014
Klummy 2014	5/21/2014	5/26/2014
Klummy 2014	6/12/2014	6/19/2014
Klummy 2014	6/23/2014	6/27/2014
Klumpa 2014	4/30/2014	5/9/2014
Klumpa 2014	5/21/2014	6/27/2014
Risslo 2014	4/22/2014	6/23/2014
Ruta 2014	4/29/2014	6/27/2014
Jarpa 2014	5/6/2014	6/23/2014
Kil-kalle 2014	4/30/2014	6/27/2014
Spjuta 2014	5/11/2014	7/1/2014
Strandas 2014	5/11/2014	6/27/2014
Tappele 2014	5/11/2014	7/1/2014
Abborrgina 2015	5/3/2015	7/1/2015
Gymasa 2015	5/13/2015	7/3/2015
Jarpa 2015	6/12/2015	7/3/2015
Kil-kalle 2015	4/27/2015	5/3/2015
Kil-kalle 2015	5/13/2015	5/16/2015
Kil-kalle 2015	5/27/2015	5/30/2015
Kil-kalle 2015	6/6/2015	6/15/2015
Kil-kalle 2015	6/24/2015	7/3/2015
Klummy 2015	4/27/2015	7/3/2015
Klumpa 2015	4/27/2015	5/25/2015
Klumpa 2015	6/6/2015	6/9/2015
Klumpa 2015	6/21/2015	6/24/2015
Lutane 2015	4/27/2015	5/31/2015
Lutane 2015	6/6/2015	7/3/2015
Risslo 2015	4/27/2015	5/22/2015
Risslo 2015	6/9/2015	6/15/2015
Risslo 2015	6/21/2015	7/3/2015
Tappele 2015	4/27/2015	6/24/2015

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