

Effect of scavenging on predation in a food web

Jarad P. Mellard^{*†} (email: jarad.p.mellard@uit.no)

Sandra Hamel, John-André Henden, Rolf A. Ims,

Filippo Marolla, Audun Stien, Torkild Tveraa, Nigel Yoccoz

January 24, 2020

This manuscript is submitted to *Journal of Animal Ecology* as a Research Article.

Keywords (5): scavenging, predation, food web, feedbacks, interference

Short running title: Effect of scavenging on predation

Number of words in abstract: 161 **Number of words in main text:** 4201

Number of words in references: 1120 **Number of figures:** 4 **Number of tables:** 0

Supporting information: Appendix A containing 9 figures and 2 tables

* Present address of corresponding author :

Department of Arctic and Marine Biology

UiT The Arctic University of Norway

9037 Tromsø Norway

Tel: +47 92262450

Abstract

Scavenging can have important consequences for food web dynamics, for example, it may support additional consumer species and affect predation on live prey. Still, few food web models include scavenging. We develop a dynamic model that includes predators, scavengers, live prey, and a carrion pool to show ramifications of scavenging for predation in simple food webs. We explicitly model carrion biomass and scavenging behavior and investigate the effect of scavenging for predation under different assumptions. Our modeling suggests that the presence of scavengers can both increase and decrease predator kill rates and overall predation in model food webs and the impact varies (in magnitude and direction) with context. In particular, we explore the impact of the amount of dynamics allowed in the predator, scavenger, and prey populations as well as the direction and magnitude of interference competition between predators and scavengers. We provide a road map to the different outcomes and link these theoretical outcomes to evidence from different empirical studies.

Introduction

Scavenging, or the use of carrion for energy gain, is an important energetic pathway in food webs. Some species are specialized scavengers, but most predators also operate as facultative scavengers by returning to scavenge their own kills or kills of others (Moleón et al., 2014). Predator-killed prey can be the most significant source of biomass for scavengers in some ecosystems (Elbroch and Wittmer, 2012; Wikenros et al., 2013). This, along with other recent evidence (Andrén et al., 2011; Krofel et al., 2012; Tallian et al., 2017), suggests a strong interaction between scavenging and predation. However, while predation has been a core subject in ecological research for decades, scavenging in a food web context has not received the theoretical or empirical attention it deserves (Moleón and Sánchez-Zapata 2015). This has led to recent calls for more focus on the link between predation and scavenging (Moleón et al., 2014; Wilson and Wolkovich, 2011).

Scavenging can impact predation in multiple ways. High availability of carcasses is likely to decrease kill rates by predators that are facultative scavengers. However, the presence of other scavenger species may increase predation rates as kills of predators get consumed by others (Andrén et al., 2011). Currently, there are conflicting ideas and varying reports on how scavenging affects predation in different vertebrate predator guilds (Allen et al., 2015; Krofel et al., 2012). In systems with wolves and bears, in both Yellowstone National Park and Scandinavia, the focal predator, the wolf, seems to kill less when scavenging brown bears are present (Tallian et al., 2017). In contrast, in the mountains of Slovenia and Croatia, lynx increase predation rates in the presence of brown bears (Krofel et al., 2012). Thus, the species of predator and scavenger seems to matter. Moreover, scavenging the kills of other species is mostly asymmetrical in food webs, with one species more likely to scavenge another species kills than vice versa (Allen et al., 2015; Krofel et al., 2012).

In a model of lynx and wolverines, Andrén et al. (2011) found that for a given abundance of lynx and wolverines, scavenging by wolverines reduced total predation. However, predation strategies and densities of both the predators and scavengers were kept constant, without the dynamical feedbacks in strategies or densities expected in natural systems. Whether total predation and other predation metrics increase or

decrease is often an important issue in wildlife management. Consequently, we build on previous work examining the interaction of predators and scavengers by creating dynamic models to address how predation rates change with respect to densities of prey and carrion and how changes in predator/scavenger population densities affect these measures. Specifically, we are interested in predation by the main predator, if their kill rates increase or decrease when a scavenger is added to the food web.

We build a generalized model that can be applied to different case studies, focusing on different combinations of two interacting species of predators/scavengers from different habitats around the world. We want to understand how the addition and increasing abundance of a scavenger to a food web affects carrion dynamics, kill rates of the primary predator, and concomitant losses of the prey species. We consider a food web with a focal predator species, and add another species that is also a predator and scavenger, since most scavengers are facultative (Moleón et al., 2014).

Many predator/scavenger populations are controlled by management to low numbers, which, may prevent many of the natural feedbacks in population growth from occurring. Even when predator and scavenger populations are controlled, prey and carrion are likely to have coupled dynamics as they are consumed. We use different constrained versions of the model to understand how variation in dynamic feedbacks affects scavenging and predation patterns and to better represent real world management scenarios. In addition, we investigate how the direction and magnitude of interference competition between the predator and scavenger affects predation rates. Thus, our models not only cover the different assumptions of feedbacks and population regulation, but also include species interactions of both exploitative competition and direct interference competition suspected to occur in real systems.

Building a model of scavenging

We develop a general model based on optimal foraging theory that allows changes in the strategies and densities of predators in response to population changes in prey and carcass availability.

Adaptive behavior of predator

According to Fryxell and Lundberg (1994), predator diet should be a sigmoid function of the density of the most profitable prey, where profitability is defined as

$$\text{Profitability} = \frac{\text{energy content}}{\text{handling time}} = \frac{e}{h}$$

following Charnov (1976); MacArthur and Pianka (1966).

We assume carrion to be more profitable than live prey (Moleón et al., 2015) because handling time h is less and energy content e can be roughly equal to live prey. Formalizing this, e/h for carrion $> e/h$ for live prey. Therefore, we make the scavenging propensity s depend on carrion density C ,

$$s(C) = \frac{zC^b}{1 + zhC^b} \quad (1)$$

where z and b are scaling coefficients that change the magnitude and shape of the scavenging response to carrion density, effectively controlling the switching response. Note that s is a rate, a scavenging response per time based on carrion availability that reflects the natural propensity to scavenge for a species. Many theoretical studies of adaptive foraging include a similar formulation (Abrams and Matsuda, 2004; Charnov, 1976; Fryxell and Lundberg, 1994; MacArthur and Pianka, 1966).

We consider two facultative scavenging species which we refer to as the focal predator and scavenger because we assume they have different scavenging propensities (Figure 1). If the attack propensity on live prey f is negatively related to scavenging propensity s , then the predator, with a lower scavenging propensity, will be more specialized on the live prey over most carrion densities, while the scavenger, with

73 a higher scavenging propensity, will be more specialized on the carrion over most carrion densities. This
 74 is a realistic tradeoff for many predator and scavenger pairs (Krofel et al., 2012) and can also be related to
 75 the handling time of carrion - e.g. a scavenger such as the wolverine can have a lower handling time than a
 76 predator such as the lynx because the lynx opens the carcass, a kind of facilitation (Kane et al., 2017).

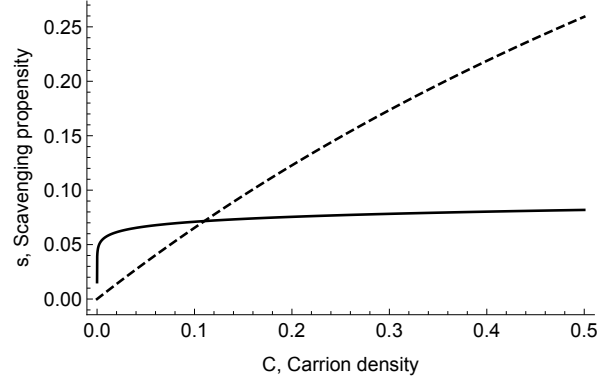


Figure 1: Scavenging propensity with carrion density for the predator (solid line) and scavenger (dashed line). Parameters for the predator P and scavenger S with corresponding subscripts are: $h_{RP} = 4; h_{RS} = 4; h_{CP} = 1.5; h_{CS} = 1; b_P = 0.1; b_S = 1; z_P = 0.1; z_S = 0.7$.

Full food web model

Calculation of predation

The equations for kill rates and scavenging rates are a form of the multispecies disc equation (Charnov, 1976; Fryxell and Lundberg, 1994). Kill rates k_P and k_S for the predator P and scavenger S respectively are

$$k_P = \frac{f_P R}{1 + f_P R h_{RP} + s_P C h_{CP}}, \quad (2)$$

$$k_S = \frac{f_S R}{1 + f_S R h_{RS} + s_S C h_{CS}}, \quad (3)$$

where R and C are the abundances of prey and carrion respectively, f_P and f_S are the predation propensities of the predator and scavenger respectively on the prey, s_P and s_S are the scavenging propensities of the predator and scavenger respectively on the carrion, h_{RP} and h_{RS} are the handling times of the predator and scavenger respectively on the prey, h_{CP} and h_{CS} are the handling times of the predator P and scavenger S respectively on the carrion. We impose the constraint that the attack propensity on live prey f_i depends on scavenging propensity s_i , so that $f_i + s_i = 1$ for $i = P$ or S . This allows us to define a tradeoff since f_i and s_i should be flexible strategies but one likely impacts the other, as is observed in wolverines for example (Mattisson et al., 2016). However, we can relax this assumption by setting f_i to a constant value and have the same qualitative results.

The total number of prey killed by the predator and scavenger per time unit as defined by Equations 2 and 3 is

$$\text{Kills}_{\text{Total}} = k_P P + k_S S \quad (4)$$

where P and S are the abundances of the predator and scavenger respectively. Results with respect to other metrics of predation are presented in Appendix A.

Full dynamical model equations

The general model topology is depicted in Figure 2.

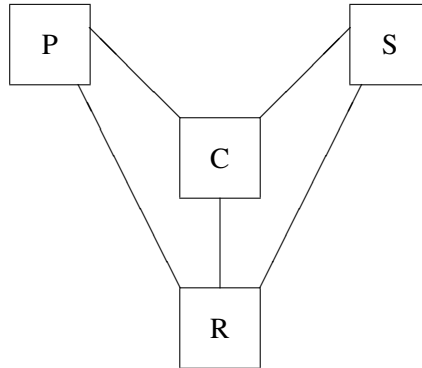


Figure 2: Full model with state variables for prey resource R , primary predator P , carrion killed by predator and scavenger C , and scavengers S . Lines connecting state variable boxes represent potential energetic (biomass) pathways.

104 The full model for the prey R , carrion C , primary predator P , and scavenger S is given by

$$\frac{dR}{dt} = g(R) - k_P P - k_S S, \quad (5)$$

$$\frac{dC}{dt} = (1 - \phi_P) k_P P + (1 - \phi_S) k_S S - q_P P - q_S S, \quad (6)$$

$$\frac{dP}{dt} = P(-m_P + \phi_P k_P a_P + q_P a_P), \quad (7)$$

$$\frac{dS}{dt} = S(-m_S + \phi_S k_S a_S + q_S a_S), \quad (8)$$

105 where ϕ_P and ϕ_S are the proportions of a killed prey immediately consumed by the predator P and scavenger
 106 S respectively (Appendix Table A1), m_P and m_S are the mortality rates of the predator P and scavenger S
 107 respectively, and a_P and a_S are conversion factors of prey or carrion to predator P and scavenger S densities
 108 respectively and are assumed to be constant, and $g(R)$ is the input of the prey to the system defined as
 109 $g(R) = R\mu(1 - R/K)$ where μ is the maximum population growth rate of the prey and K represents prey
 110 carrying capacity or set to constant input $g(R) = I - \nu R$, where I is the influx and ν is the efflux rate.
 111 Scavenging rates are defined for the predator and scavenger to be

$$q_P = \frac{s_P C}{1 + f_P R h_{RP} + s_P C h_{CP}}, \quad (9)$$

$$q_S = \frac{s_S C}{1 + f_S R h_{RS} + s_S C h_{CS}}. \quad (10)$$

112 *Interference competition*

We add interference competition in the model so that presence and density of the scavenger affects the handling time of carrion by the predator (Allen et al., 2014; Elbroch and Wittmer, 2013; Kane et al., 2017; Tallian et al., 2017). We use the parameter n_P to determine the direction and magnitude of the effect of the scavenger on predator handling time. Handling time of the predator on the carrion takes the form

$$h_{CP}(S) = h_{CP0} + \frac{n_P y_P S}{1 + y_P S} \quad (11)$$

where h_{CP0} is the handling time for the predator in isolation, S is density of the scavenger and y_P is a scaling parameter for how much the density of the scavenger affects handling time of the predator. Handling time of the predator can be positively ($n_P > 0$) associated with scavenger density, as has been observed for example in brown bears scavenging wolf kills (Tallian et al., 2017), or negatively ($n_P < 0$) associated with scavenger density, as has been observed for example in bears (Krofel et al., 2012) or wolverines scavenging lynx kills (Mattisson et al., 2011a). It has been proposed that this has to do with the direct antagonistic interactions between predator species that take place near a carcass. The predator may also affect the scavenger through the parameter n_S so the handling time of the scavenger on the carrion takes the form

$$h_{CS}(P) = h_{CS0} + \frac{n_S y_S P}{1 + y_S P} \quad (12)$$

where h_{CS0} is the handling time for the scavenger in isolation, P is density of the predator and y_S is a scaling parameter for how much the density of the predator affects handling time of the scavenger. However, we usually neglect interference by the predator on the scavenger by setting $n_S = 0$. This is for simplicity and to focus on the primary predator. See Appendix Section 1.4 for when $n_S \neq 0$.

Simplified models and further assumptions

We reduce the full model into two simplified models (Appendix Section 1.3.2 and 1.3.3) representing limiting cases that allow for some analytical methods and perhaps more important, to better approximate real systems, giving three models in total:

- Full dynamics model using equations 5-8,
- R and C dynamics model allows only resource R and carrion C dynamics using equations 5 and 6 and setting the predator and scavenger populations to constant values, and
- No dynamics model similar to Andr  n et al. (2011) where R , C , S , and P , are set to constant values and kill rates and total kills are calculated using equations 2, 3, and 4.

We make further simplifying assumptions to focus on the impact of the scavenger on the predator. We

assume the carrion pool, C , is generated by the predator with the proportion of prey biomass left as carrion given by $1 - \phi_P$. We assume the scavenger leaves no carrion, $\phi_S = 1$, assuming this to be inaccessible to the main predator, for example due to caching behavior (Mattisson et al., 2016). This generates some asymmetry between the predator and scavenger, as both the predator and scavenger can feed from the carrion pool generated by the predator. See Appendix Section 1.4 where we consider the carrion pool generated also by the scavenger killing prey, with $\phi_S < 1$. We consider the carrion pool to be available until it is completely scavenged, that is there is no loss or decay due to other scavengers, decomposition, or the environment. We assume processes to operate in continuous time (Focardi et al., 2017; O'Bryan et al., 2019).

We ran numerical simulations of each model using NDSolve in Mathematica v11 (Wolfram Research, Inc.). Simulations are arrayed along a gradient of scavenger mortality for the Full model, allowing us to determine the role of scavenger density on predation. For the two simpler models without dynamics of predators and scavengers, scavenger density was manipulated manually. Initial conditions for each state variable were set to small values and simulations were allowed to run until no further change was observed in the state variables. We then assessed the resulting predation rates and pool sizes from these equilibrium conditions. We conducted a local stability analysis to show that this equilibrium is stable by looking at the sign (all negative) of the eigenvalues of the Jacobian matrix evaluated at the equilibrium (Appendix section 1.1). For the Full model and two simpler models, we focused on parameter values that lead to positive values for densities of both the scavenger and predator in order to compare across models (see Appendix Table A1).

Results

In the Full dynamics model, an increase in the scavenger population density has relatively little effect on total predation (Figure 3a). However, in the models with reduced dynamic feedbacks, i.e. the model with R and C dynamics only (Figure 3b) or No dynamics model (Figure 3c, Appendix Table A2), total predation increases with an increase in scavenger density. The effect of interference competition by the scavenger on the predator, n_p , has a small effect on total predation for the Full dynamics model, R and C dynamics model (Figure 3b), and No dynamics model (Figure 3c). Relative to $n_p = 0$, we see a decrease in total predation for $n_p > 0$ (i.e. positive relation between handling time and scavenger density), and an increase in total predation for $n_p < 0$ (i.e. negative relation between handling time and scavenger density).

Predator kill rate, k_p increases with increasing scavenger density S for the Full dynamics model (Figure 3d), whereas it increases and then decreases with S for the R and C dynamics model (Figure 3e), and is relatively constant with S for no dynamics the model (Figure 3f). Relative to $n_p = 0$, we see a small increase in predator kill rate for $n_p > 0$ and a decrease in predator kill rate for $n_p < 0$ in the Full dynamics model. This contrasts with a decrease in predator kill rate for $n_p > 0$ and an increase in predator kill rate for $n_p < 0$ in the models with reduced dynamics. The combined effects of the amount of dynamics and species interactions on predator kill rate can be seen in Appendix Table A2 and Figure 4. We see that how predator kill rate changes with scavenger density is strongly determined by the amount of dynamics allowed in the model. However, the effects of interference competition by the scavenger on the predator determines the sign of the effect in the No dynamics model. Some of the relationships of predator kill rates to scavenger density reflect the nonlinear changes in pool sizes of resources. In the Full dynamics model, pool sizes are changing with scavenger density but to different degrees (Appendix Figure A2). Predator kill rate increases in the Full model as both carrion declines and prey increases as predators are competitively replaced by scavengers (Appendix Figure A2). In the R and C dynamics model, as scavenger density increases, both R and C decline while P is constant (Appendix Figure A5). Total predation increases with scavenger density (Figure 3b). Predator kill rate goes up sharply initially because C declines sharply as scavenger density increases in the system. Since scavenging strategy follows changes in carrion density closely, the predator

171 must kill more because there is less C . As S further increases, R decreases too and kill rate decreases. Thus
172 the predation pattern is driven by depletion of C and depletion of overall resources by S .

173 The effect of increasing scavenger density on the kill rate of the predator in the No dynamics model
174 depends on n_P , the interference competition as manifested by the scavenger affecting the carrion handling
175 time of the predator. Scavenger density S affects predator carrion handling time h_{PC} and scavenging strategy
176 s in opposite ways, which makes it difficult to predict how kill rates are affected. However, we are able
177 to show analytically that under certain assumptions, S decreases predator kill rate if it increases predator
178 handling time (Appendix Section 1.3.3). Analytical techniques are especially useful if h_{PC} is not in the
179 scavenging strategy equation, s , that is for a predator behaving non-adaptively. This may be the case for
180 wolves and bears, but is unlikely to be true for lynx, wolverines, or cheetahs (Hilborn et al., 2018). If h_{PC}
181 is not in the scavenging strategy equation, s , increasing h_{PC} always decreases predator kill rate, so if $n_P > 0$
182 and scavenger density S increases, predator kill rate will always decrease (Appendix Section 1.3.3).

183 The food-web topology in our model resembles real systems, thus we are able to match our assumptions
184 and predictions with many empirical examples (Figure 4). Most interspecific interactions are asymmetric,
185 with one species more likely to gain access to and stay at a carcass, e.g. lynx and wolverines (Mattisson et al.,
186 2011a) and in wolves (Tallian et al., 2017) or solitary cats (Hilborn et al., 2018) and ursids (Krofel et al.,
187 2012), The interaction between lions and hyenas is perhaps the only approximately symmetrical interaction.
188 In this case, the scavengers contribute significantly to the carrion pool and the predators affect scavenger
189 handling times (see Appendix Section 1.4).

190 The real-world examples of Predator-Scavenger pairs (Krofel et al., 2012) appear to be spread throughout
191 the model parameter space when we overlay the empirical examples on to the phase plot of how predator
192 kill rate is affected by scavenger density (Figure 4). For example, in the lynx and wolverine interaction, lynx
193 appear to quickly abandon a carcass when a wolverine is present, thus a negative n_P effect on handling time.
194 This can decrease the time until their next kill, thus there can be an increase in kill rate (colored region) and
195 exploitative competition can be high (López-Bao et al., 2016). In a lynx and bear system, bears found 32%
196 of lynx-killed prey and lynx lost 15% of their prey biomass to bears, which resulted in a 23% increased lynx
197 kill rate (colored region). The increased kill rate, however, did not fully compensate for their losses to bears

198 (Krofel et al., 2012). In the wolf and bear interaction, the direct interference competition can be high, which
199 may affect kill rates (colored region) (Tallian et al., 2017). Bears appear to be dominant and able to displace
200 wolves from a carcass, however wolves may linger and increase time until their next kill, thus a positive n_P
201 effect on handling time. The interaction between wolves and brown bears in Yellowstone is likely important
202 in understanding the whole ecosystem effects of the return of wolves there (Massey et al., 2013). Species
203 identity is important when considering these interactions (Allen et al., 2015), for example, unlike brown
204 (grizzly) bears, black bears often lose prey to wolves.

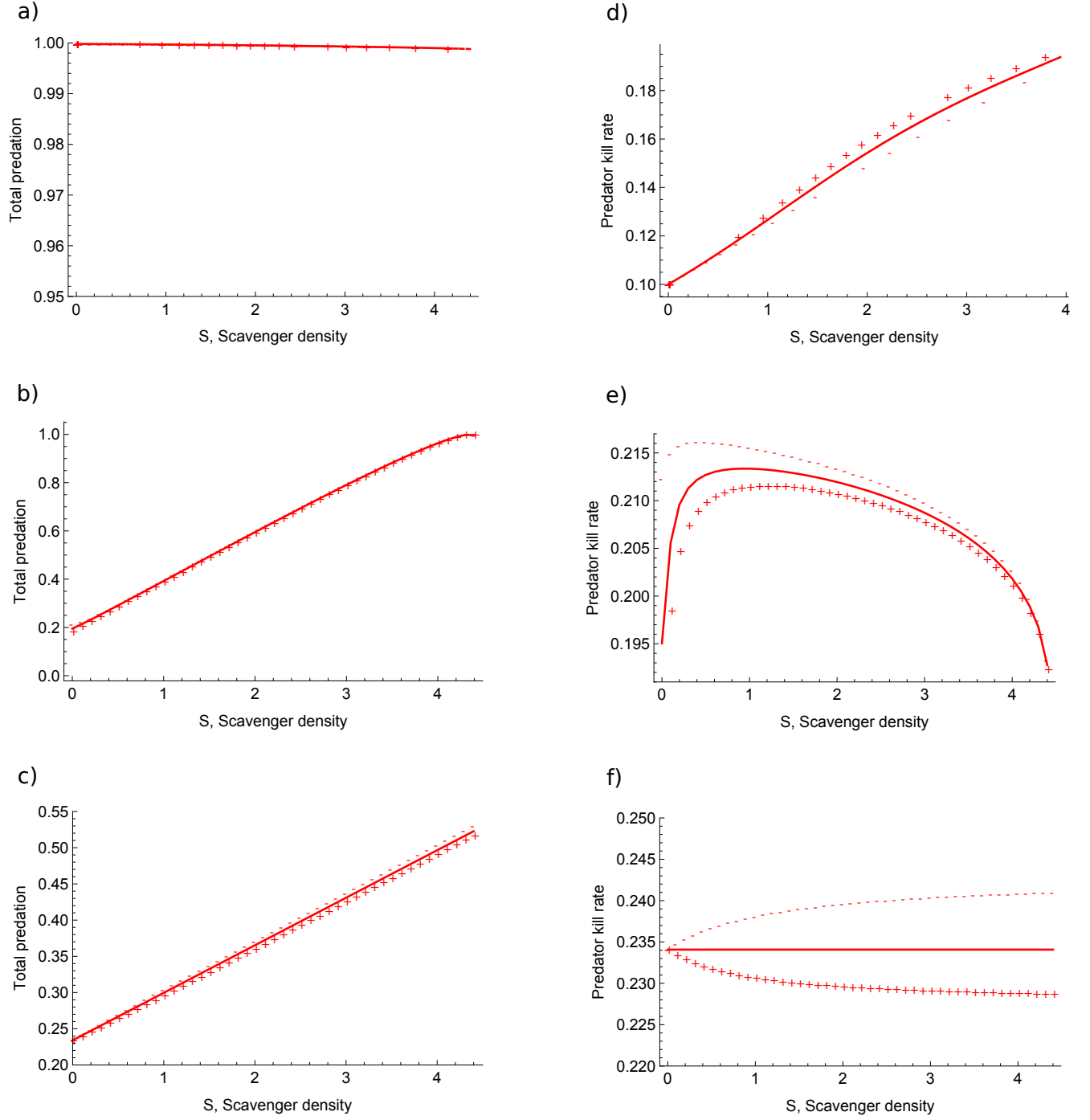


Figure 3: Change in total predation with increase in scavenger density when there is a) Full dynamics, b) only R and C dynamics, and c) No dynamics. Change in predator kill rate with increase in scavenger density when there is d) Full dynamics, e) only R and C dynamics, and f) No dynamics. Solid line: $n_p = 0$, +: $n_p = 1$, and -: $n_p = -1$, where n_p is the effect of scavenger on predator handling time. Parameter values are with accompanying figures for each model in Appendix Sections 1.3.1, 1.3.2, 1.3.3.

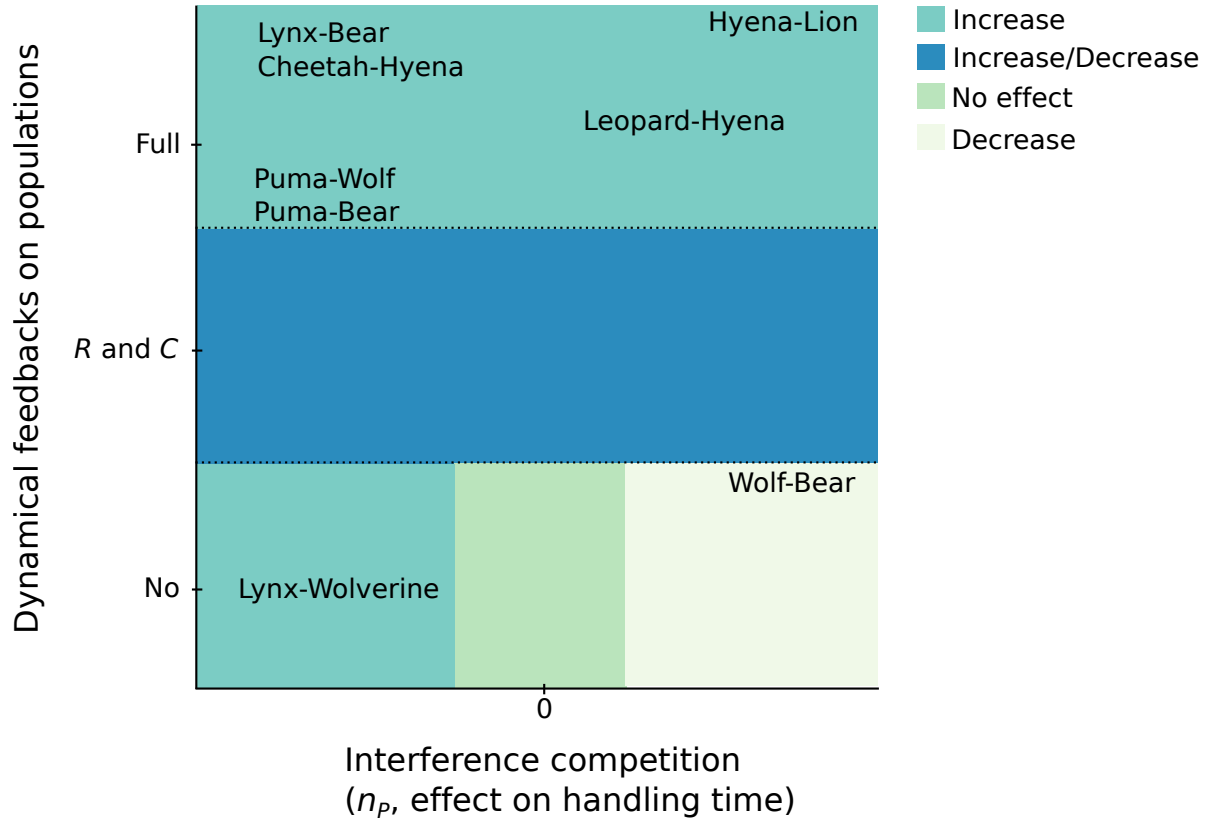


Figure 4: Effect of an increase in scavenger population density on predator kill rate as determined by interference competition (horizontal axis) and dynamical feedbacks on populations in the food web (vertical axis). Interference competition is defined as n_p , scavenger influence on predator handling time. Dynamical feedbacks on populations is distinguished by the three models: Full is Full dynamics model, R and C is resource and carrion dynamics model, and No is No dynamics model. Colored regions indicate the relationship of predator kill rate with scavenger density. Increase/Decrease denotes an increase followed by a decrease with scavenger density. Text on top of the phase plot are real-world examples of Predator-Scavenger pairs taken from the literature. Placement of the coupled Predators-Scavengers is based on evidence from the literature, with some being predictions based on parameters and others being results based on hypothesized parameters. The “Lynx-Bear” comes from Krofel et al. (2012) and is an observed net effect with hypothesized mechanisms. The “Wolf-Bear” comes from Tallian et al. (2017) and is an observed net effect with hypothesized mechanisms. The “Lynx-Wolverine” comes from Mattisson et al. (2011a) and is an observed net effect (usually 0, but can be +) with some mechanisms measured in López-Bao et al. (2016). All other pairs are taken from Krofel et al. (2012) and original sources within and are predictions of the net effects, while the real net effects remain unknown. Note that all pairs are arrayed along the vertical axis based on the hypothesized natural density regulation, and this may vary across different management regimes.

Discussion

We built a dynamical model of scavenging based on foraging theory. Building on previous work, we provide new insights showing that the effect of the interaction between predators and scavengers on equilibrium population sizes can vary depending on the context (Abrams, 1987). Generally, the addition of a scavenger to a food web has effects on the kill rate of the predator. The magnitude and sign of those effects depend on the architecture of the system, primarily determined by the management regime that affects the population dynamics of the predators and scavengers (Figure 4). Only under some circumstances should the abundance of scavengers have absolutely no effect on kill rates: when they result in both no changes in the predation strategy of the main predator and no changes in predator and prey densities, perhaps a highly unlikely scenario. Scavengers still increase total losses in this case (Figure 3c).

When predator, scavenger, and prey abundances are kept constant by management (No dynamics model), scavengers have minimal effects on predator kill rate. With the inclusion of dynamics in predators, scavengers and/or prey, this changes. For example, the addition of scavengers forces the predators to kill more over the entire abundance range of scavengers in the Full dynamics model and over some abundance range of scavengers in the R and C dynamics model (Figures 3, 4). This should be a fundamental prediction - scavengers most likely increase predator kill rates, especially if there are feedback effects on the prey or carrion resources.

For the No dynamics model, the relationship of predator kill rate with scavenger density is flat if the effect of scavengers on predator handling time is negligible ($n_p = 0$), with some small effect for $n_p > 0$ or $n_p < 0$ (Figure 3f). This means that most effects from the addition of scavengers on predator kill rates are through dynamical feedbacks. It is noteworthy that interference competition (n_p) has relatively more of an effect in the simple model with no dynamics than in the other models.

Andrén et al. (2011) defined kill rate as the number of reindeer killed per predator per time unit, but they kept total number of predators (lynx) and scavengers (wolverines) constant and just changed the ratio of predators to scavengers. They found that the expected number of reindeer killed per predator increases as there are more lynx (less wolverines) in the system. Our No dynamics model is somewhat comparable

because it lacks population feedbacks, while behavioral strategy feedbacks always exist in our models. We find relatively constant predator kill rates with increases in scavenger numbers, but we do not hold total number of predators and scavengers constant. Our Full dynamics model is also similar to the model of Andrén et al. (2011) - the total number of predators and scavengers combined is constrained by the total energy in the ecosystem. However, we find relatively constant total predation as we shift the ratio of predators (lynx) to scavengers (wolverines). Our models contribute to a more full understanding of predation on reindeer by building on Andrén et al. (2011) to predict which factors are important and what the overall outcome is when multiple predator species live in proximity to one another and prey on this ecologically and economically important species (Mattisson et al., 2011b; Pedersen et al., 1999; Tablado et al., 2014).

Large carnivores acting as predators have major impacts on ecosystems (Ripple et al., 2014) but scavengers, represented by many of the same and different species spread across all biomes (Moleón and Sánchez-Zapata, 2015), may have similar impacts. Other types of scavengers should be examined as well since they can have an even bigger role than carnivorous mammals in some systems (Henden et al., 2014). An ecosystem may be able to support more obligate-type scavengers if the primary predator/scavenger does not use all the carrion. If these additional scavengers remove carrion that the primary predator/scavenger would intend to use, then we predict that this can also increase kill rates of the predator (Appendix Table A2). Vultures may be one of only a few obligate scavengers in terrestrial systems, but they consume a small or negligible portion of biomass compared to lions and hyenas, and large carnivores in general are able to defend their kills from vultures (Moleón et al., 2014). The savannah system has a number of exemplary predator/scavenger species including vultures, hyenas, lions, jackals and many herbivores like zebra, springbok, wildebeest, oryx, elephants (Getz, 2011). Vultures, lions, and hyenas generally consume 100% of medium and large carcasses in this system (Moleón and Sánchez-Zapata, 2015). Thus, scavenging and the interactions between predator species play a large role in biomass transformation rates in many different ecosystems.

For wildlife management purposes, we would reiterate that the importance of the predator/scavenger interaction depends on the goal of the management. Pool sizes of predators, scavengers, or prey may all be the target of management. In addition, the ratio of predators to scavengers has been suggested as a potential

management target (Andrén et al., 2011; Mattisson et al., 2011a). Management may also be targeted towards ecosystem processes or rates, such as kill rates. Here, we show that while often discussed and measured, these rates are complex aggregate measures of many interacting underlying ecological processes that vary with context. This may make it difficult to understand changes in ecosystem structure based strictly on these rates.

Management that controls predator and scavenger populations to keep them at low numbers as well as regulates prey and carrion abundance prevents many natural ecosystem feedbacks. Such actions reduce the probability that predators increase their kill rate when their prey carrion is eaten by scavengers. This is also where human harvesting of the same prey population can have some influence on the dynamics. However, for more natural systems or in situations where management is not controlling predator and prey numbers, feedbacks make it likely that predators may increase kill rates when their prey carrion is eaten by scavengers. This can occur even if only prey and carrion abundance is allowed to respond dynamically due to consumption, as seen in the *R* and *C* dynamics model (Figure 3e).

Managers of prey populations likely care most about total losses and need to know if expected kill rates from predators/scavengers should be tallied independently of one another to get the total losses in the prey population in an area. We show that in many cases, losses from predator/scavengers are additive, for example lynx and wolverines together are likely additive. However, in other cases or where feedbacks occur, total losses are relatively constant (Figure 3a), so the predators compensate for one another. In some cases, for example wolves and bears together, although wolf (predator) kill rates may go down, total losses may still increase (Appendix Table A2), a previously unknown insight (Tallian et al., 2017). The question that follows is whether managers should try to manage the predators/scavengers in a way that keeps them spatially separated. We suggest that it depends on the predators and if management will allow the populations to grow to their full potential. The general result is, however, given by the total energy constraint on the ecosystem, more predators/scavengers are not supported by keeping them together (Figure A2).

We provide a roadmap to outcomes (Figure 4). Our models are able to reproduce the different patterns observed in predator/scavenger pairs in nature. This ability provides some support to our model, meaning

we may use it to explain the cases and differences between the predator-scavenger pairs. Future empirical studies could be designed to evaluate these predictions. Based on our analysis, data collection efforts should be focused on quantifying the scavenger effect on handling time of the predator, and the amount of population feedbacks in the systems, which perhaps can be extracted from the numerical response. These are the key variables that distinguish the systems and allow us to predict if scavenging will increase or decrease kill rates. One of the fundamental differences we use to distinguish the systems is how the species interaction affects handling times. However, we note that interference competition may interact with exploitative competition through the carrion pool size. This suggests that exploitative competition needs to be evaluated, thus carcass density is important and should be measured. Furthermore, if the z and b parameters related to scavenging rate could be measured in real systems, they would provide key information.

Conclusion

Scavenging can impact predation through multiple direct and indirect pathways: by changing the kill rates of predators, by decreasing available carrion, by bringing predators/scavengers into more direct contact and causing interference, and by changing growth rates of predator/scavenger populations. The importance of these pathways will vary between food webs depending on the identity of the predator/scavenger pairs, which determines their interactions, and how the populations of predators/scavengers are controlled. We suggest this is the reason for the different, and sometimes opposite effects seen, of the presence of scavengers on predator kill rates. Our hope is that this modeling provides a useful framework for predicting and understanding the effect of scavenging on predation across food webs in different types of ecosystems.

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1 Appendix A

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1.1 Equilibrium analysis

The formulation for the equilibrium solution for Equations 5-8 is difficult to read, thus we simplify the equations in order to show the algebraic formulation here. We assume simpler Type I forms for $k_i(R)$ and $q_i(C)$. Furthermore, we reduce the number of variables by assuming $a_P = 1$ and $a_S = 1$. The non-trivial equilibrium for all pools of biomass with positive values has the following expressions for \hat{R} , \hat{C} , \hat{P} , and \hat{S}

$$\hat{R} = \frac{m_S q_P - m_P q_S}{\alpha}, \quad (\text{A1})$$

$$\hat{C} = \frac{k_P m_S \phi_P - k_S m_P \phi_S}{-\alpha}, \quad (\text{A2})$$

$$\hat{P} = \frac{\gamma(-k_P m_S \phi_P q_S + k_S(m_S(-1 + \phi_S)q_P + m_P q_S))}{\beta}, \quad (\text{A3})$$

$$\hat{S} = \frac{\gamma(k_S m_P \phi_S q_P - k_P(m_S q_P + m_P(-1 + \phi_P)q_S))}{\beta}, \quad (\text{A4})$$

where

$$\alpha = k_S \phi_S q_P - k_P \phi_P q_S, \quad (\text{A5})$$

$$\beta = (k_S m_S - k_P m_P)(-m_S q_P + m_P q_S) \alpha \quad (\text{A6})$$

$$\gamma = -v m_S q_P + I k_S \phi_S q_P + v m_P q_S - I k_P \phi_P q_S. \quad (\text{A7})$$

We tested the local stability as determined by the Jacobian matrix evaluated at the equilibrium

$$J = \begin{pmatrix} -v - k_P \hat{P} - k_S \hat{S} & 0 & -k_P \hat{R} & -k_S \hat{R} \\ k_P(1 - \phi_P)\hat{P} + k_S(1 - \phi_S)\hat{S} & -q_P \hat{P} - q_S \hat{S} & q_P \hat{C} + k_P(1 - \phi_P)\hat{R} & q_S \hat{C} + k_S(1 - \phi_S)\hat{R} \\ k_P \phi_P \hat{P} & q_P \hat{P} & -m_P + q_P \hat{C} + k_P \phi_P \hat{R} & 0 \\ k_S \phi_S \hat{S} & q_S \hat{S} & 0 & -m_S + q_S \hat{C} + k_S \phi_S \hat{R} \end{pmatrix}$$

to calculate the eigenvalues, which, we evaluated numerically to check that all eigenvalues are negative, indicating a stable equilibrium.

1.2 Additional calculations

1.2.1 Parameter values

Table A1: Parameter definitions and values used in analyses unless noted otherwise.

Variable or Parameter	Definition	Value (Range)
R	prey resource population	state variable
C	carrion	state variable
P	predator population	state variable
S	scavenger population	state variable
h_{Ci} [time ⁻¹]	handling time of carrion by P or S for $i = P$ or S	function of S or P
h_{Ri} [time ⁻¹]	handling time of prey by P or S for $i = P$ or S	4 (1:8)
n_i [Dimensionless]	interference competition coefficient for P or S for $i = P$ or S	0 (-1:1)
y_i [Dimensionless]	scaling coefficient for interference P or S for $i = P$ or S	1 (0.1:2)
ϕ_i [Dimensionless]	proportion immediately consumed by P or S for $i = P$ or S	0.465 (0:1)
f_i [time ⁻¹]	predation propensity of P or S for $i = P$ or S	function or (0.1:1)
s_i [time ⁻¹]	scavenging propensity of P or S for $i = P$ or S	function of C
b_i [Dimensionless]	scaling coefficient for s_i for $i = P$ or S	1 (0:3)
z_i [Dimensionless]	scaling coefficient for s_i for $i = P$ or S	1 (0:1)
m_i [time ⁻¹]	mortality rate of P or S for $i = P$ or S	0.1,0.21 (0.03:0.5)

401 Calculation of $n_{P,S}$:

402 The interference competition parameter, $n_{P,S}$, affects handling time and thus kill interval, the sum of handling time
 403 of current prey and time spent searching and killing next prey (Tallian et al., 2017). The effect of bears on lynx has
 404 been found to result in 1.5 days shorter feeding (handling) time (Krofel et al., 2012). The effect of bears on wolves
 405 has been found to result in 7.6 hours longer kill interval (handling) time (Tallian et al., 2017). Assuming a kill interval
 406 of two to three days (Tallian et al., 2017), the maximum impact on handling time is thus a 75% decrease or increase
 407 so we present results where we have constrained $n_{P,S}$ to be between -1 and 1.

408 Calculation of $\phi_{P,S}$:

409 The proportion a predator immediately consumes, $\phi_{P,S}$, varies with context. It is possible that a predator kills a
 410 prey and does not consume any of the carcass ($\phi_{P,S} = 0$). Typically however, some proportion is consumed and that
 411 proportion consumed varies between species. For example, a minimum predator consumption based on metabolic
 412 requirements has been calculated for a lynx to be 1.7 kg (Andrén et al., 2011), for a wolverine to be 1.2 kg (Andrén
 413 et al., 2011), and for a wolf to be 3.25 kg (Wikenros et al., 2013). If we consider an average reindeer mass to be 32

414 kg, then percent immediately consumed based on metabolic requirements for a wolf is about 10%, lynx is 5% and
415 wolverine 4% of the carcass biomass. Lynx-killed reindeer are rarely consumed entirely but up to 20-90% can be
416 consumed as lynx use reindeer carcasses for an average of two to three nights and may consume about 2.5 kg per night
417 (Pedersen et al., 1999). A wolverine may consume up to 70% of its kill (Andrén et al., 2011). Andrén et al. (2011)
418 estimate a value of 41% for lynx consumption of slaughter weight of a reindeer since lynx do not usually consume all
419 edible parts. Thus we focus on values between 0.4 and 0.5 but also consider a range of 0 to 1 for $\phi_{P,S}$.

420 Calculation of $z_{P,S}$:

421 The scaling parameter, $z_{P,S}$, affects the relatively fixed propensity to scavenge and may vary between species.
422 Although we generally assume that $z_P > z_S$, we also explore conditions where $z_P = z_S = 1$. For the wolverine, the
423 majority (61%) of its food can come from scavenging lynx killed reindeer (Mattisson et al., 2011a), while for some
424 species we assume this value can be much less so we use the range of 0 to 1 for $z_{P,S}$.

425 *1.2.2 Other metrics of predation*

426 We also calculate several other metrics of predation and report the results in the sections that follow for each model.

427 Prey killed per predator is total predation per predator:

$$\text{Kills}_{\text{Total}}/\text{predators} = k_P + \frac{k_S S}{P}. \quad (\text{A8})$$

428 Per-capita prey killed per predator is total predation per prey per predator:

$$\text{Kills}_{\text{Total}}/\text{prey}/\text{predators} = (k_P P + k_S S)/R/P. \quad (\text{A9})$$

429 Per-capita prey killed by predators per predator is predator kill rate per prey:

$$\text{Kill rate}_{\text{Predator}}/\text{prey} = k_P/R \quad (\text{A10})$$

1.3 Additional results

Table A2: Effect of amount of dynamics allowed in the model on total predation and predator kill rate as scavenger density increases. The interference competition specified by n_P , the effect of scavenger on predator handling time, also affects predation metrics and is why the predator kill rate for the No dynamics model has increases, 0, decreases for $n_P = -1$, $n_P = 0$, $n_P = 1$ respectively.

	Full dynamics	R and C dynamics	No dynamics
Total predation	slight decrease	increases	increases
Predator kill rate	increases	increases/decreases	increases, 0, decreases

1.3.1 Model with full dynamics

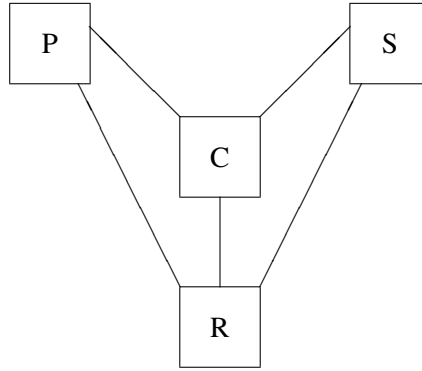


Figure A1: Full model with state variables prey resource R , primary predator P , carrion killed by predator C , and scavengers S . Lines connecting state variable boxes represent potential energetic (biomass) pathways.

In this model, we generally used a fixed prey resource input (Jansen and Van Gorder, 2018), $g(R) = I - \nu R$, to simplify the model and speed up simulations.

For this model with full dynamics:

Increasing scavenger abundance decreases predator abundance until predators go extinct (Figure A2). This is because in the model with full dynamics, there is strong exploitative competition between the predators and scavengers for the prey and carcasses.

Increasing scavenger abundance increases prey abundance until the predators go extinct (Figure A2). Further increases in scavengers then decreases prey abundance because then they are the main predator. This is comparable to the influence of predator/scavenger mortality m on equilibrium prey density in the simple model with only one predator/scavenger. Increasing scavenger abundance decreases carcass abundance until the predators go extinct and carcasses abundance reaches zero (Figure A2). Further increases in scavengers has no effect on carcass abundance because this carcass pool is generated only from the primary predator of the prey (this assumption is relaxed in Appendix Section 1.4).

We now look at predation metrics within the range of parameters where the predators and scavengers coexist to compare to the other models where both guilds are present:

Total predation is relatively constant with increases in scavengers (Figure 3a). Positive n_P (increase in handling time with scavenger abundance) can have a small negative effect on total predation and negative n_P (decrease in handling time with scavenger abundance) can have a small positive effect on total predation. Although total predation is relatively constant, there is a very slight decline with increases in scavengers, and this decline depends on ν , the

457 prey efflux rate from the system. Larger values of v create larger declines. As v approaches I , the prey influx, total
458 predation can become more nonlinear and have a more pronounced decline with increases in scavengers.

459 Predator kill rate increases with scavengers (Figure 3d). Positive n_P (increase in handling time with scavenger
460 abundance) can have a small positive effect on predator kill rate, while negative n_P (decrease in handling time with
461 scavenger abundance) can have a small negative effect on predator kill rate. What is interesting is that the “+” are
462 on the upside part of line, meaning increased handling time actually increases kill rate. However, prey have higher
463 abundance and predators have lower abundance with increased handling time so this makes sense.

464 Prey killed per predator increases with scavengers (Figure A3). Positive n_P (increase in handling time with scav-
465 enger abundance) can have a small positive effect on predation per predator, while negative n_P (decrease in handling
466 time with scavenger abundance) can have a small negative effect on predation per predator. Per capita prey killed
467 per predator decreases and then increases with scavengers (Figure A3). Positive n_P (increase in handling time with
468 scavenger abundance) makes per capita prey killed per predator decrease and then increase even more with scav-
469 engers, while negative n_P (decrease in handling time with scavenger abundance) makes per capita prey killed per
470 predator decrease and then increase less with scavengers. Per capita prey killed by predators per predator decreases
471 with scavengers (Figure A3).

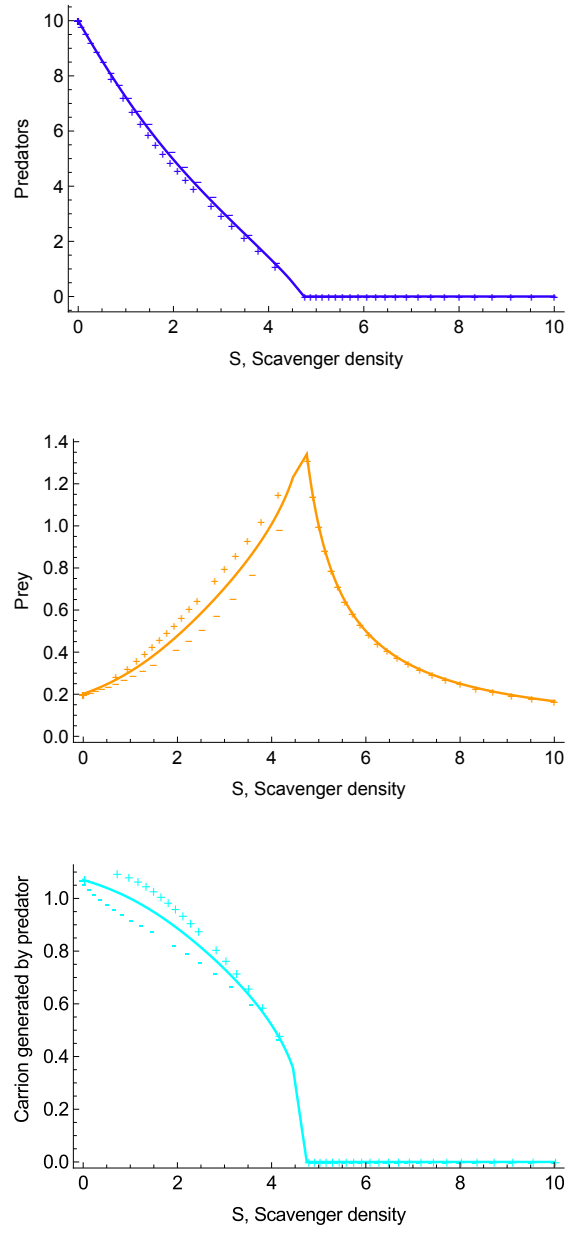


Figure A2: P, R, C. Solid line is $n_P = 0$, + points are for $n_P = 1$ and - are for $n_P = -1$.

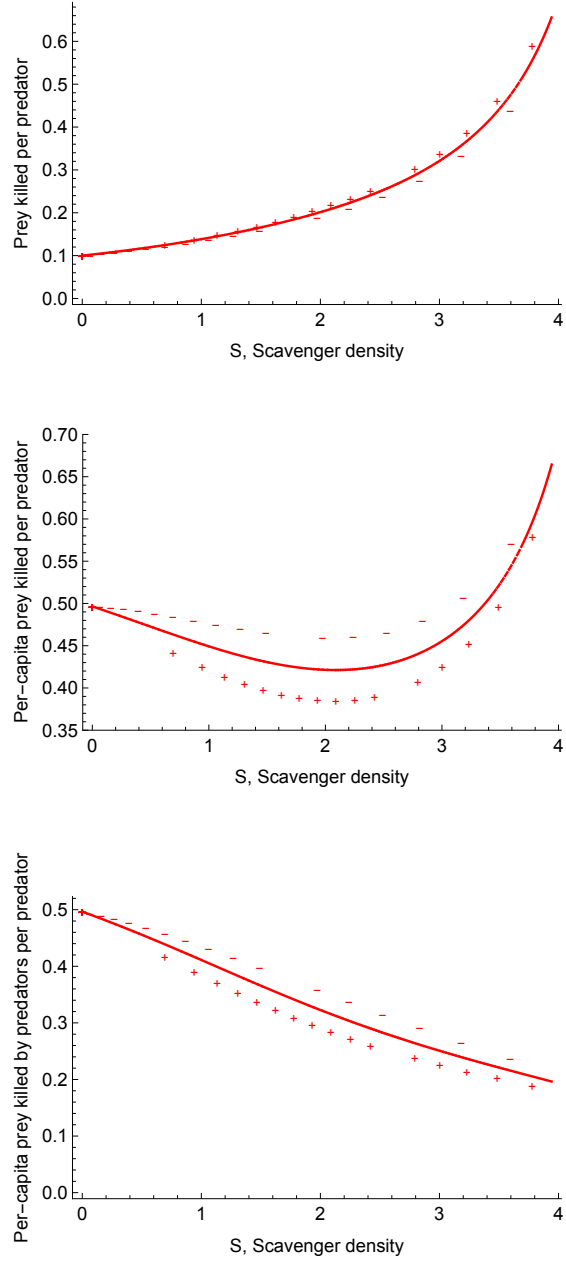


Figure A3: Parameter values for figures of this model are $K = 1, \phi_P = 0.465, \phi_S = 1, m_P = 0.1, h_{RP} = 4, h_{RS} = 4, h_{CP0} = 1, h_{CS} = 1, b_P = 0.1, b_S = 1, z_P = 0.1, z_S = 0.7, a_P = 1, a_S = 1, I = 1, v = 0.001$.

1.3.2 Model with only R and C dynamics



Figure A4: R and C dynamics model with state variables prey resource R and carrion killed by predator C

In this model, we only use equations 5 and 6, setting predator and scavenger populations to constant values. We used a nonlinear growth rate for the prey where the input of the prey to the system is defined as $g(R) = R\mu(1 - R/K)$, however, we find the same qualitative results when we use a fixed prey resource input, $g(R) = I - \nu R$.

For this model with only R and C dynamics:

Increasing scavenger abundance decreases prey abundance and carcass abundance (Figure A5). We have not found population cycles for this model where, although predators are not growing themselves, they are switching between prey types. Total predation increases with scavengers (Figure 3b). Predator kill rate increases and then decreases with scavengers (Figure 3e). There is a small effect of n_P (change in handling time with scavenger abundance). Prey killed per predator increases with scavengers (Figure A6). Remember that the number of predators remains the same in this model. Per-capita prey killed per predator increases with scavengers (Figure A6). Per-capita prey killed by predators per predator increases with scavengers (Figure A6).

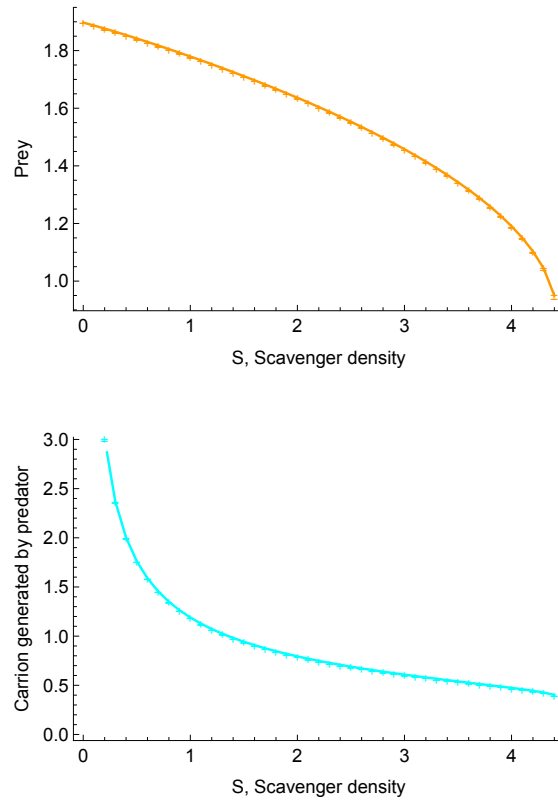


Figure A5: R and C . Solid line is $n_p = 0$, $+$ points are for $n_p = 1$ and $-$ are for $n_p = -1$.

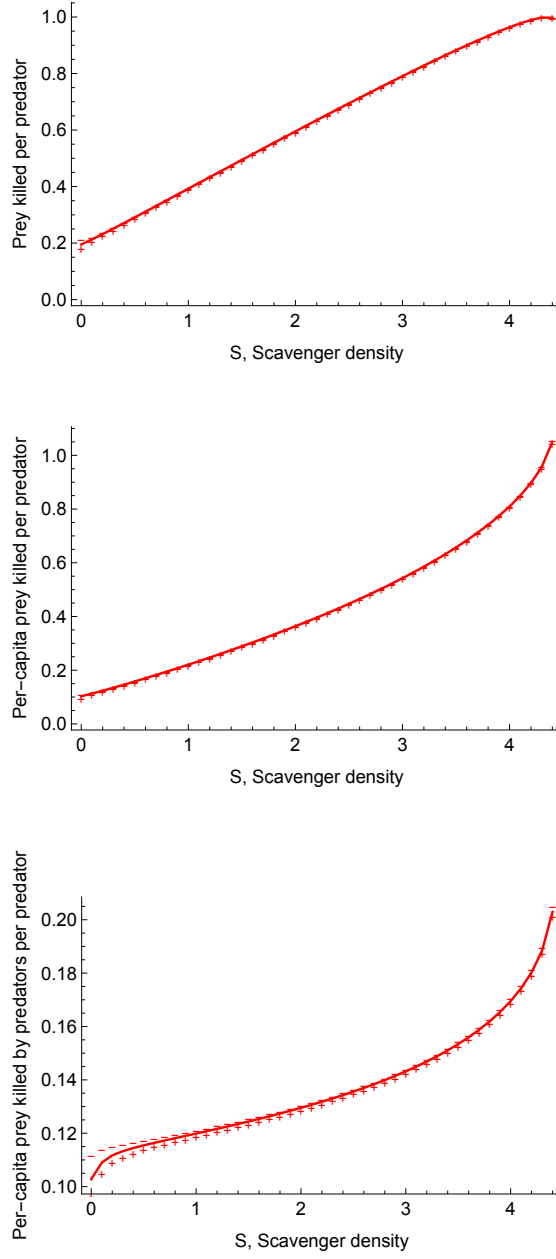


Figure A6: Parameter values for figures of this model are $P = 1, K = 2, \mu = 2, m_P = 0.1, h_{RP} = 4, h_{RS} = 4, h_{CP0} = 1, h_{CS} = 1, b_P = 0.1, b_S = 1, z_P = 0.1, z_S = 0.7$.

1.3.3 Model with no dynamics

For this model with no dynamics:

Total predation increases with scavengers (Figure 3c). Predator kill rate is relatively constant with scavengers (Figure 3f). However, positive n_P (increase in handling time with scavenger abundance) can have a small negative effect on predator kill rate, while negative n_P (decrease in handling time with scavenger abundance) can have a small positive effect on predator kill rate. Prey killed per predator increases with scavengers (Figure A7). This is because number of predators remains the same in this model. Per-capita prey killed per predator increases with scavengers (Figure A7). Per-capita prey killed by predators per predator is constant with scavengers (Figure A7) with a similar small effect of n_P on predator kill rate.

In this simple model, R and C are constant, as is h_{RP} . Recall that $f = 1 - s$, thus predator kill rate is proportional to $\frac{1-s_P}{2+s_P(h_{CP}-1)}$. Therefore kill rate is a function of s_P and h_{CP} . If h_{CP} is not in the equation for s_P (see Appendix Section 1.5 for more discussion of this), increasing handling time h_{CP} always decreases kill rate. With this assumption, if $n_P = 0$, S has no effect on predator kill rate. However, a positive value for n_P increases handling time, and thus increases in S decreases predator kill rate. A negative value for n_P decreases handling time, and thus increases in S increases predator kill rate.

We include h_{CP} in the equation for s_P though because we expect predators to generally behave adaptively (Hilborn et al., 2018). Recall the equation for $s_P(C) = \frac{z_P C^{b_P}}{1+z_P h_{CP} C^{b_P}}$, thus handling time of the predator affects the scavenging rate, which, also affects kill rate. For the moment let us assume that $z_P = 1$ and $b_P = 0$. Then a positive value for n_P means that S increases predator handling time, and thus predator scavenging rate decreases. A negative value for n_P decreases handling time, and thus scavenging rate increases. It can be easily shown that predator kill rate is proportional to $\frac{1}{1+s_P h_{CP}}$. Therefore, because S affects both s_P and h_{CP} , it is not immediately obvious if increasing S will increase or decrease kill rate. However, it can be shown that under these assumptions, h_{CP} is more strongly affected than s_P by S so increases in S decreases predator kill rate for $n_P > 0$ if the predator strategy in scavenging behavior is adaptive to S density. Note this is the same result as above when the predator strategy in scavenging behavior is non-adaptive (does not affect decision) in response to S density so we can conclude that, under these assumptions, S decreases predator kill rate if it increases predator handling time.

For other assumptions on z , b , and C , there are certain combinations of values that preserve this relationship of S always decreases predator kill rate for $n_P > 0$ and increases predator kill rate for $n_P < 0$ (see Appendix section 1.4). This is the result of handling time being in both the equation for s and in the denominator in the functional response.

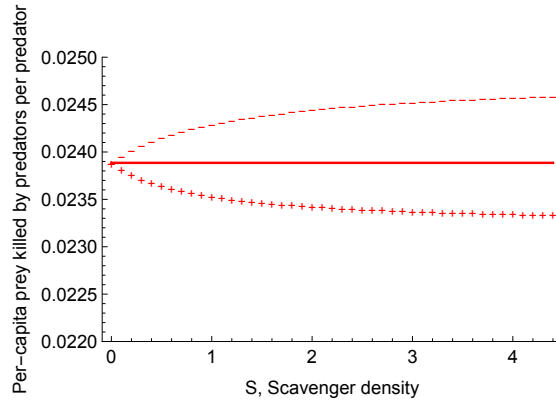
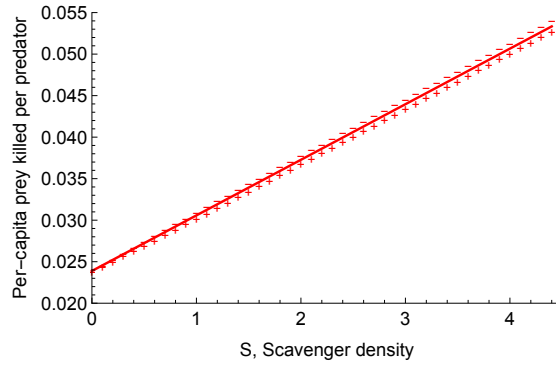
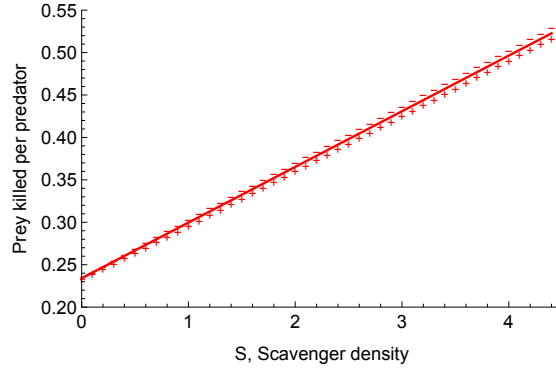


Figure A7: Parameter values for figures of this model are $P = 1, C_P = 12, R = 9.8, h_{RP} = 4, h_{RS} = 4, h_{CP0} = 1, h_{CS} = 1, b_P = 0.1, b_S = 1, z_P = 0.1, z_S = 0.7$.

1.4 Parameters that model more symmetry in the interactions between predator and scavenger

Here we allow the scavenger to contribute to the carrion pool by setting $\phi_S > 0$. This is likely important in the interaction between some species such as the lion and hyena. We also consider $n_S \neq 0$ for added realism of the interaction between species such as the lion and hyena.

These assumptions do make small quantitative differences in the predation patterns we observe, but we do not find any qualitative differences, for example, in comparing the following figures (Figure A8) with the figures in the main text for the full model (Figure 3). For the R and C dynamics model, we also found no qualitative differences with these assumptions.

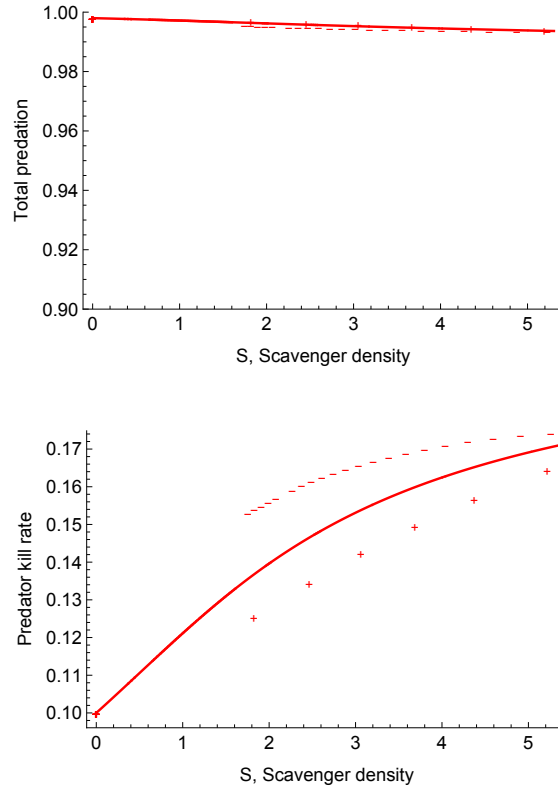


Figure A8: Solid line is $n_P = n_S = 0$, + points are for $n_P = n_S = 1$ and - are for $n_P = n_S = -1$. Parameter values for figures of this model are $K = 1, \phi_P = \phi_S = 0.465, m_P = m_S = 0.1, h_{RP} = 4, h_{RS} = 4, h_{CP0} = 1, h_{CS} = 1, b_P = 0.1, b_S = 1, z_P = 0.1, z_S = 0.7, a_P = 1, a_S = 1, I = 1, v = 0.01$.

1.5 Form of scavenging s equation

529 Here, we investigate the impact of the form of the scavenging s equation if we consider other values of z , b , and C .
530 We know that if we remove handling time h from the scavenging s equation so we only have h in the denominator of
531 kill rate, then kill rate is negatively related to handling time. However, there is a parameter range that allows us to
532 change the handling time and keep the relationship intact of kill rate negatively related to handling time as can be seen
533 in the following figures in the blue regions. Fryxell and Lundberg (1994) have handling time in the preference and the
534 functional response and the step function that resembles ours. They also have a z parameter that dictates the closeness
535 of diet choice to optimal step function, which is what our b exponent does.

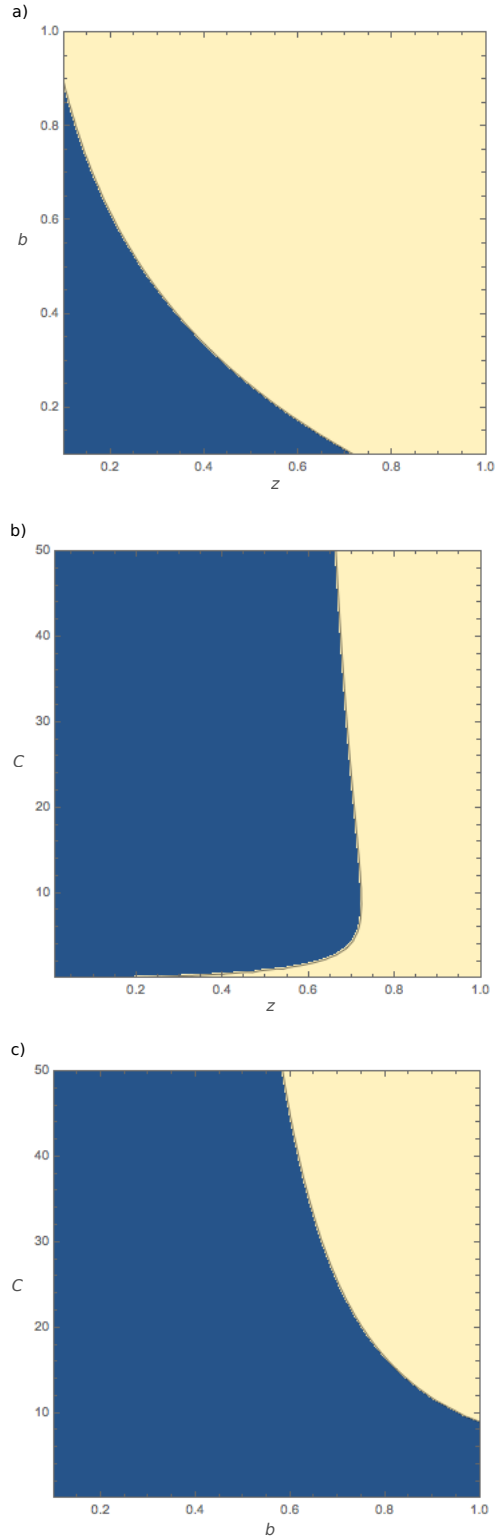


Figure A9: Predator kill rate decreases with handling time (blue region), specifically the derivative of the predator kill rate < 0 . Parameter values for these figures are a) $h = 1, C_P = 12$, b) $h = 1, b = 0.1$, and c) $h = 1, z = 0.1$, with other parameters $P = 1, R = 9.8, h_{RP} = 4, h_{RS} = 4, h_{CP0} = 1, h_{CS} = 1, b_P = 0.1, b_S = 1, z_P = 0.1, z_S = 0.7$.