

Topic: Beaver (*Castor fiber*, *Castor canadensis*) predator avoidance behavior in foraging and territory defense.

#### Annotated Bibliography.

The bibliography is organized by theme, starting from background context of predator avoidance in mammals, followed by the balance between profitability and predation risk, importance of olfactory cues in beavers, and how predation affects beaver territory defense.

#### **Overview of mammalian predator avoidance behavior.**

##### Citation

Hegab, I. M., Kong, S., Yang, S., Mohamaden, W. I., & Wei, W. (2015). The ethological relevance of predator odors to induce changes in prey species. *Acta Ethologica*, 18(1), 1–9. <https://doi.org/10.1007/s10211-014-0187-3>

##### Article summary

In response to predation risk, prey employ morphological, physiological, and behavioural defense strategies. Predator avoidance behaviours are employed early and when their benefits outweigh the costs. Previous studies used an integrated approach to understand the adaptiveness and mechanisms of predator avoidance behaviours. The objective of this review was to explore whether predator odors from different sources cause different prey behavioural responses, outline common predator avoidance behaviours in response to predator odors, explore the behavioural effects of constant predation risk, and whether varying predator odor strengths result in appropriate prey responses that reflect threat level. These questions were answered by reviewing studies relevant to each topic. Predator odors from fur and skin may produce stronger anti-predator behaviours compared to odors from feces and urine because the two types of odors may convey different amounts of risk. Furthermore, although the specific chemical in predator fur that causes avoidance is not known, sulfurous compounds in feces and urine may be the culprit in causing avoidance. To avoid run ins with predators, odor detection is often used before other defense strategies. Common responses to predator odors and periods of high predation risk include reduction in movement and range in the absence of a shelter, reduction in non-defensive behaviours, and moving to a safe area when predator abundance is too high for escape strategies. More constant exposure to predation cues may result in habituation and sensitization when predation risk is low and high respectively. Prey respond more to stronger predator odors, suggesting they can modify responses based on risk levels. By comparing findings from studies, this review suggests that predator avoidance behaviours are sensitive to predation risk levels, follow patterns, and are varied. It identified the need to investigate the physiological mechanisms of prey decision-making under varying levels of predation risk.

##### Contribution

This review compared studies with both contradicting and supporting results which revealed new insights, such as the importance of habitat and escape strategies on odor induced anti-predator behaviours. Avoidance behaviour is suggested to be patterned, highly variable, and modified to match amount of threat from findings that support each other. The importance of olfaction in rodent predator avoidance is highlighted which supports previous studies on beaver predator avoidance. Study organisms were often rodents which means beaver anti-predator

behaviours can be hypothesized from review findings. Beaver specific studies may be conducted to compare beaver anti-predator behaviour to other prey animals.

### **Beavers balance predation risk against profitability when foraging on land.**

#### Citation

Basey, J. M., & Jenkins, S. H. (1995). Influences off predation risk and energy maximization on food selection by beavers (*Castor canadensis*). *Canadian Journal of Zoology*, 73(12), 2197–2208. <https://doi.org/10.1139/z95-260>

#### Article Summary

Studies on beaver foraging have focused on models that take energy acquirement, but not predation risk into account. Such studies have not considered whether their results could be explained by predation risk or balancing of risk and energy consumption. The purpose of this study was to test three beaver foraging models based on increasing energy consumption, reducing predation risk or a balance of both. From September tenth to October 23<sup>rd</sup> at two beaver ponds, each with a family of beavers, two transects perpendicular to the pond with two horizontal rows of different sized aspen trees were prepared. Trees were either 1.5cm or three cm in diameter, with larger trees further away or equidistant compared to smaller trees from the shore. Tree distances were manipulated for each trial but were set up such that profitability was always greater for larger trees and predation risk was always lower for smaller trees. Time required for travel, cutting and consuming trees, speed of beavers and their main predator, coyotes, were measured for model predictions on which trees should be foraged. Water temperatures, location and speed of aspen consumption, and type of tree foraged was also recorded. Each trial lasted until beavers foraged at least 30 trees which took three to five nights. Beavers changed their preference of tree size with changing distances as predicted by the model hypothesizing a balancing of profitability and predation risk. Beavers also consumed aspen almost exclusively in water and increased consumption speed as water temperature dropped which supports the balancing model because increasing consumption rate in cold water minimizes energy loss due to low temperatures and reduces risk from land predators. These results suggest beaver foraging behavior is shaped by a balance between profitability and predation risk. Future studies should focus on testing trade-off foraging models in other animals.

#### Contribution

Previous studies only considered profitability based foraging models which led to results that could be explained by profitability, but by trade-offs with predation risk as well. This study tested three foraging models and results suggest profitability and predation risk shapes beaver foraging. This study supports previous findings that suggested beaver foraging distance and choice changed due to predation. It also supports findings that suggested beavers use predator cues to reduce risk when foraging. This study suggests beaver predator avoidance is balanced with energy intake and that it involves foraging closer to shore and consumption in water, away from land predators.

#### Citation

Smith, D. W., Trauba, D. R., Anderson, R. K., & Peterson, R. O. (1994). Black bear predation on beavers on an island in Lake Superior. *American Midland Naturalist*, 132(2), 248.  
<https://doi.org/10.2307/2426580>

#### Article Summary

Beavers are not typically preyed upon by black bears despite overlapping territories. Beavers settled on Stockton and Outer Islands of Lake Superior followed by bears only on Stockton, where they were found to eat beavers. The study objective was to investigate the extent of black bear predation and beaver foraging and population response to the increasing bear population. Aerial surveys, ground surveys and trappings were conducted to determine beaver population sizes. Radio collars and observations were used to measure bear population, habitat choice and ranges. Beaver forage availability and activity was measured by recording cut and uncut tree species, shrubs, saplings, and their distances from water along 30m transects perpendicular to beaver ponds. Number of beaver lodges disturbed by bears and presence of beaver hairs in collected bear scat was recorded. The study was conducted from 1984 to 1992. The declining beaver population was correlated with a bear population increase on Stockton while beaver population increased on Outer. This finding suggests bear predation may be driving beaver population decline on Stockton. Most beaver lodges were partially destroyed by bears and bears ate trapped beavers multiple times. Six percent of bear scat contained beaver hairs. These findings suggest that beavers are being preyed upon by bears, perhaps due to poor food variety and availability. Beavers on Stockton foraged fewer trees, closer to shore, and foraged more shrubs compared to beavers on Outer. This finding suggests that Stockton beavers are reducing foraging distance and choosing easier forage items like shrubs to reduce bear predation risk. Stockton beaver habitat choice was restricted to deeper waters, unlike Outer beavers which may be in response to bear predation risk. Bears preferred beaver flowages as their habitat where plant foods were more available. This preference may have led to more bear-beaver run ins, increasing beaver predation.

#### Contribution

This study shows evidence for novel bear predation on beavers. It also suggests beavers may prefer deeper water habitats when predation risk is high. It presents evidence for changes in beaver foraging behavior in response to predation risk not seen before which may be due to greater risk posed by bears compared to wolves that have larger ranges and food choice. Previous studies on beavers preyed upon by wolves showed no increase in shrub foraging and foraging distance didn't decrease as dramatically. This study suggests beaver foraging distance, food choice and habitat may change in response to predation risk.

#### Citation

McClintic, L. F., Wang, G., Taylor, J. D., & Jones, J. C. (2014). Movement characteristics of American beavers (*Castor canadensis*). *Behaviour*, 151(9), 1249–1265.  
<https://doi.org/10.1163/1568539X-00003183>

#### Article Summary

American beavers (*Castor canadensis*) are central place foragers that forage around a lodge. Two hypotheses describe movement of central place foragers. The deliberate movement hypothesis predicts that to minimize predation risk, greater speed and wider turns are employed

with increasing distance from the central location by central place foragers. The bimodal foraging trip hypothesis predicts two distances at which central place foragers feed. Shorter distances are used to feed and defend young, while longer distances are travelled to feed the adults themselves. Another hypothesis predicts that sub-adults have larger home ranges because they explore before and after natal dispersal. The study objective was to determine whether beaver movement supports these hypotheses. Using triangulation, hourly distance moved, turning angles, distance from lodge by age group and season, wet and dry, were recorded for 26 radio tagged beavers across nine wetlands in Redstone Arsenal, Alabama for 12 months. Passive integrated transponders were used for identification. Hourly moving speed was positively related to distance from the lodge only in wetland areas, potentially due to alligators hunting beavers. Turn angles decreased with distance only during the wet season. These findings partially support the deliberate movement hypothesis. Lack of correlation in terrestrial areas may be due to usage of multiple refuges and lack of land predators. Beavers showed a bimodal distribution of hourly distance from lodge in months when birthing rates were highest. This finding supports the bimodal foraging trip hypothesis as defending and feeding young may result in shorter foraging distances. Sub-adult average core range was larger compared to yearlings. This finding supports the hypothesis that ranges of sub-adults may be larger due to exploration prior to and after dispersal from the natal group. Future studies should focus on foraging time, feeding habitat and its predation risks for better understanding movement ecology of beavers.

#### Contribution

Movement characteristics of central place foragers have not been adequately studied. This study was first to provide evidence supporting the deliberate movement and bimodal foraging trip hypotheses of central place foragers using small scale movement data in mammals. It supports previous studies that proposed movement speed is affected by predation risk and bimodal foraging in other animals like birds. It also supports findings that sub-adult mammals have greater home ranges, potentially due to exploratory behaviours. The study highlights the potential role of predation risk on shaping beaver behaviour out of the lodge, specifically movement speed which relates to foraging time.

#### Citation

Salandre, J. A., Beil, R., Loehr, J. A., & Sundell, J. (2017). Foraging decisions of North American beaver (*Castor canadensis*) are shaped by energy constraints and predation risk. *Mammal Research*, 62(3), 229–239. <https://doi.org/10.1007/s13364-017-0312-6>

#### Article summary

Herbivores balance predation risk with energy intake when foraging. These factors are used to explain foraging behaviour of central place herbivores that forage around a central location. Optimal and central place foraging models predict that herbivores maximize their net rate of energy intake however it is unknown how energy constraints and predation risk may affect beaver terrestrial foraging range and choice. The objective of the study was to determine the effects of predation risk and energy constraints on beaver (*Castor canadensis*) foraging behaviour. Specifically, it was to test whether beavers use odors for predator avoidance, observe the size of trees foraged with increasing distance from the water, and to test whether foraging distance is affected by predation risk, energy constraints, or both. Natural beaver foraging

behavior was observed by recording the species, distance from shore, and diameter of trees in transects around beaver ponds in the Evo area of Southern Finland. Also, an experimental study was conducted where six beaver sites in the Evo area were surrounded by rows of aspen sticks treated with water, vinegar or wolf urine and sticks taken were recorded over 20 days. Quaking aspen was preferred the most while coniferous species were avoided. This finding may be explained by the greater energetic value and digestibility of aspen. Foraging was greater closer to shore which supports optimum foraging theory and foraging models that reduce predation risk. The diameter of cut trees was smaller further from the shore which contradicts classical central place foraging models that do not consider cost of moving large trees. Sticks treated with water had significantly higher chance of being taken than urine treated sticks however there was no significant difference between vinegar and the other treatments. This finding suggests that beavers could potentially detect predator odors to reduce predation risk.

### Contribution

This article was chosen because it suggests that predation risk may influence beaver foraging behavior by showing beaver avoidance of urine treated aspen. Also, it shows that foraging is greatest near the shore, which may be explained by greater predation risk further from water. These findings agree with previous studies that show avoidance of foraging trails with predator odors and decreased foraging distance when predation is high. The study invites further examination into the effects of predation risk in foraging behavior as most beavers completely avoided urine treated aspen, preventing assessment of how predation risk influenced foraging range.

### Importance of odor cues in predator avoidance.

#### Citation

Engelhart, A., & Müller-Schwarze, D. (1995). Responses of beaver (*Castor canadensis* Kuhl) to predator chemicals. *Journal of Chemical Ecology*, 21(9), 1349–1364.  
<https://doi.org/10.1007/BF02027567>

#### Article Summary

Prey may determine predation risk by detecting predator cues such as feces and urine. Some prey avoid local predator cues more than non-local predator cues. The study objective was to assess whether beavers detect predator chemicals for predator avoidance when foraging and whether sympatric predators cause greater avoidance than allopatric predators. For five nights, 180 families of beavers from either Allegeny State Park or Huntington Wildlife Forest were each presented with 12 aspen sticks, treated with various predator chemicals, diesel, neem oil and controls without chemicals. Predator chemicals were collected from feces and urine. The sticks taken after each night were recorded and were not replaced. The study was conducted in the summer and fall seasons between June to November. Predator chemical sticks were avoided the most and there was no significant difference in usage, although sympatric predator cues were avoided slightly more. This finding suggests that beavers do detect predator chemicals to reduce risk during foraging however are mostly indiscriminate in avoiding sympatric and allopatric predators. Slightly higher avoidance of sympatric predator cues suggests past selection pressures

or learning may be influencing avoidance. There were differences in level and type of predator cue avoidance as well as overall stick usage between the two populations. This finding suggests differences in local predator type and abundance, food availability, and genetic heritage may be influencing foraging behaviour. Sticks were used more in the fall compared to the summer which may be due to more non-woody foods being available in the summer and increased foraging in the fall for food storage. Sticks sometimes had incomplete bark stripping which suggests taste may also be used for predator avoidance. Future studies should focus on identifying the components in predator feces and urine that deter beavers from foraging.

### Contribution

This study suggests olfaction and taste of predator chemicals is important in assessing risk when beavers forage. It also suggests past selective pressures and learning shape current behavior, resulting in behavioral differences among populations. This study agrees with previous findings of mammals using predator chemical cues for avoidance. It also agrees with findings suggesting mammals can be discriminate or indiscriminate in avoiding allopatric and sympatric predators as beavers showed a mix of both behaviors. This study's findings led to subsequent experiments that agreed with the importance of olfaction and the largely indiscriminate avoidance of predator species by beavers.

### Citation

Swinnen, K. R. R., Hughes, N. K., & Leirs, H. (2015). Beaver (*Castor fiber*) activity patterns in a predator-free landscape. What is keeping them in the dark? *Mammalian Biology*, 80(6), 477–483. <https://doi.org/10.1016/j.mambio.2015.07.006>

### Article Summary

Temporal activity patterns are adaptations shaped by processes within and outside an animal such as competition, physiology, and predation. Activity pattern plasticity may increase fitness however it can be restricted by various factors including past predation pressures. Beavers were hunted by Pleistocene humans and were nearly wiped out by modern humans. Beavers under predation display nocturnal and crepuscular activity despite greater energy costs of low temperatures and lack of low light adaptations such as the tapetum lucidum. The study investigated beaver activity patterns in the absence of predators and its response to changes in night length, brightness, and season. From January 2012 to October 2013, 97 camera traps recorded beavers in 34 areas across five types of terrestrial locations expected to have activity. Time of recording, location, and night brightness were used to compare activity between periods of varying night lengths, brightness, and seasons. Activity patterns were nocturnal, like beavers under predation. Activity pattern differences between long and short nights were similar to differences between similar night lengths. These findings suggest beavers can function in light just as well in the dark and therefore past predation pressure from humans may be responsible for nocturnal activity. Beavers displayed more activity during brighter nights which may be due to better foraging outweighing costs of greater predation risk. Activity pattern did not change with the seasons, perhaps due to stored food making increased winter foraging unnecessary. Alternatively, larger family size in the summer may be responsible for an absence of greater number of recordings in winter despite greater foraging caused by a lack of non-woody food sources. Future studies should investigate effects of moonlight brightness on activity patterns for



beavers under predation. These studies would allow comparisons to predator-free beaver behavior for a better understanding of the effects of predation risk on activity patterns.

### Contribution

This article suggests beaver predator avoidance behavior remains despite a current lack of predation. It also suggests behavioural plasticity of beavers is limited by past predation and that current behaviours are molded by present and past factors. This study contradicts previous findings that suggest mammals in colder climates should be diurnal, and that they should be less active in bright nights due to predation risk. It supports previous studies suggesting current phenotypes are shaped by past selection pressures. This article suggests beaver nocturnal activity is to avoid predators and that understanding beaver behaviour requires analysis of past pressures.

### Citation

Severud, W. J., Belant, J. L., Bruggink, J. G., & Windels, S. K. (2011). Predator cues reduce American beaver use of forage trails. *Human – Wildlife Interactions*, 5(2), 296–305.  
<https://doi.org/10.26077/N3Q0-7352>

### Article Summary

Herbivores need to balance energy intake with predation risk to maximize fitness and many mammals use odor cues for predator avoidance. The risk allocation hypothesis predicts that predator avoidance will be greater when prey are under short periods of increased risk compared to long, high risk periods interspaced by short, low risk periods. The objective was to determine whether beavers used odor cues for predator avoidance when foraging on land and to test the risk allocation hypothesis. From September 18<sup>th</sup> to November 13<sup>th</sup> forage trail use is high, 15 beaver lodges in wetlands of Seney National Wildlife Refuge each had two forage trails monitored for activity using infrared cameras. One trail had wolf urine applied while the other trail did not. The number of beavers and other fauna detected was recorded. Beaver duration of stay before and after urine treatment was measured for each trail. The number of beavers detected and duration of stay decreased following urine treatment while the untreated trail had no change in activity. This finding suggests beavers detect and use predator odors to avoid them during terrestrial foraging. It also suggests beavers either reduce foraging or use safer trails when predators are present. Decrease in trail use also supports the risk allocation hypothesis since beavers aren't at high risk of wolf predation at all times. Carnivore species richness increased after urine treatment. This finding may be due to carnivores detecting odors of the same or different species individuals to prevent conflict or to meet. Muskrat and raccoon activity was not affected by wolf urine. This finding suggests that only prey respond to predators or alternatively, muskrats and raccoons are in danger all the time and thus display little predator avoidance behaviour. Beaver avoidance of wolf urine suggests using predator urine can be an effective beaver deterrent.

### Contribution

This article suggests beavers, like other prey mammals, use odor cues for predator avoidance. It also suggests prey display greater predator avoidance when under infrequent, short durations of higher risk compared to when exposed to constant risk. Study findings agree with previous findings that suggest beavers use olfaction to monitor predation risk on land. It also

agrees with the risk allocation hypothesis. This article suggests beavers use odors to detect predation risk and may avoid predators by either reducing foraging or using other trails when the risk is not worth the benefits of foraging along a certain trail.

### **Predation risk and territory defense.**

#### Citation

Rosell, F., & Sanda, J. (2006). Potential risks of olfactory signaling: The effect of predators on scent marking by beavers. *Behavioral Ecology*, 17(6), 897–904.

<https://doi.org/10.1093/beheco/arl022>

#### Article Summary

Beavers are territorial, defending their territory from unfamiliar beavers. Territoriality increases fitness by allowing a monopoly over territory resources. Beavers mark their territory with scents. Territory defense involves overmarking and destroying intruder scent mounds. The scent matching hypothesis predicts that intruders recognize scents of territory owners to avoid fights. Previous lab experiments suggest predator presence may inhibit territory defense behaviors that increase predation risk. No studies have provided evidence for predator effects out in nature. The threat sensitive hypothesis predicts that prey responses are proportional to threat levels. The objective was to determine the effect of predator and non-predator odors on beaver territory defense behavior. Scent mounds were constructed next to 60 active beaver lodges. The mounds only had invading beaver scents or also had predator or non-predator feces. Wolf, lynx, horse, and eland feces were used. Overnight and direct observations of aggressive mound destroying, scent overmarking frequencies, and sniffing was conducted in Telemark, Norway for two consecutive summers. Mound destruction and overmarking frequencies were greatest when beaver scent mounds were absent of other odors, followed by mounds with non-predator odors and those with predator odors. These findings suggest there is selection against territory defense in presence of predators due to increased predation risk. Risk may increase during mound destroying and when reinforcing prey odors by scent overmarking. Avoidance of non-predator odors may reduce parasite infection risks from feces. Sniffing duration was longer when predator odors were present. Beavers may need more time to distinguish two odors compared to when encountering only conspecific odors. There was no significant difference in response to wolf and lynx odor despite wolves being absent in the area. This finding may be due to past predation and instinctual predator avoidance behaviors. Effects of inhibiting territory defense for long durations, especially on fitness, should be studied.

#### Contribution

This study provided evidence supporting inhibition of territory defense behaviours by predators in a natural setting. This finding supports previous studies on mice scent marking however contradicts findings on voles that did not reduce scent marking in response to predators. This study showed that animals may avoid non-predator scents, supporting previous studies that suggested reindeer avoid sheep feces to avoid parasitic infections. This study supports previous studies on beaver predator avoidance relies heavily on olfaction. This study suggests territoriality and predation risk exerts opposing selective pressures on beavers resulting in a trade-off between predator avoidance and keeping intruders out.