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COVER: Dr. Thomas Reimchen recording data for his long-term study on the effects of Pacific salmon carcasses on growth of old (average age ~300 years) Sitka Spruce (*Picea sitchensis*; the moss-covered large tree to his left) on the coast of British Columbia, Canada. Also note the canister of bear spray to his right. See the article Reimchen (145–162). Photo: Dr. Bristol Foster, 5 September 1999 at Princess Royal Island, British Columbia.

## Little evidence that Beach Pea (*Lathyrus japonicus*) toxins cause gait abnormalities in Sable Island Feral Horse (*Equus ferus caballus*)

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### Abstract

*Lathyrus* is a leguminous plant genus notable for its synthesis of lathyrogens, a group of nonprotein amino acids. Lathyrogens can have a range of toxic effects on mammals when consumed in large quantities, but research on lathyrogens has occurred primarily in an agricultural context and on the syndromes (osteo-, angio-, and neuro-lathyrism) that *Lathyrus* consumption causes in humans and livestock. We know relatively little about whether the lathyrogens in uncultivated *Lathyrus* species are more broadly consequential to the ecology of natural ecosystems. For example, the unmanaged Feral Horse (*Equus ferus caballus*) population inhabiting Sable Island, Nova Scotia, Canada relies on forage from coastal maritime plant communities, including Beach Pea (*Lathyrus japonicus*). Horses have a strong sensitivity to lathyrogens compared with many other mammals, and symptoms of lathyrism (gait abnormalities, hernias, hoof malformation) are sometimes observed in Sable Island horses. However, it is unclear whether Beach Pea on Sable Island produces lathyrogens at sufficient concentrations to cause disease. Using liquid chromatography–mass spectrometry (LC-MS), we tested immature, mature, and senescent Sable Island Beach Pea samples for two of the most common lathyrogens: L-β-N-oxalyl-α,β-diaminopropionic acid (β-L-ODAP) and β-aminopropionitrile (BAPN). We detected only trace amounts of β-L-ODAP and no BAPN, causing us to conclude that lathyrogens are unlikely to be the cause of the physical abnormalities observed in Sable Island horses. These results from an iconic Canadian ecosystem provide useful toxicological data for a common coastal maritime plant.

Key words: Lathyrigen; lathyrism; liquid chromatography–mass spectrometry; ODAP; BAPN; DABA; equine; zoopharmacognosy; Beach Pea; *Lathyrus japonicus*; Sable Island; horse; *Equus ferus caballus*

### Introduction

Species of the leguminous genus *Lathyrus* L. (Fabaceae) are notable for producing toxins (lathyrogens) that cause a range of eponymous diseases in mammalian herbivores when consumed in large quantities (Stunkard 1974). One of these, neuro-lathyrism, is among the earliest recorded diseases in humans, dating to writings by Hippocrates (Dastur and Iyer 1959). Neurolathyrism is caused by L-β-N-oxalyl-α,β-diaminopropionic acid (β-L-ODAP), a nonprotein amino acid found in most *Lathyrus* species, most notably Grass Pea (*Lathyrus sativus* L.), a staple crop in some parts of the world (Manna *et al.* 1999). In people affected by malnutrition, prolonged consumption of β-L-ODAP can cause motor neuron degeneration in the distal corticospinal tract (Spencer

*et al.* 1986). This results in a stiff or spastic gait and, in severe cases, leg and arm contractures, irreversible atrophy of leg muscles, and spastic paraparesis (Rao *et al.* 1967; Stunkard 1974; Misra *et al.* 1993).

Other species of *Lathyrus* have been found to produce different toxic nonprotein amino acids. For example, Sweet Pea (*Lathyrus odoratus* L.) synthesizes β-aminopropionitrile (BAPN; Wiley and Joneja 1976). Unlike β-L-ODAP, BAPN interferes with collagen formation (Brüel *et al.* 1998). In doing so, BAPN causes osteolathyrism and angiolathyrism, diseases characterized by bone deformation, hernia formation, and increased risk of aortic rupture (Strong 1966; Conner and Peacock 1973).

Most *Lathyrus* species tested have been found to contain β-L-ODAP or BAPN (Ghosh *et al.* 2015);

however, testing efforts have been heavily biased toward *Lathyrus* species used in agriculture or as ornamentals. As a result, we have little understanding of how the consumption of lathyrogens affects wild animal populations.

Beach Pea (*Lathyrus japonicus* Willdenow) is an uncultivated *Lathyrus* species that has a circumpolar distribution and is found predominantly in temperate coastal environments (Lechowicz *et al.* 1980). Although Beach Pea is not a cultivated crop, its colourful flowers and large pea pod (legume) fruits are sometimes harvested for food on a non-commercial basis (Chinnasamy *et al.* 2004; Egebjerg *et al.* 2018). In the non-peer-reviewed recreational foraging literature, there are conflicting reports as to whether Beach Pea is safe to consume, or if, like other *Lathyrus* species, it is toxic (Turner and von Aderkas 2009; Seymour 2020). Chavan *et al.* (2003) detected small amounts of  $\beta$ -L-ODAP in the seeds of Beach Pea samples collected from Bellevue Beach, Newfoundland and Labrador, Canada, but none in Beach Pea leaves or pods. However, in Grass Pea,  $\beta$ -L-ODAP concentrations can differ with genotype (Kumar *et al.* 2011), abiotic conditions, or developmental stage (Jiao *et al.* 2011). Therefore, it is unclear whether the observations made by Chavan *et al.* (2003) near the northern extent of the Beach Pea's range and at a single developmental stage are broadly representative of the ability of Beach Pea to synthesize lathyrogens. Similarly, it is unclear whether Beach Pea plants might instead produce other lathyrogens (e.g., BAPN) at greater concentrations than  $\beta$ -L-ODAP.

We have recorded gait abnormalities (upward fixation of the patella) in Sable Island Feral Horse (*Equus ferus caballus*; estimated rates and age distribution of

this condition in the population not currently available although observed in both mature and immature horses), which we hypothesized might be symptomatic of neurolathyrism (see Video S1). Furthermore, hernia (Figure 1a) and hoof malformations (Figure 1b) are observed frequently enough that the size, shape, and placement of these abnormalities can be used as diagnostic features to identify individual horses on Sable Island (~3% and 25% of the population, respectively; Welsh 1975; Mellish *et al.* 2021). Both hoof malformations and hernias could be symptoms of the collagen-disrupting effects of BAPN. However, gait abnormalities can also be caused by poor conformation or poor quadriceps muscle tone (Jeffcott and Kold 1982; Andersen and Tnibar 2016). Similarly, hoof malformation and hernias could be caused by environmental or nutritional deficiencies (Verschooten *et al.* 1994; Pollitt 2004). Determining whether biologically relevant levels of lathyrogens are present in Beach Pea plants on Sable Island is useful in testing competing hypotheses about the mechanisms underlying abnormal trait variation observed in Sable Island Feral Horses.

Mammalian species differ in their resistance to lathyrogens. Ruminants are relatively tolerant compared with humans and hindgut fermenters (Hanbury *et al.* 2000), and horses are highly sensitive to *Lathyrus* consumption (Holbrook *et al.* 2015). In horses, neurolathyrism is typically characterized by dyspnoea, as well as gait abnormalities caused by the stiffening and eventual paralysis of the hindlimbs (Enneking 2011). However, the clinical presentation of BAPN poisoning in horses is unknown, because the most well-studied BAPN-producing *Lathyrus* (Sweet Pea) is an ornamental species (Bao *et al.*



**FIGURE 1.** Representative cases of a. umbilical hernia and b. hoof malformation commonly observed in Feral Horse (*Equus ferus caballus*) on Sable Island, Nova Scotia, Canada. Photo a: Mason R. Stothart. Photo b: Alice Liboiron.

2020). Here, we sought to test whether gait and physiological (e.g., hoof deformation, hernias) abnormalities observed in Sable Island horses might be caused by lathrogens, by quantifying  $\beta$ -ODAP and BAPN concentrations in immature and mature Beach Pea plants from Sable Island. If detected, the consumption of Beach Pea plants by Sable Island horses could present a useful opportunity to study the ecology of lathrogen production and detoxification in nature.

## Methods

### *Sable Island study system*

Horses were first introduced to Sable Island, Nova Scotia, Canada (43.932°N, 59.938°W) in the mid-1700s, and they have since remained largely unmanaged, with legal protection after a 1961 amendment to what is now the *Canada Shipping Act (2001)* and, after 2013, under the *Canada National Parks Act*. Since 2007, this horse population has also been the focus of a long-term individual-based ecological study (Regan *et al.* 2020). American Beachgrass (*Calamagrostis breviligulata* (Fernald) Saarela subsp. *breviligulata* [formerly *Ammophila breviligulata* Fernald]) and various forbs, including such species as Seabeach Sandwort (*Honckenya peploides* (L.) Ehrhart) and Common Yarrow (*Achillea millefolium* L.), comprise most of the diet of horses on Sable Island (Welsh 1975). However, the horses also consume Beach Pea plants, which are found in locally high abundance across the island (Figure 2; Tissier *et al.* 2013).

### *Sample collection and preparation*

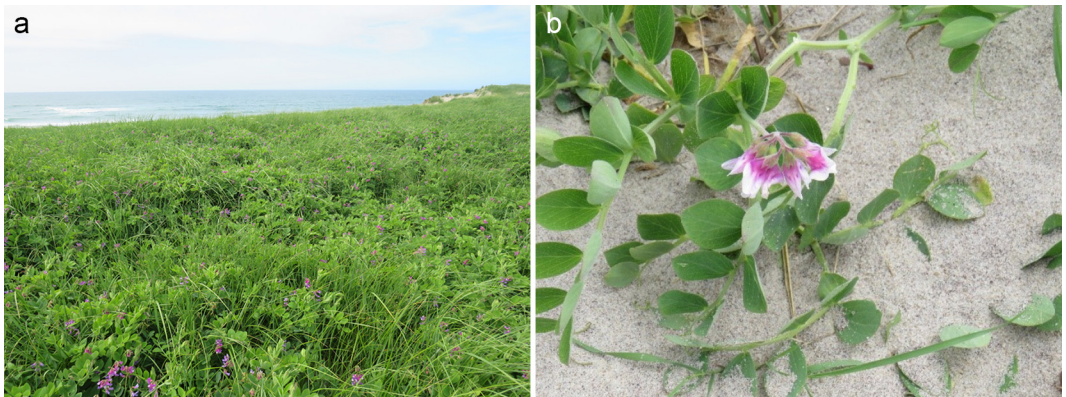
In August 2020, samples of Beach Pea plants were collected opportunistically from five sites across Sable Island. Each site represented a patch of Beach Pea plants, generally intermixed with other vegetation, and all samples were collected within an area of ~10 m  $\times$  10 m. At each site, we collected samples

of young shoots (new growth on small plants), flowering shoots, mature shoots with pods, and senescent shoots (with pods). These shoots were categorized as “young” ( $n = 5$ ) or “old” ( $n = 5$ ; bearing either inflorescence or fruit). Samples were stored at  $-20^{\circ}\text{C}$  for several months, before being lyophilized and ground to a fine powder using a coffee grinder. Storage at  $-20^{\circ}\text{C}$  preserves the stability of  $\beta$ -L-ODAP (Bento-Silva *et al.* 2019).

### *Determination of $\beta$ -ODAP and BAPN by liquid chromatography–mass spectrometry (LC-MS)*

For measurement of  $\beta$ -L-ODAP and BAPN, individual samples (25–50 mg of fine ground material) were extracted in 70% ethanol in three cycles (overnight, 1 h, 1 h) while shaking at room temperature and combined extracts were evaporated to dryness, followed by re-dissolving in 1 mL of  $\text{dH}_2\text{O}$ . This extraction protocol has been validated for  $\beta$ -L-ODAP recovery (Xiong *et al.* 2015; Emmrich *et al.* 2019), although others report reliable extractions can also be obtained using only  $\text{dH}_2\text{O}$  (Bento-Silva *et al.* 2019). Three replicate extractions were performed for each sample. We derivatized 20  $\mu\text{L}$  of amino acids in a 100- $\mu\text{L}$  reaction using Waters AccQ-Tag reagent (Waters, Milford, Massachusetts, USA) following the manufacturer’s protocol. The derivatized samples were diluted 100-fold, and 5  $\mu\text{L}$  samples were analyzed by LC-MS. The LC-MS estimates were normalized by starting sample mass.

Quantification was performed using a Xevo triple quadrupole TQ-S instrument (Waters) as previously described (Emmrich *et al.* 2019). The declustering potential, the collision energy, and the collision cell exit potential were optimized individually using standards and the automated method development tool (Intellistart) in the Waters MassLynx software. The test standards of  $\beta$ -L-ODAP (Lathyrus Technologies,



**FIGURE 2.** a. A plant community dominated by Beach Pea (*Lathyrus japonicus*) on Sable Island, Nova Scotia, Canada. b. A Beach Pea plant. Photos: Mason R. Stothart.

Hyderabad, India) were allowed to isomerize to create a mixture of  $\alpha$ -L-ODAP and  $\beta$ -L-ODAP and BAPN (VWR International). The mass transitions used were 347.16 > 171.099 (ODAP) and 241.108 > 171.099 (BAPN).

Beach Pea extracts were spiked with standards to determine the limit of detection of ODAP and BAPN. To this end, 18  $\mu$ L of young Beach Pea extract was mixed with 2  $\mu$ L of 50 ng/ $\mu$ L  $\alpha$ / $\beta$ -L-ODAP or BAPN standards, in three technical replicates.

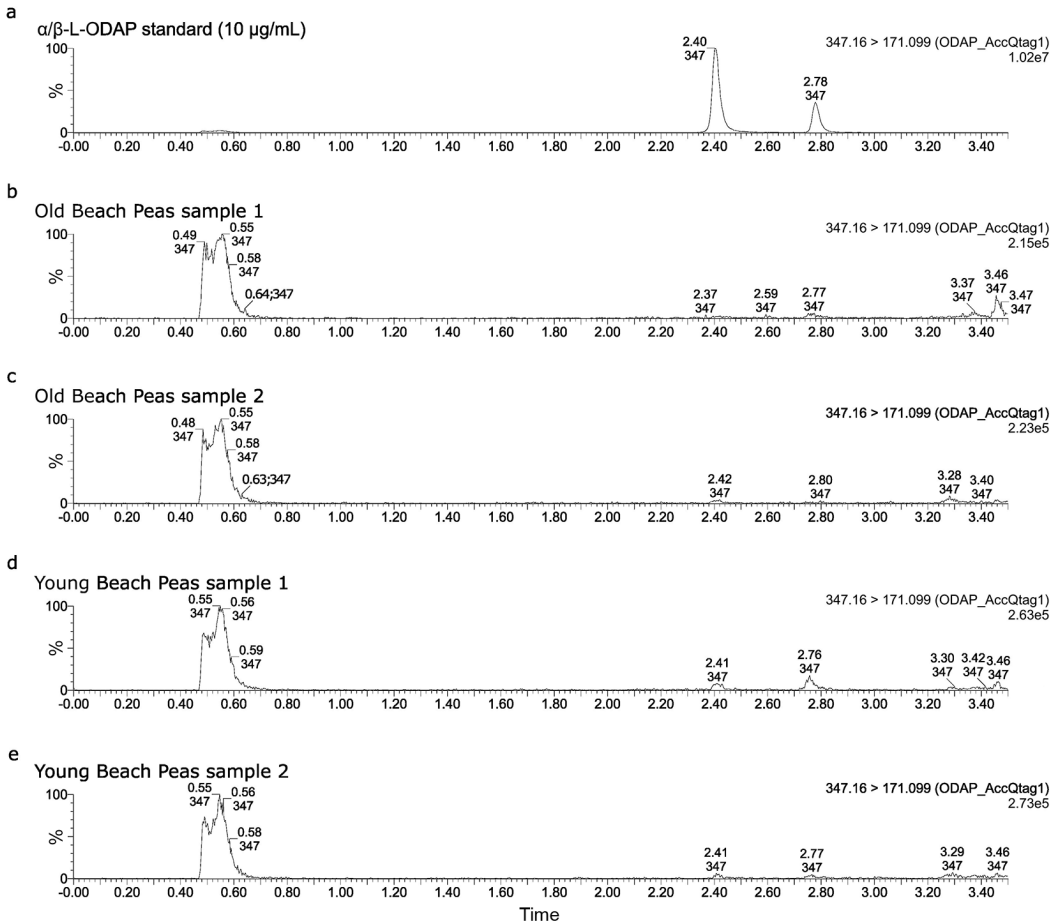
## Results

Spiking of young Beach Pea samples with both  $\alpha$ / $\beta$ -L-ODAP and BAPN at a level of 5 ng/mL produced measurable responses, indicating a level of detection of 200 parts per billion (ppb; Figure S1, S2). Trace levels of  $\beta$ -L-ODAP (<10 parts per million [ppm]) were observed in both young and mature

Beach Pea samples (Figure 3). However, no BAPN (at a level of detection of 200 ppb) was observed in any of the samples (Figure S3).

## Discussion

We observed no evidence of BAPN and only trace amounts of  $\beta$ -L-ODAP in Beach Pea plants collected from Sable Island, regardless of stage of maturity. These results agree with previous findings reported in the literature for the species under a different name (*Lathyrus maritimus* Bigelow, a synonym of *L. japonicus*) and a different chemical name ( $\beta$ -N-oxalylamino-L-alanine, a synonym for  $\beta$ -L-ODAP; Chavan *et al.* 2003). Chavan *et al.* (2003) did not detect  $\beta$ -L-ODAP in the leaves or pods of Beach Pea samples collected from Bellevue Beach; however, they did observe trace amounts in Beach Pea branches (0.65 mg/100 g of dried material), fresh seeds (2.90



**FIGURE 3.** Detection of oxalyl- $\alpha$ , $\beta$ -diaminopropionic acid (ODAP) in Beach Pea (*Lathyrus japonicus*) on Sable Island, Nova Scotia. For each age class, two liquid chromatography–mass spectrometry traces are shown (mass transition 347.16 > 171.099).

mg/100 g of dried material), and mature seeds (4.02 mg/100 g of dried material). In our samples, which comprised a homogenous mixture of leaf, stem, pod, and seeds,  $\beta$ -L-ODAP was only detectable because of the high sensitivity of the LC-MS method (Emmrich *et al.* 2019). The  $\beta$ -L-ODAP might have been present in higher concentrations in seeds of Sable Island Beach Pea plants; however, the leaf-stem-pod-seed mixtures that we assayed are more ecologically realistic approximations of how Beach Pea plants are consumed by the horses on Sable Island, which do not discriminate in terms of what parts of the plant they consume. Regardless, using either our estimates of  $\beta$ -L-ODAP in Beach Pea seeds or those made by Chavan *et al.* (2003), we expect the ingestion of lathyrogens by Sable Island horses to be negligible. Previous estimates of  $\beta$ -L-ODAP concentrations in Beach Pea plants are 10–50-fold lower than what is reported in the seeds of “low  $\beta$ -L-ODAP” cultivars of Grass Pea (Das *et al.* 2021). For comparison, Grass Pea seeds with  $\beta$ -L-ODAP-concentrations of ~20–2590 mg/100 g of material are widely consumed as human food and only pose a health risk if used as a staple food source during times of prolonged malnutrition.

Beach Pea plants on Sable Island do not appear to contain biologically significant concentrations of  $\beta$ -L-ODAP, but we cannot rule out the possibility of seasonal variation in lathyrogen content, because all samples were collected in August. Lathyrogen concentration can be higher in young than old plants (Jiao *et al.* 2011), and so, it is possible that  $\beta$ -L-ODAP concentrations may be greater in the early spring than in August. Similarly, environmental conditions, such as drought, salinity, toxic heavy metals, and symbioses with *Rhizobium* bacteria, could also affect  $\beta$ -L-ODAP content (Jiao *et al.* 2011).

Nonetheless, our results do not support the theory that Beach Pea consumption causes gait abnormalities, hernias, and hoof malformation in feral Sable Island horses. The gait abnormalities we see in Sable Island horses are also consistent with upper fixation of the patella (locking stifles). Locking stifles can be caused by deformations in femur, patella, or tibia, and poor tone in the quadriceps muscles, preventing patellar ligaments from being released from the medial trochlear ridge (Jeffcott and Kold 1982; Labens *et al.* 2005; Andersen and Tnibar 2016). These symptoms are consistent with osteolathyrism and neuro-lathyrism, respectively (Stunkard 1974), but they can also be caused by injury or have a genetic basis (Kidd 2017). Similarly, although the frequency of hernias and hoof malformation in this population could signal disrupted collagen formation, hernias in horses can be congenital or caused by blunt trauma or pregnancy and parturition (Moustafa *et al.* 2022) with

many of the hernias we observe in horses on Sable Island appearing to be umbilical hernias. Meanwhile, hoof malformations can be linked to dietary imbalances or laminitis, which itself can be indicative of systemic disease (Verschooten *et al.* 1994; Pollitt 2004; Patterson-Kane *et al.* 2018). The sandy substrate of Sable Island may also contribute to hoof overgrowth, because horses do not have access to hard substrate (e.g., rock, gravel) which might otherwise wear hooves. However, hoof abnormalities are sometimes observed among young horses (~1 year of age) on Sable Island, while older horses (>15 years of age) can present a normal hoof phenotype.

Although we did not detect harmful concentrations of lathyrogens, genomic analysis would be necessary to conclude that Beach Pea plants are entirely incapable of BAPN synthesis. Similarly, we are also unable to reject the hypothesis that Beach Pea plants produce some other, yet unidentified disease-causing nonprotein amino acid. As an uncultivated plant species that is not commonly used as forage for livestock, a novel compound in Beach Pea plants is less likely to have been previously characterized. For example, while we tested for two of the most common lathyrism-causing compounds, Grass Pea has been found to produce the lathyrogen 2,4-diaminobutyric acid (DABA; Foster *et al.* 1987). The DABA inhibits ornithine decarboxylase and thereby prevents ammonia from entering the urea cycle (O’Neal *et al.* 1968), resulting in acute or chronic hyperammonemia (Rowe *et al.* 1993; Auron and Brophy 2012). The abnormalities in Sable Island horses that motivated our study are not consistent with acute hyperammonemia (Sharkey *et al.* 2006). However, Feral Horses living under challenging environmental conditions might be unlikely to survive to the point of acute presentation of this disease, and the symptoms of chronic hyperammonemia might be hard to detect using observational methods (Dunkel *et al.* 2011). In the future, Beach Pea plants should be assayed for DABA to provide a more comprehensive toxicological profile.

### Author Contributions

Writing – Original Draft: R.J.G. and M.R.S.; Writing – Review & Editing: A.E., P.M.F.E., P.D.M., J.P., R.J.G., and M.R.S.; Conceptualization: P.D.M., J.P., R.J.G., and M.R.S.; Investigation: A.E., P.M.F.E., and R.J.G.; Methodology: A.E. and P.M.F.E.; Formal Analysis: A.E. and P.M.F.E.; Funding Acquisition: P.D.M. and J.P.

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**SUPPLEMENTARY MATERIALS:**

**VIDEO S1.** Gait abnormality in a Sable Island Feral Horse (*Equus ferus caballus*), Sable Island, Nova Scotia, Canada. Video taken on 17 July 2021, by Mason R. Stothart.

**FIGURE S1.** Oxalyl- $\alpha,\beta$ -diaminopropionic acid spiking experiment.

**FIGURE S2.**  $\beta$ -aminopropionitrile spiking experiment.

**FIGURE S3.** Detection of  $\beta$ -aminopropionitrile (BAPN) in Beach Pea (*Lathyrus japonicus*) on Sable Island, Nova Scotia.

## Note

### Displacement of migratory Bull Trout (*Salvelinus confluentus*) spawning by a newly constructed beaver (*Castor canadensis*) dam in a west-central Alberta stream

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#### Abstract

Despite broad overlap of the ranges of Bull Trout (*Salvelinus confluentus*) and North American Beaver (*Castor canadensis*), relatively little is published in the peer-reviewed literature on their interaction. Beavers are ecosystem engineers with the potential to transform lotic environments, while Bull Trout are of conservation concern and subject to various protective measures throughout their range. The impact of beaver activity on trout populations is context dependent, and our appreciation of the scope of this impact depends on documentation. We report on the disruption of Bull Trout spawning migration by a newly constructed beaver dam in Fall Creek, a west-central Alberta stream in the North Saskatchewan River drainage system. Large Bull Trout have been documented travelling up to 74 km to spawn in Fall Creek. Since 2007, we have used autumn redd counts to monitor the abundance of spawning Bull Trout in the stream. In 2022, we documented displacement of Bull Trout spawning in Fall Creek by a newly constructed beaver dam. Over 60% of Bull Trout redds were observed in a reach downstream of the dam rarely used by spawning fish. We also observed seven post-spawn Bull Trout, representing over 10% of the spawning run, apparently stranded in a shallow impoundment upstream of the dam. It is unclear whether this displacement will have a long-term impact on the Fall Creek Bull Trout population. However, the seasonal impact on spawning adults is unprecedented in the 15 years we have monitored the population.

Key words: North American Beaver; *Castor canadensis*; Bull Trout; *Salvelinus confluentus*; spawning; redd; migratory; Alberta; impact

Bull Trout (*Salvelinus confluentus*) is a char native to western Canada and the United States Pacific Northwest. The species has declined in abundance and distribution and is subject to various protective measures throughout much of its range (COSEWIC 2012). The Saskatchewan-Nelson Rivers designatable unit (DU) of Bull Trout occurs entirely within Alberta and is listed as Threatened under the Canadian *Species at Risk Act* (Sinnatamby *et al.* 2020; SARA Public Registry 2024). As a member of the family Salmonidae (i.e., trout, salmon, char, grayling, and whitefish), Bull Trout often exhibit a migratory life history and require sediment-free gravel and cobble substrates to reproduce successfully (Beechie *et al.* 2008; COSEWIC 2012).

Beavers (*Castor* spp.) are ecosystem engineers, and their dam building behaviour can transform lotic environments (Johnson-Bice *et al.* 2018; Larsen *et al.* 2021). Appreciation of the role of beavers in the restoration of degraded river habitats is growing, but the use of beaver-related restoration practices for recovery of native salmonids can be controversial (Pilliod *et al.* 2018; Larsen *et al.* 2021; Wolf *et al.* 2024). Beaver dams impound flowing water and can impede fish migration and increase sedimentation, reducing salmonid spawning success (Johnson-Bice *et al.* 2018; Larsen *et al.* 2021). However, these impacts are context specific and vary widely, largely precluding universal statements on the impact of beaver dams on salmonid populations (Collen and Gibson 2000;

Kemp *et al.* 2012; Larsen *et al.* 2021). This complexity fosters uncertainty, which can generate controversy when stakeholder perspectives on the positive and negative aspects of beaver activity differ (Larsen *et al.* 2021).

Despite broad overlap with the range of North American Beaver (*Castor canadensis*), surprisingly little has been published in the peer-reviewed literature on the interaction between Bull Trout and beavers (but see Jakober *et al.* 1998, 2000; DuPont *et al.* 2007; Wolf *et al.* 2024). Here we report on the displacement of spawning Bull Trout by a newly constructed beaver dam in Fall Creek, a west-central Alberta stream in the Saskatchewan-Nelson Rivers DU. Documentation of field observations, such as ours, provides context for assessing the scope of salmonid–beaver interactions generally (Kemp *et al.* 2012; Johnson-Bice *et al.* 2018) and a useful case study for management of Bull Trout specifically.

Fall Creek (coordinates at the mouth: 52.2639°N, 115.5521°W) provides the only known spawning habitat for migratory Bull Trout in the Ram River watershed. The stream is of high conservation value and has been the focus of various conservation measures including a closure to angling and removal of off-highway vehicle stream crossings (reviewed in Judd *et al.* 2023). The stream is a fifth-order tributary (September mean discharge  $\sim 0.37$  m<sup>3</sup>/s) of the Ram River in the foothills of Alberta  $\sim 44$  km southwest of Rocky Mountain House. A waterfall, 7.5 km upstream of the mouth, constitutes a barrier to fish passage, and the headwaters of Fall Creek were historically fishless. Below the falls, Fall Creek has a moderate gradient (1.6%), is dominated by gravel and cobble substrates, and is heavily influenced by groundwater (Rodtka *et al.* 2010), characteristics typical of Bull Trout spawning habitat (COSEWIC 2012). Alberta Conservation Association documented large (i.e., mean fork length  $\sim 58$  cm, 1.8 kg) Bull Trout travelling up to 74 river km from the Ram, North Saskatchewan, and Clearwater rivers to spawn in Fall Creek (Rodtka *et al.* 2010). This population averages 73 Bull Trout annually (Rodtka *et al.* 2010; Judd *et al.* 2023).

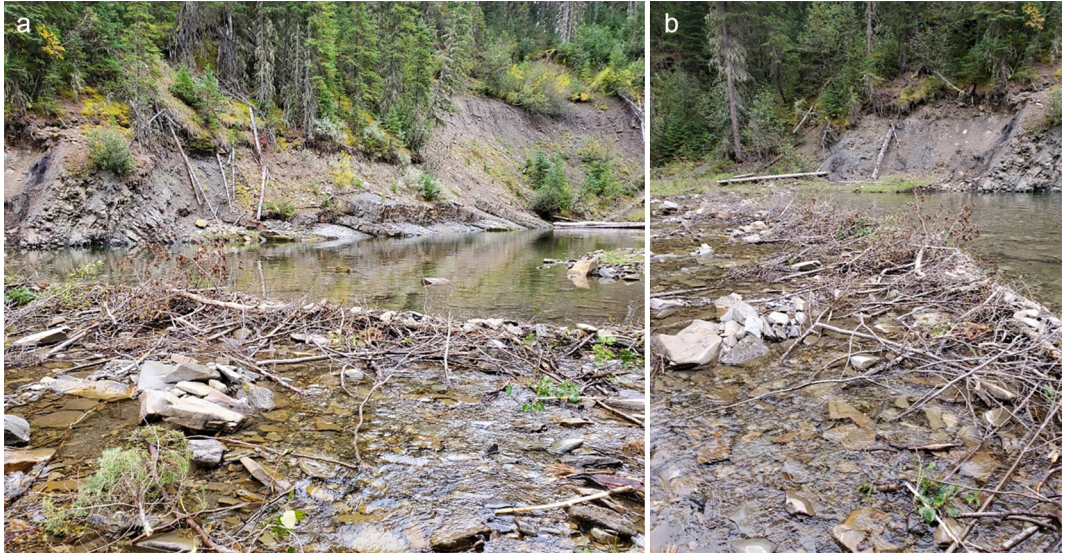
Since 2007, we have used autumn redd counts to monitor the annual abundance of spawning Bull Trout in Fall Creek. Redds are the gravel nests constructed by female salmonids while spawning and can be used as an index of abundance (Beechie *et al.* 2008; Howell and Sankovich 2012; Kaeding and Mogen 2023). Although suitable spawning habitat appears to occur throughout much of the 7.5 km of stream below the barrier falls,  $>95\%$  of Bull Trout redds occur in the upper 3.2 km (“survey reach” hereafter; Rodtka *et al.* 2010; Judd *et al.* 2023). We have observed adult Bull Trout entering Fall Creek as early as April,

but most migrants enter in mid- to late August and redd building begins in early September. Spawning peaks around mid-September and is complete by the first week of October, at which point essentially all migratory Bull Trout have left the stream (Rodtka *et al.* 2010; Judd *et al.* 2023). The timing and location of Bull Trout spawning activity in Fall Creek has remained consistent since we started monitoring the population (Judd *et al.* 2023), which is characteristic of many salmonid populations (Beechie *et al.* 2008). Autumn flows in Fall Creek are usually low and clear, which aids in redd detection.

Although survey methods have varied over the years, in a typical year, we count redds in the survey reach only once in early October. However, from 2018 to 2022 we conducted biweekly surveys to reassess the timing of Bull Trout spawning in the stream first documented over a decade earlier. Our survey season started in early September and ended the first week of October. During surveys, an experienced crew of two walked upstream identifying redds as either definite (i.e., displaying clean substrate, defined pit, and tail spill) or probable (i.e., missing one of the attributes of a definite redd; Bonar *et al.* 1997). Redd locations were marked with a global positioning system waypoint and flagged on a nearby bank. The accumulated count of flagged, definite redds represented our estimate of annual redd abundance in the survey reach. On our last survey of each year (except 2020), we walked all 7.5 km of Fall Creek accessible to migrating Bull Trout to identify any redds downstream from the survey reach. The number and location of any Bull Trout observed was also recorded during every survey.

During our first survey of 2022 on 9 September, we observed a newly constructed beaver dam in the survey reach (Figure 1). This was the first beaver dam we had observed in the stream, although we had noted signs of beaver activity in the survey reach since 2018. The dam was  $\sim 17$  m wide, 0.4 m high, spanned the full width of the stream with no spill over, and was constructed of large gravel, cobble, and deciduous tree branches. The channel downstream of the dam was heavily braided and consistently shallow (i.e.,  $< 0.2$  m). We observed a group of 30 Bull Trout in a 30 m long section of 1 m deep run habitat 185 m downstream of the dam. Although staging of Bull Trout in similar habitat throughout the survey reach in early September is not unusual, the high density of fish we observed in a single run was unprecedented.

During our second survey of 2022 on 16 September, we counted 23 Bull Trout in the same run below the dam at a time when we expected most fish to be at spawning sites upstream of the dam. We also observed redds and actively spawning Bull Trout downstream



**FIGURE 1.** Upstream (a) and profile (b) views of a newly constructed beaver dam in Fall Creek, Alberta, 9 September 2022. Photos: M. Rodtka.

of the dam in an area rarely used by spawning fish since our survey began in 2007. Although spawning was still occurring upstream of the dam, we noted far fewer Bull Trout and redds than usual.

Results of our final survey on 4 October confirmed our suspicion that 2022 was an exceptional year. Most Bull Trout redds occurred downstream of the dam, in areas where there had been essentially no spawning activity in past years (Figure 2). Although we expected almost all migratory fish to have left the stream by October (Roldtka *et al.* 2010), we observed seven large (50–60 cm), Bull Trout in the shallow (<1.5 m) impoundment upstream of the dam, representing >10% of the estimated 2022 spawning run of 63 fish (Judd *et al.* 2023). We also observed a newer, partly completed dam, 100 m downstream from the original. No redds or Bull Trout were observed downstream of the survey reach.

Apparently, the newly constructed beaver dam was displacing Bull Trout spawning downstream and may have impeded downstream migration. The redds we observed upstream of the dam were most likely constructed by early-season migrants that had moved into the reach before the dam became impassible. We are unsure when the dam was completed, but it was first documented on 16 August and was noted as being “fairly fresh” at the time with spill-over and gaps likely capable of passing an adult Bull Trout (M. Banko pers. comm. 10 May 2023), and we have documented adults moving upstream as early as April. Regardless of when, or if, the dam became a full barrier to Bull Trout migration, >60% of the redds

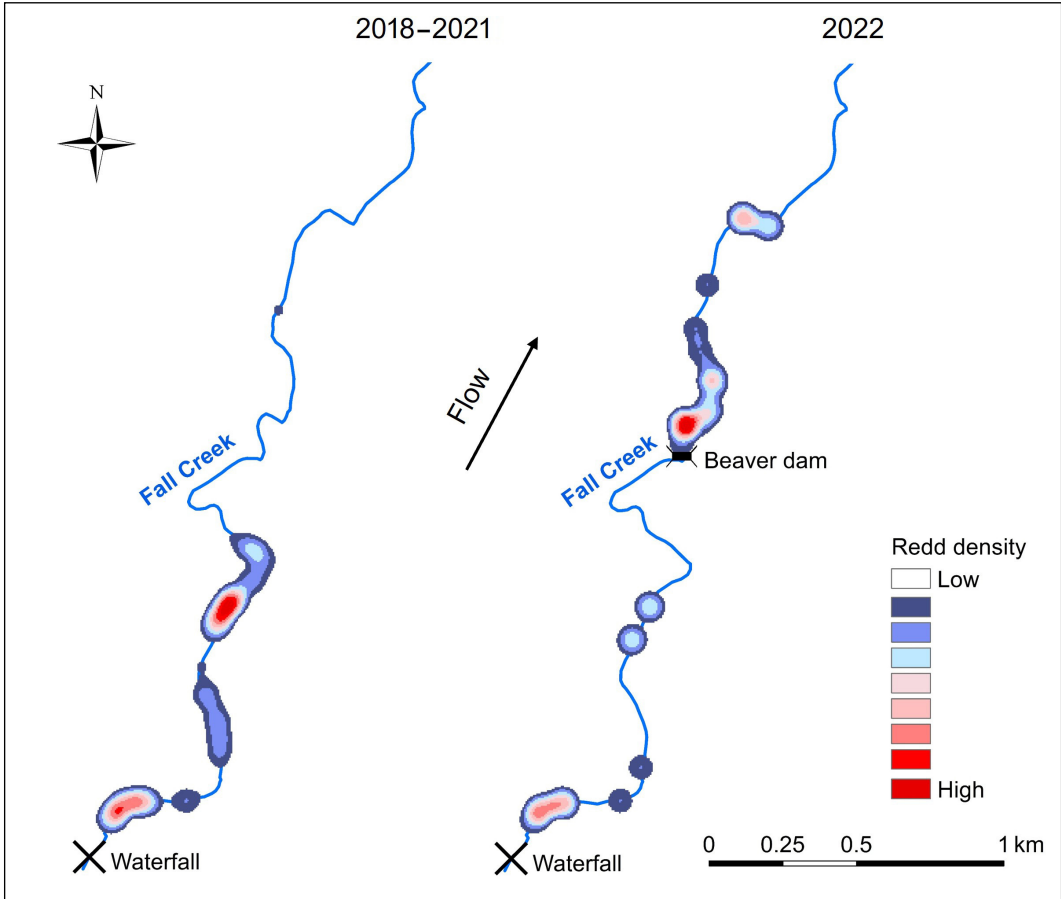
counted in 2022 occurred downstream of the dam in a reach rarely used by spawning Bull Trout. This represents a substantial displacement of Bull Trout spawning which is most plausibly attributed to creation of the beaver dam. It remains to be seen what, if any, long-term impact this disruption has on the Fall Creek Bull Trout population. However, the seasonal impact on spawning adults is unprecedented in the 15 years we have monitored the population.

### Author Contributions

Writing – Original Draft: M.C.R. and C.S.J.; Writing – Reviewing & Editing: M.C.R., C.S.J., and P.K.M.A.; Conceptualization: M.C.R., C.S.J., and P.K.M.A.; Investigation: C.S.J. and M.C.R.; Funding Acquisition: M.C.R. and P.K.M.A.

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**FIGURE 2.** Displacement of Bull Trout (*Salvelinus confluentus*) redds in response to a newly constructed beaver dam in Fall Creek, a tributary to the Ram River in the headwaters of the North Saskatchewan River watershed, Alberta. Redd density was calculated using the kernel density function in ArcGIS 10.6 (ESRI, Redlands, California, USA) in 2022 ( $n = 54$ ) and 2018–2021 ( $64.3 \pm 15.4$ ; mean  $\pm$  SD) redds, respectively.

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## Note

### Northern Pintail (*Anas acuta*) hens exhibit irrational behaviour, returning to their nests after apparent loss of their broods

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#### Abstract

Two Northern Pintail (*Anas acuta*) hens were observed returning alone to their upland nest sites after hatching their broods and taking them to water. Both instances were the result of apparent loss of their broods shortly after reaching water. The hens' behaviour was irrational and demonstrates that there is an attachment to nest sites that does not immediately cease after hatch and taking their broods to water.

Key words: Northern Pintail; *Anas acuta*; duck; nest site; brood loss; behaviour

Diving duck hens and broods often return to their overwater nests within a few days of hatching (Evans *et al.* 1952; Mendall 1958; Weller 1959), but dabbling duck hens do not (Weller 1964). Post-hatch use of overwater nests by diving ducks is not surprising because these sites would provide safe, familiar locations for brooding or roosting. However, use of terrestrial nest sites by dabbling duck hens and broods would require additional time and travel on land where there is an increased risk of predation to both hen and ducklings compared to water (Afton and Paulus 1992; Chouinard and Arnold 2007; Arnold *et al.* 2012). Gates (1958) reported an anomalous instance of a Gadwall (*Anas strepera*) hen returning to its nest after taking its brood to water; in that case, the nest was close (~5 m) to water, and the hen returned to incubate some nonviable eggs after losing her brood.

In this note, I report two instances of Northern Pintail (*Anas acuta*) hens returning to their upland nest sites located hundreds of metres from water after the apparent loss of their broods. These observations were made during a study of dabbling duck brood survival in southern Alberta using radio-marked hens captured on their nests (see Duncan 1986 for methods and study area).

The first instance involved a hen that nested ~300 m from water. She and her brood left their nest

the day after hatching and were observed that evening on a wetland. Early the next morning, the hen was located standing alone beside her empty nest in the upland. Later that day and on subsequent days, the hen was observed alone on the wetland, apparently having lost her brood sometime during the first evening after reaching water.

The second instance involved a hen that had taken her ducklings ~400 m from the nest to a wetland the day after they hatched. In an ill-fated attempt to count the ducklings in very dense emergent vegetation that same day, another observer and I disturbed the hen and dispersed the brood. Our presence resulted in numerous nearby nesting Black Tern (*Chidonas niger*) mobbing us vociferously. There was also a brisk wind at that time, which, combined with noise from the terns, made it extremely difficult to hear the vocalizations of the ducklings. The hen performed distraction displays for several minutes and then flew away from the wetland in the direction of her nest. After a few minutes, the hen returned to the wetland, flew low over the area where she and her ducklings had been disturbed, and then again flew away into the uplands toward her nest site. Shortly thereafter, we observed the hen standing beside her nest, which contained one nonviable egg. After less than a minute, the hen flew back to the water of her own volition. The following day and on subsequent days, the hen was

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found in the company of ducklings, having apparently reunited with her brood.

The return of both pintail hens to their nests was a response to the apparent “loss” of their broods, albeit only temporarily in the second case. In that instance, the noise from the agitated terns and wind would have precluded the hen from hearing her ducklings. Because chick vocalizations and visual cues are known to change or elicit parental behaviour in birds (e.g., Conover *et al.* 1980; Evans 1992; Rumpf and Tzschentke 2010), the hens’ behaviour was likely a response to the absence of such stimuli from ducklings. These observations and that of Gates (1958) demonstrate that dabbling duck hens maintain an attachment to the nest site for at least one or two days after hatching their eggs and taking their broods to water. In response to the loss of their broods, the hens acted on this continuing, residual attachment to their nest sites.

The return of dabbling duck hens to their upland nest sites following brood loss might be rational and adaptive if viable eggs or young remained in the nest. However, viable eggs or ducklings seldom remain in a nest after the hen and brood have departed, because ducks exhibit strong hatch synchronicity (Afton and Paulus 1992) and brood cohesion (Collias and Collias 1956). In the first instance I report, there were no eggs or ducklings remaining in the nest after the hen and brood had departed, demonstrating a lack of rational awareness by the hen. In the second incident, the hen prematurely abandoned her ducklings and temporarily returned alone to her nest, thereby leaving her ducklings at a higher risk of predation. In both of these instances, the hens exhibited irrational behaviour as opposed to conscious, logical thought.

Residual nest-site attachment of hens after they have departed from the nest with their broods could be maladaptive if it prompts premature abandonment of broods. For example, in the second instance reported here, the hen temporarily abandoned her brood but they ultimately reunited; however, in other cases it is reasonable to assume that such abandonment could result in brood loss. Duncan (1986) noted that duck broods were most susceptible to human disturbance within three days of hatch. The first few days after hatch are when duckling mortality in pintails and other ducks is highest (Grand and Flint 1996; Guyn and Clark 1999; Sedinger *et al.* 2018 and references therein), with the primary causes of early duckling mortality being predation and inclement weather (e.g., Grand and Flint 1996; Chouinard and Arnold 2007). This residual attachment to the nest site, combined with an imperfect hen–brood bond shortly after hatch (Weller 1964), could well exacerbate the risk of duckling mortality in the first few days after hatch.

Why might hens behave in such an illogical manner? Incubation drive and nest-site attachment of birds does not come to an abrupt halt after hatch, but rather gradually wanes, with a transitory period when both incubation and brooding behaviours may be expressed (Beer 1966; Richard-Yris *et al.* 1998). Because hormones have a strong influence on parental breeding behaviour in birds (e.g., Eisner 1960; Boos *et al.* 2007), the irrational actions I observed could be a result of the time it takes for hormones to attain certain levels and shift birds to new behavioural states (Henschke *et al.* 2016). It is unlikely that the occasional short flights of dabbling duck hens to their nests after brood loss incurs a large selective cost; irrational behaviour in birds presumably only occurs in the absence of strong pressures against such behaviours (Leniowski *et al.* 2013; Henschke *et al.* 2016; Turzańska and Chachulska 2017). The more frequent return of diving duck hens and broods to their nests within a few days of hatch could well be another manifestation of the slow waning of the incubation drive.

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## Video-documentation of American Black Bear (*Ursus americanus*) foraging on algae in livestock tanks on a conservation property in western Montana, USA

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### Abstract

Algae is an important food for many wildlife species. For ursids, marine algae is documented in Polar Bear (*Ursus maritimus*) diets, but freshwater algae has not been reported in American Black Bear (*Ursus americanus*) diets. We installed remote cameras at livestock tanks, in which freshwater algal blooms grew, to document Black Bear foraging behaviour. We video-documented algae foraging by four unique bears of both sexes and of different age classes. Algae foraging by two cubs and one adult female likely represented exploratory sampling because these three bears minimally foraged and did not subsequently return to the livestock tanks to forage on algae again. One adult male foraged on algae during three separate occasions, indicating his algae foraging was non-exploratory. We discuss possible hypotheses to explain freshwater algae consumption by Black Bear, including nutritional benefit, physiological relief, and parasite expulsion. Our study is the first to report algae foraging by American Black Bear, and our findings suggest that the benefits of *Cladophora* species for wild animals may be greater than is currently understood.

Key words: Algae; behaviour; *Cladophora* species; foraging; remote cameras; *Ursus americanus*

### Introduction

Algae is an important food resource for many marine (Arthur and Balazs 2008; Hata and Umezawa 2011; Reverter *et al.* 2020; Meekan *et al.* 2022) and terrestrial (McKnight and Hepp 1998; Holgerson *et al.* 2017; Bassett *et al.* 2022) wildlife species. For North American ursids, consumption of marine algae by Polar Bear (*Ursus maritimus*) is well documented (Harrington 1965; Russell 1975; Gormezano and Rockwell 2013), but consumption of freshwater algae by terrestrial bears is less well understood. A review of 178 papers, reports, dissertations, and theses on Grizzly Bear (*Ursus arctos*) diet in the Greater Yellowstone Ecosystem during 1891 through 2013 found only one documented case of freshwater algae in Grizzly Bear scat (Gunther *et al.* 2014). For this one case, the authors suggested that algae ingestion was unintentional (i.e., the bear was feeding on other foods) or represented exploratory sampling (i.e., the bear was sampling algae while searching for new

foods). Studies of American Black Bear (*Ursus americanus*) diet based on scat (e.g., Tisch 1961; Raine and Kansas 1990; Lesmerises *et al.* 2015; McLaren *et al.* 2021) and stable isotope (Hatch *et al.* 2011; Hopkins 2011; Dykstra 2015) analyses have similarly reported no evidence of algae consumption by Black Bear.

Beyond scat and stable isotope data, observations of bears foraging in the wild can provide insight into their diet. However, direct observation of foraging by wild Black Bear is challenging because they are wary and have relatively large spatial requirements (Powell *et al.* 1997). Remote photography, increasingly used to estimate wildlife occupancy, density, and survival (Karanth and Nichols 1998; O'Brien *et al.* 2010; O'Connell *et al.* 2011; Reynolds-Hogland *et al.* 2022a,b), may also provide opportunities to document wildlife foraging behaviour. We installed a network of remote cameras on a conservation property in western Montana, USA to document and evaluate Black Bear behaviour (Sawaya *et al.* 2017;

Reynolds-Hogland *et al.* 2023a,b), including foraging activity. Here, we present video-documentation of five cases of algae foraging by three Black Bears and photo-documentation of one case of presumed algae foraging by another bear.

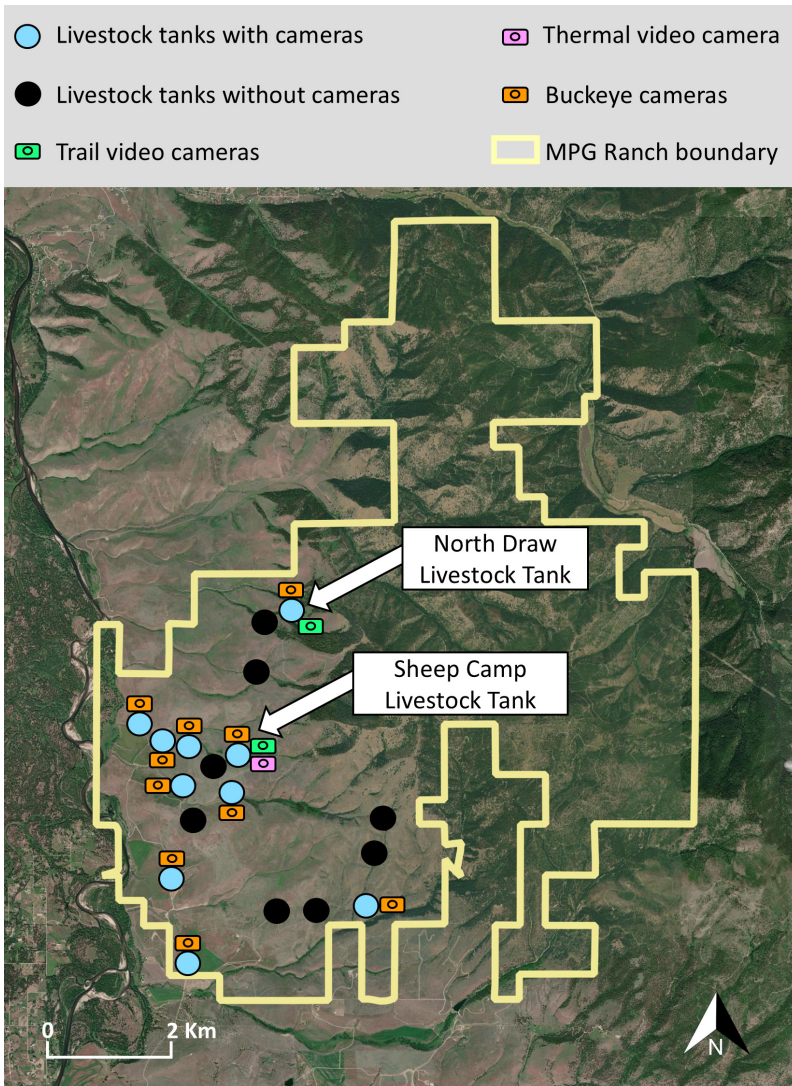
## Methods

### Study site

Our study was conducted on MPG Ranch (46.70722°N, 114.00444°W), a 6191-ha conservation property in the Northern Sapphire Mountains in western Montana, USA (Figure 1). Historically, the

property had been intensively managed for livestock for 100+ years, but was purchased in 2009 and transitioned to a conservation property with ongoing ecological restoration (Lekberg *et al.* 2013; Durham *et al.* 2017; Mummey *et al.* 2018; Sheng *et al.* 2022). Livestock fencing was removed, but artificial livestock tanks that existed in 2009 were retained to provide drinking water and aquatic habitat for wildlife (Sawaya *et al.* 2017).

The elevation at MPG Ranch ranges from 966 to 1833 m. Dominant tree species on the eastern and northern portions of the property include Douglas-fir



**FIGURE 1.** MPG Ranch, a 6191-ha conservation property in the Northern Sapphire Mountains in western Montana, USA. At the Sheep Camp livestock tank, we video-documented algae foraging by four unique Black Bear (*Ursus americanus*) of both sexes and of different age classes, during 2012–2022.

(*Pseudotsuga menziesii* (Mirbel) Franco), Ponderosa Pine (*Pinus ponderosa* Douglas ex Lawson & C. Lawson), Subalpine Fir (*Abies lasiocarpa* (Hooker) Nuttall), and Trembling Aspen (*Populus tremuloides* Michaux). The southern and western portions are dominated by agricultural land, open grass-covered slopes, sagebrush steppe, dry open forests, and narrow deciduous woody draws that lead to bottomland riparian cover types (Noson and Rodrigues 2015; Durham *et al.* 2017). MPG Ranch provides habitat for a wide variety of songbirds, corvids, raptors, insects, reptiles, amphibians, small mammals, mesocarnivores, and large mammals, including American Black Bear, Mountain Lion (*Puma concolor*), White-tailed Deer (*Odocoileus virginianus*), Mule Deer (*Odocoileus hemionus*), Moose (*Alces americanus*), and Elk (*Cervus canadensis*).

#### Video cameras

During 2011–2022, we installed video cameras at 88 camera stations to observe and document bear behaviour. A camera station was defined as one or more video cameras aimed at one unique feature, such as a livestock tank, pond, wildlife trail, rub tree, etc. We used Browning models 8FHD-P and BTC-7A (Morgan, Utah, USA), Stealth Cam models STC-DVIRHD and STC-G42NG (Grand Prairie, Texas, USA), Reconyx XR6 UltraFire (Grand Prairie, Texas, USA), and Bushnell model 1197678 (Overland Park, Kansas, USA) video camera systems. For our broader

Black Bear research program, we evaluated video data from camera stations aimed at all features to estimate bear demography (Reynolds-Hogland *et al.* 2022a,b). Herein, we focus on video data collected from only camera stations aimed at livestock tanks, which documented bear algae foraging events (Figure 1).

We installed four camera stations at four different livestock tanks. One camera station was installed in 2012, one in 2013, and two in 2014. The two camera stations installed during 2012 and 2013 were removed after one year owing to unproductivity (Table 1). The other two camera stations, aimed at the Sheep Camp livestock tank and the North Davis livestock tank (Figure 1), successfully video-captured Black Bear and were active during 2014–2022. Video cameras recorded for one-minute intervals at up to 60 frames/s, were motion-activated, had a one-minute time delay, and were operational 24 hr/day. Video settings were selected to maximize detection of animal behaviours, individual identification, and camera battery life. Video data were stored on secure digital (SD) cards. We checked all video cameras every 2–3 weeks during the summers of 2011–2014 and replaced camera batteries at least four times annually. During 2015–2022, we checked cameras and replaced camera batteries every six weeks from March to November, annually.

#### Thermal video camera

In summer 2016, we installed one AXIS Q1931-E thermal network camera (AXIS, Lund, Sweden) at the

**TABLE 1.** Duration of time that trail, Buckeye, and thermal cameras were active at each livestock tank on MPG Ranch in western Montana, USA, 2012–2022. NA means not applicable.

Livestock tank ID	Trail camera	Buckeye camera	Thermal camera
Waley Tank 1	2012	NA	NA
Waley Tank 2	2013	NA	NA
Sheep Camp Tank	2014–2022	2013–2022	2016–2022
North Draw Tank	2014–2022	2013–2022	NA
Woodchuck Ridge Stock Tank	NA	2013–2022	NA
Lower Sheep Camp Tank	NA	2013–2022	NA
Tongue Creek Stock Tank (L)	NA	2013–2022	NA
Tongue Creek Tank (U)	NA	2014–2022	NA
Sainfoin Bench Stock Tank	NA	2014–2022	NA
Orchard Stock Tank	NA	2016–2022	NA
Entrance Tank scale	NA	2017–2022	NA
Middle Sheep Camp Tank	NA	2017–2022	NA
Baldy Draw	NA	NA	NA
West North Draw Tank	NA	NA	NA
Mid Woodchuck Creek Tank	NA	NA	NA
Lower Woodchuck Creek Tank	NA	NA	NA
South Sheep Camp Stock Tank	NA	NA	NA
South Tongue Creek Stock Tank	NA	NA	NA

Sheep Camp livestock tank (Figure 1) to monitor thermoregulation of wildlife that immersed in this water source and because wildlife activity was relatively high at this livestock tank (P.W.R. unpubl. data). The thermal camera at the Sheep Camp livestock tank provided a view of wildlife that differed from the view provided by the non-thermal video camera station that was also aimed at the Sheep Camp livestock tank. The thermal camera was motion-triggered, had no time delay, and was powered by batteries with a solar charger. Videos were stored on a SD card, which we regularly maintained during 2016–2019.

#### *Still photos*

During 2013–2022, we installed Buckeye Orion and Buckeye X80 Wireless cameras (Buckeye Cam, Athens, Ohio, USA) at 77 Buckeye stations (Figure 1). Ten of the 77 Buckeye stations were aimed at 10 different livestock tanks. Five Buckeye stations aimed at livestock tanks were active from 2013 to 2022, two were active from 2014 to 2022, one was active from 2016 to 2022, and two were active from 2017 to 2022 (Table 1). Buckeye cameras collected still images, were motion-triggered, had a 10–15-s time delay, and sent images through a wireless network using radio frequency. Images were received by a PC Base antenna and stored onto an Apple Mac mini, during 2013–2022. Buckeye cameras were remotely monitored continuously throughout the study period. If a Buckeye camera was moved by an animal or if a battery was low, we immediately readjusted the camera position and replaced batteries.

#### *Genetic data*

We installed hair collection stations (Kendall *et al.* 2009) to determine genetic identity, maternity, and paternity of individual Black Bear (Reynolds-Hogland *et al.* 2022b). We used genetics and unique physical characteristics to determine individual identity of algae-foraging bears. During 2013–2022, we collected >1500 bear hair samples at 36 rub posts and rub trees. Details of genetic analyses, which were conducted by the National Genomics Center for Wildlife and Fish Conservation (Missoula, Montana, USA), are provided in Ramsey *et al.* (2019). No animal care protocol was required for the non-invasive collection of photo and genetic data that we collected.

#### *Classifying capture events*

We scrutinized every video and still photo to identify individuals and to document and classify bear behaviours. The vast majority of bears on our study site had unique traits (e.g., chest blazes, ear notches, head and snout shapes, distinct coat patterns, scars and bare spots, eyebrow colours, relative ear sizes, profile snout shapes, snout moustaches, snout colours, and temporalis and masseter sizes), which we used to help

identify individuals (Ramsey *et al.* 2019; Reynolds-Hogland *et al.* 2022a). We also linked visual markers of individuals with their genetic identifications, following Ramsey *et al.* (2019). We classified individual bears into four age classes: cub (<1 year old), yearling (1–2 years old), subadult (2–4 years old), and adult ( $\geq 5$  years old; Hebblewhite *et al.* 2003; Obbard and Howe 2008). We used a 1-hr threshold to separate capture events when an individual moved out of the camera frame and then returned (Reynolds-Hogland *et al.* 2023b).

## Results

#### *Video cameras*

During 2012–2022, we documented 381 bear visits to the Sheep Camp and North Draw livestock tanks. Algae grew in both of these but algae-foraging by Black Bear was observed only at the Sheep Camp livestock tank. Thus, we focus on Black Bear video-captures at only the Sheep Camp livestock tank. At least 22 individual bears visited the Sheep Camp livestock tank 148 times during 2015–2022 (Table S1). Algae was present in the Sheep Camp livestock tank during 46 visits by 16 different bears. We identified the algae growing in the livestock tanks to the genus *Cladophora*.

We documented one adult male (Bear M2) foraging on algae in the Sheep Camp livestock tank during three separate events in fall 2019 (Figures 2–4). During all three occasions, the livestock tank was full of water with a relatively large algal bloom. Bear M2 immersed himself in the water and grabbed algae with either his mouth or forepaws. Then, Bear M2 chewed the algae. After Bear M2 ate algae the first time on 8 September, he returned to the Sheep Camp livestock tank on 12 September and 5 October and consumed algae during both subsequent visits (Videos S1–S3).

#### *Thermal video camera*

We documented >60 thermal video-capture events of Black Bear at the Sheep Camp livestock tank. On 25 September 2019, adult female Bear F2 and her two cubs visited this tank. One of Bear F2's cubs put its forepaws into the water and pulled algae out of the tank and chewed it. The cub appeared to spit out at least some of the algae, which dropped to the ground (Video S4). On 1 October 2019, a different adult female (Bear F11) and her three cubs visited the tank. One of Bear F11's cubs used its mouth to grab algae from a metal grate that was placed in the tank to allow small animals to escape (Video S5).

#### *Still photos*

During 2012–2022, we classified >140000 still images from Buckeye cameras. Algae was found in all 10 livestock tanks that had Buckeye cameras. We

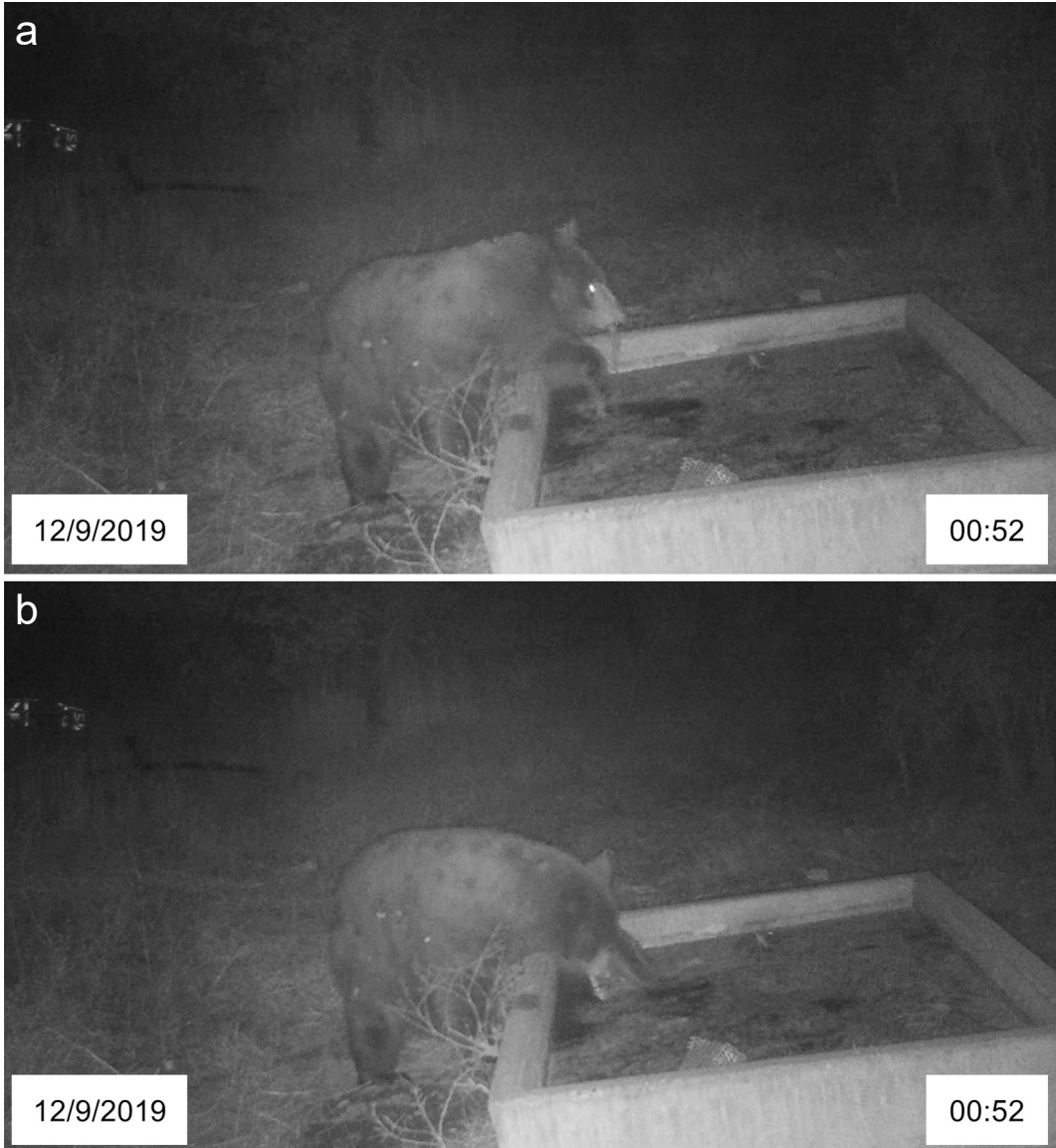


**FIGURE 2.** Frames from a video-capture (Video S1) of adult male American Black Bear (*Ursus americanus*) M2 foraging on algae on 8 September 2019, in a livestock tank on MPG Ranch in western Montana, USA. Photos: MPG Ranch.

documented several wildlife species foraging on algae in livestock tanks (Figure 5), including White-tailed Deer, Mule Deer, Elk, and Black-billed Magpie (*Pica hudsonia*). At 1:50 on 8 October 2019, one Buckeye image documented adult female Bear F2 at the Sheep Camp livestock tank with material that appeared to be algae dangling from her mouth (Figure 5f). The video camera that was also aimed at the Sheep Camp livestock tank failed to video-capture this algae foraging event.

## Discussion

American Black Bear is an opportunistic omnivore (Benson and Chamberlain 2006; McLaren *et al.* 2021) with a broad dietary niche (Hatch *et al.* 2011) that shifts with seasonally available foods (Powell *et al.* 1997; Bowersock *et al.* 2021). To date, algae has not been reported in Black Bear diets. Here, we video-documented two cases of algae foraging by two different Black Bear cubs and three separate cases of algae foraging by one adult male Black Bear (Bear M2). We



**FIGURE 3.** Frames from a video-capture (Video S2) of adult male American Black Bear (*Ursus americanus*) M2 foraging on algae on 12 September 2019, in a livestock tank on MPG Ranch in western Montana, USA. Photos: MPG Ranch.

also photo-documented one adult female Black Bear (Bear F2) with material that appeared to be algae dangling from her mouth.

Algae foraging by the two cubs and the adult female (Bear F2) was likely exploratory or unintentional. Both cubs chewed very little algae and did not subsequently return to the livestock tank to forage on algae again. Similarly, adult female Bear F2 was photo-captured with algae-like material dangling from her mouth only once.

Alternatively, Bear M2 foraged on algae in the Sheep Camp livestock tank during three separate occasions in fall, 2019: on 8 September (Figure 2), 12 September (Figure 3), and 5 October (Figure 4). This repeated foraging behaviour indicates that Bear M2 was not sampling algae during at least the last two algae foraging events.

We identified the algae in the livestock tanks to the genus *Cladophora*, a globally widespread, macroscopic, freshwater green algae (van den Hoek *et*



**FIGURE 4.** Frames from a video-capture (Video S3) of adult male American Black Bear (*Ursus americanus*) M2 foraging on algae on 5 October 2019, in a livestock tank on MPG Ranch in western Montana, USA. Photos: MPG Ranch.

*al.* 1995; Boedeker *et al.* 2010) consisting of >183 species (Munir *et al.* 2019; Michalak and Messyasz 2021). Seasonal blooms of *Cladophora* species can create detrimental environmental and recreational issues in freshwater bodies (Messyasz *et al.* 2015; Nutautaitė *et al.* 2021; Michalak and Messyasz 2021), but *Cladophora* species can also benefit wildlife because they contain biologically active ingredients (Nutautaitė *et al.* 2021). For example, the commonly occurring *Cladophora glomerata* contains

carotenoids (Khuantrairong and Traichaiyaporn 2012); minerals such as calcium, potassium, and selenium (Peerapornpisal 2007; Michalak and Messyasz 2021); vitamins A, C, E, B1, and B2 (Khuantrairong and Traichaiyaporn 2011; Michalak and Messyasz 2021); fatty acids (Laungsuwon and Chulalaksanakul 2014; Messyasz *et al.* 2015); glycosides (Khalid *et al.* 2012); enzymes (Verdel *et al.* 2000; Messyasz *et al.* 2015); amino acids and protein (Rani 2007; Messyasz *et al.* 2015; Michalak and Messyasz



**FIGURE 5.** Photo-captures of wild animals foraging on algae in livestock tanks on MPG Ranch in western Montana, USA. Photos: MPG Ranch.

2021). Thus, it is possible that Bear M2 foraged on algae for nutritional benefit.

Bear M2 foraged on *Cladophora* species during the fall, the time of hyperphagia for Black Bear. Common plants that Black Bears consume during fall in western Montana include Choke Cherry (*Prunus virginiana* L.), hawthorn (*Crataegus* L.), Service

Berry (*Amelanchier alnifolia* (Nuttall) Nuttall ex M. Roemer), huckleberry (*Vaccinium* L.), Red-osier Dogwood (*Cornus sericea* L.), Bristly Black Currant (*Ribes lacustre* (Persoon) Poirét), Bracted Honeysuckle (*Lonicera involucrata* (Richardson) Banks ex Sprengel), angelica (*Angelica* L.), and fruits of trees in the *Sorbus* (L.) genus (Tisch 1961). The protein

(20%) and fat (5%) content in *Cladophora* species (Peerapornpisal 2007) are similar to, or higher than, that in most common plants that Black Bear consume in fall. For example, the protein and fat content in Choke Cherry (7% protein, 4.2% fat; Costello *et al.* 2016), Service Berry (3.3% protein, 3.4% fat; Gunther *et al.* 2014), Bristly Black Currant; (5.6% protein, 3% fat; Gunther *et al.* 2014), and huckleberry (4–10% protein, 3–6% fat; Gunther *et al.* 2014) are lower or similar to that found in *Cladophora* species.

We do not know if Black Bear can digest *Cladophora* species. They are omnivores with short, simple digestive tracts (Stevens and Hume 1995; Gillman *et al.* 2020), so they are unable to fully digest plant matter (Bowersock *et al.* 2021). Humans are also omnivores, and they consume both fresh and dried forms of *Cladophora* species (Choobthaisong and Oupathumpanont 2021). Also, freshwater algal blooms can be digested by several livestock mammals including the omnivorous domestic Pig (*Sus domesticus*; Michalak and Chojnacka 2008). Black Bear, humans, and domestic Pig all have simple monogastric digestive systems. Thus, it is possible that Black Bear, like humans and domestic Pig, could digest *Cladophora* species.

In addition to containing proteins, carbohydrates, fat, minerals, and vitamins, *Cladophora* species also have anti-inflammatory and analgesic properties (Peerapornpisal *et al.* 2006). We observed Bear M2 limping throughout 2018 (Reynolds-Hogland *et al.* 2022b), and Bear M2 was still favouring his back left leg during 2019. It is possible that Bear M2 consumed *Cladophora* species in fall 2019 to help alleviate physical discomfort. Other wild animals such as elephants, birds, lizards, and some great apes self-medicate (Shurkin 2014). For example, Fruth *et al.* (2014) studied self-meditative behaviours by Bonobo (*Pan paniscus*) which occasionally consumed the leaf of *Manniophyton fulvum*. This plant has anti-inflammatory properties, which the authors suggest could provide physiological relief.

Alternatively, Bear M2 may have consumed algae to aide in the removal of intestinal parasites. Similar behaviour has been widely documented in African great apes (Huffman 2003). For instance, the consumption of whole leaves of non-nutritive plants by Chimpanzee (*Pan troglodytes*) has been linked with the expulsion of parasites (Wrangham 1995; Huffman *et al.* 1996; Huffman and Caton 2001; Huffman 2003).

It is also possible that the algae foraging we documented by Bear M2 was unintentional. Insects, an important component of the Black Bear diet (Tisch 1961; Graber and White 1983; Powell *et al.* 1997; Lesmerises *et al.* 2015), could have been present in the algal blooms that Bear M2 consumed. If so, Bear

M2 may have unintentionally consumed algae while he was foraging on insects. Incidental algae consumption is reported in Manatee (*Trichechus manatus*; Castelblanco-Martinez *et al.* 2009), where algae live in the leaves and roots of macrophytes that Manatees consume (Colares and Colares 2002; Guterres-Pazin *et al.* 2012). Although consumed inadvertently, algae is thought to provide protein or other nutrition to Manatees (Best 1981; Packard 1981; Guterres-Pazin *et al.* 2012). If Bear M2 unintentionally consumed algae, it is possible that algae provided nutritional benefit to Bear M2.

In conclusion, we documented American Black Bear and other wildlife foraging on freshwater algae in livestock tanks. In addition to providing water and opportunities for wildlife to thermoregulate (Sawaya *et al.* 2017), livestock tanks provided opportunities for algae to grow. The nutritional benefits of freshwater algae in the *Cladophora* genus are increasingly added to improve feed for domestic animals (Mihranyan 2011; Zulkiffly *et al.* 2013; Messyasz *et al.* 2015; Nutautaité *et al.* 2021). Our findings suggest that the benefits of *Cladophora* species extend to wild animals. This finding has implications for wildlife conservation and management.

### Author Contributions

Writing – Original Draft: M.J.R.-H.; Writing – Review & Editing: M.J.R.-H., C.B., G.S., A.B.R., R.A.D., K.T., M.V., and P.W.R.; Conceptualization: M.J.R.-H., C.B., G.S., A.B.R., and P.W.R.; Investigation: M.J.R.-H., C.B., G.S., A.B.R., R.A.D., K.T., and M.V.; Supervision: M.J.R.-H., A.B.R., and P.W.R.; Visualization: M.J.R.-H., C.B., G.S. and M.V.; Funding Acquisition: P.W.R.

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## SUPPLEMENTARY MATERIALS:

**TABLE S1.** Video-documentation of wild American Black Bear (*Ursus americanus*) that visited stock tanks when algae blooms were and were not present, size of algae blooms, and if the individual ate the algae from the Sheep Camp livestock tank, on MPG Ranch in western Montana, USA, 2015–2022.

**VIDEO S1.** Video of adult male Black Bear (*Ursus americanus*) M2 foraging on algae in the Sheep Camp livestock tank on 8 September 2019 on MPG Ranch in western Montana, USA, posted at [https://youtu.be/VJPRSVPo\\_7Y](https://youtu.be/VJPRSVPo_7Y).

**VIDEO S2.** Video of adult male Black Bear (*Ursus americanus*) M2 foraging on algae in the Sheep Camp livestock tank on 12 September 2019 on MPG Ranch in western Montana, USA, posted at <https://youtu.be/znTg50s2Svw>.

**VIDEO S3.** Video of adult male Black Bear (*Ursus americanus*) M2 foraging on algae in the Sheep Camp livestock tank on 5 October 2019 on MPG Ranch in western Montana, USA posted at <https://youtu.be/zSbaJZ3SUHA>.

**VIDEO S4.** Video of adult female Black Bear (*Ursus americanus*) F2 with her two cubs of the year, one of which forages on algae in the Sheep Camp livestock tank on 25 September 2019 on MPG Ranch in western Montana, USA, posted at <https://youtu.be/Zqj-UbtFB04>.

**VIDEO S5.** Video of adult female Black Bear (*Ursus americanus*) F11 with her three cubs of the year, one of which forages on algae in the Sheep Camp livestock tank on 1 October 2019 on MPG Ranch in western Montana, USA, posted at <https://youtu.be/lia5HFNGWJM>.

## The carcass zone: salmon contribution to tree rings in old-growth Sitka Spruce (*Picea sitchensis*) throughout coastal British Columbia

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### Abstract

The contribution of Pacific salmon to riparian forest biodiversity is widely recognized, yet the direct influence on conifer annual growth rings is less well-established. I examined broad spatial and temporal trends (1945–1999) in ring width, basal area increments (BAI), and nitrogen signatures in heartwood rings of 282 old-growth riparian Sitka Spruce (*Picea sitchensis*; average age ~300 years) from 79 watersheds in three regions of coastal British Columbia. Several large yearly fluctuations in salmon biomass entering streams were positively but weakly correlated with tree growth, lagged one to four years. General linear models indicate that tree age and salmon carcass proximity were the major growth predictors, while tree distance to stream and riparian slope were not significant. Average annual BAI (marginal means) in carcass zones were 80%, 150%, and 55% higher than adjacent control sites on the Mainland, Mid-coast Islands, and Haida Gwaii, respectively. Nitrogen isotope signatures ( $\delta^{15}\text{N}$ ) in heartwood rings ranged from  $-8.6\text{‰}$  to  $8.0\text{‰}$  and were about 3‰ higher in carcass trees than control trees. Total nitrogen (TN) ranged from 0.03% to 0.15% and was largely independent of salmon carcass occurrence. Bivariate plots ( $\delta^{15}\text{N}$  against TN) indicate a geographical clustering of elevated TN in Haida Gwaii watersheds, lower  $\delta^{15}\text{N}$  and TN in the Mid-coast Islands, and elevated  $\delta^{15}\text{N}$  and TN in watersheds with exceptionally high salmon carcass transfer and bear activity. These cumulative data robustly quantify accentuated conifer growth from salmon-derived nutrients in riparian zones that are largely independent of climatic influences and tree age.

Key words: Basal area increment; old-growth; *Oncorhynchus*; ring width; riparian zone; salmon carcass; Sitka Spruce; stable isotopes; total nitrogen; *Ursus*

### Introduction

The temperate rainforests of western North America are a globally unique ecosystem characterized by high biodiversity and high plant biomass and include some of the largest conifers on the planet (Orians and Schoen 2013). While precipitation and maritime climate contribute to the productivity of these ancient forests, marine-derived nutrients, including salmon (*Oncorhynchus* spp.), Pacific Herring (*Clupea pallasii*), and shellfish can be transferred by predators and scavengers into the riparian zone. This is known to increase productivity and biodiversity in select localities (Ben-David *et al.* 1998; Cederholm *et al.* 1999; Hilderbrand *et al.* 1999; Reimchen 2000; Helfield and Naiman 2001; Drake *et al.* 2002, 2011; Hocking and Reynolds 2012; Fox *et al.* 2014; Trant *et al.* 2016; Cox *et al.* 2020).

In coastal British Columbia, nutrient studies in riparian zones have focussed on sharp spatial gradients in salmon-derived nutrients such as below and

above waterfalls that are impassable to salmon. These studies show differences in plant species assemblage above and below falls (Mathewson *et al.* 2003; Wilkinson *et al.* 2005) as well as corresponding differences in marine-derived nitrogen isotope signatures in diverse taxa of soil invertebrates (Hocking and Reimchen 2002; Hocking *et al.* 2009) and in songbirds (Christie and Reimchen 2008). Tree ring analyses also show salmon isotopic signatures (Reimchen *et al.* 2003), with a 19% to 30% greater annual growth in the presence of salmon nutrients (Reimchen and Fox 2013; Reimchen and Arbellay 2019). These results are relevant to understanding primary productivity in old-growth coastal forests but need to be given a broader geographical context.

In the current study, 79 watersheds from throughout coastal British Columbia (Mainland, Mid-coast Islands, Haida Gwaii) with old-growth Sitka Spruce (*Picea sitchensis* (Bongard) Carrière) were surveyed. In each watershed, tree cores were taken from the

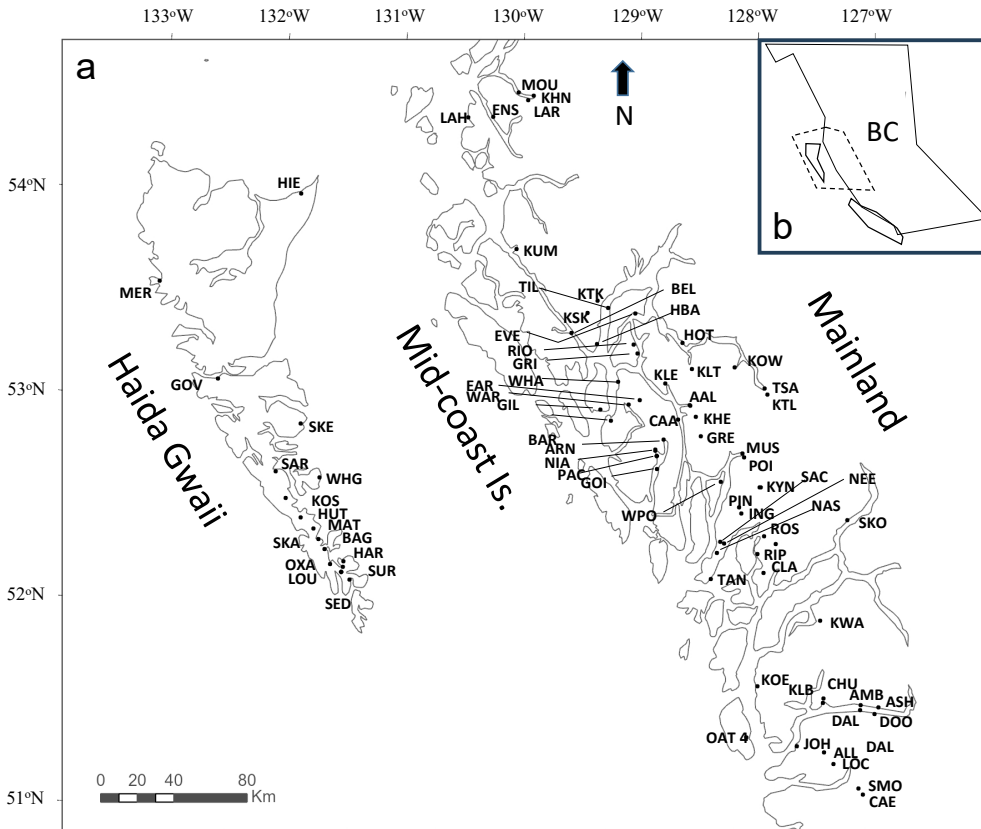
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largest spruce trees adjacent to spawning gravels and from adjacent trees as control. I quantified annual ring width and basal area increment (BAI) over five decades (1945–1999) and isotopic nitrogen ( $\delta^{15}\text{N}$ ) and total nitrogen (TN) during two time blocks (1950–1954, 1975–1979) on a subset of cores. The early time block comprises the first years when salmon counts were obtained for most streams (NuSEDS 2019), while the second time block corresponds to the outer edge of the heartwood and does not include the sapwood in which nitrogen levels greatly increase (Reimchen and Fox 2013; Reimchen and Arbellay 2019). These attributes are assessed in relation to tree size (diameter at breast height [DBH]), tree age, yearly salmon biomass entering the river, presence or absence of salmon carcasses, distance of the focal trees from the stream, and slope of the riparian zone. The results provide direct quantification of the contribution of salmon-derived nutrients to yearly growth rings of old-growth Sitka Spruce among and within watersheds throughout coastal British Columbia.

## Methods

### Study sites and sample collection

Surveys of 94 watersheds in coastal British Columbia were undertaken from 1999 to 2008 (Mainland,  $n = 55$ ; Mid-coast Islands,  $n = 23$ ; Haida Gwaii,  $n = 16$ ) during the September and October salmon spawning season. Edaphic features for these sites are reported in Reimchen *et al.* (2003). I excluded 15 of these watersheds because there was evidence for historical logging in the vicinity of riparian old-growth Sitka Spruce (hereafter referred to as “spruce”). This left 79 watersheds for sampling (Figure 1, Table S1); three of these had no spawning salmon due to impassable waterfalls at the river mouth and the remaining had populations of spawning salmon. Depending on availability, up to six of the largest spruce were selected for coring; this included trees immediately adjacent to spawning gravels, usually within 50 m of the stream which characterizes the zone of carcasses. I also chose a control tree and for this, I typically walked about 50 m further into the forest beyond the



**FIGURE 1.** a. Watersheds surveyed in coastal British Columbia to examine the relationship between salmon carcasses and Sitka Spruce (*Picea sitchensis*) growth. Full locality names and number of Sitka Spruce trees used in tree ring analyses are listed in Table S1. b. Outline of British Columbia (BC) and study area (in dashed line).

last carcass and chose the largest spruce for coring. In the three watersheds with impassable waterfalls, the largest riparian trees immediately above the waterfalls and adjacent to the stream were cored. Obtaining cores from trees in close proximity to each other with and without exposure to salmon-derived nutrients largely removed the correlated influences of climatic factors such as rainfall and temperature.

For all trees, distance to the stream ( $\pm 1$  m; DISTFOR), riparian slope (SLOPE), and presence/absence of salmon carcass remnants (CARCASS) in the vicinity of the tree were recorded. The carcasses largely originate from the foraging activities of bears (Reimchen 2000) although other taxa including marten (*Martes* spp.), river otter (*Lutra* spp.), and wolves (*Canis* spp.) can also be vectors (Ben-David *et al.* 1998; Darimont *et al.* 2003; Reimchen 2017). Most salmon carcasses occur within 20 m of the stream with occasional carcasses up to 50 m because bears prefer to maintain visual contact with stream activity, particularly that of other bears (Reimchen 2000, 2017; Reimchen and Fox 2012). I scored three categories of CARCASS for each target tree as (1) carcass-near: carcass remnants present within 10 m of the trunk; (2) carcass-far: no carcasses visible (visibility usually  $\sim 10$  m) from the target tree but present at nearby trees; and (3) control: no evidence of carcass remnants. My replicated yearly surveys at Bag Harbour, Haida Gwaii, showed that fresh bony remnants are generally overgrown with mosses by the following year but occasionally I found old jaws with moss growth from previous years. Categories 1 and 2 are referred to as the "carcass zone". The method is described more fully in Reimchen (2000).

As a proxy for historical salmon abundance, I used databases of spawning salmon (NuSEDS 2019). For each stream, I used yearly adult salmon abundance and calculated total biomass (SALMBIO) using average biomass of each species (pink: *Oncorhynchus gorbuscha*, 2.2 kg; chum: *Oncorhynchus keta*, 3.0 kg; sockeye: *Oncorhynchus nerka*, 2.7 kg; coho: *Oncorhynchus kisutch*, 3.2 kg; chinook: *Oncorhynchus tshawytscha*, 13.6 kg; Groot and Margolis 1991). Average salmon biomass (kg  $\pm$  SD) per stream (1950–1998) differed among regions (Mainland, 73 800 kg  $\pm$  75 000; Mid-coast Islands, 16 000  $\pm$  16 000; Haida Gwaii, 37 800  $\pm$  32 000, ANOVA on square root normalized SALMBIO,  $F_{2,72} = 9.2$ ,  $P < 0.001$ ).

Tree circumference was measured at breast height (150 cm) and converted to DBH. Using a 1.2  $\times$  40 cm increment borer, one or two cores were extracted from each tree, excluding dead trees as well as those with a noticeable lean. I chose the cleanest core if two were taken. Average core length was 34 cm (range 7–40 cm). Four to six trees were cored in most watersheds.

Cores were prepared using standard dendrochronological methods (see Reimchen and Fox 2013). They were dried for a minimum of three weeks at 60°C, then transferred to a grooved board and smoothed using a progression from coarse to fine grit sandpaper, following which the cores were placed in individual PVC troughs and then scanned at 720 dpi. Cores that were broken, or had growth anomalies from branch whorls or decay, were excluded. Rings (1945–1999) on 502 trees were measured and cross-dated using CooRecorder and CDendro 9.2 (Cybis Elektronik & Data AB, Saltsjöbaden, Sweden). I did not determine the repeatability of the ring width (RW) measurements because these were done directly from the CooRecorder software that defines the rings and the distances between them. I cross-referenced multiple ring measurements from the software directly under the microscope and the software measurements were either the same or more consistent than my own.

I determined BAI using:

$$\text{BAI} = \pi r_i^2 - \pi r_{i-1}^2$$

where  $r_i$  is the tree radius at the end of the annual increment and  $r_{i-1}$  the radius at the beginning of the annual increment which partially corrects for tree size effects (Dietrich and Anand 2019). To obtain nitrogen data, individual rings were removed (detailed method in Reimchen and Fox 2013). In the current study, for each of 234 trees, I processed 10 heartwood rings covering the years 1950–1954, the earliest period where salmon abundance is known for most watersheds, and 1975–1979, the latest period within the heartwood prior to the transition to sapwood where nitrogen levels greatly increase (Reimchen and Fox 2013). Each of the rings was powdered and 30 mg packaged in tin capsules. In trees with very small growth, occasionally two adjacent rings were combined to yield sufficient volume. Isotopic data were extracted at the University of California Davis Stable Isotope Facility using a PDZ Europa ANCA-GSL elemental analyzer interfaced to a PDZ Europa 20-20 isotope ratio mass spectrometer (Sercon Ltd., Cheshire, United Kingdom). Total nitrogen (TN) values represent percentage of total nitrogen in the wood sample, whereas  $\delta^{15}\text{N}\text{‰}$  values were calculated by:

$$\delta^{15}\text{N}\text{‰} = (R_{\text{sample}} / R_{\text{standard}}) - 1$$

where  $R$  equals the ratio of  $^{15}\text{N}/^{14}\text{N}$  stable isotopes.  $R_{\text{standard}}$  is the ratio of  $^{15}\text{N}/^{14}\text{N}$  stable isotopes in atmospheric  $\text{N}_2$ . Repeatability of TN and  $\delta^{15}\text{N}$  values (average of the raw mean differences between the two replicates) on wood reference samples ( $n = 135$ ) averaged  $\pm 0.012\%$  and  $\pm 1.0\%$ , respectively (Reimchen *et al.* 2003).

Because of the large size of most trees, few of the cores reached the pith and this limited direct aging. As a result, tree age (AGE) was extrapolated for these

larger trees based on Altman *et al.* (2016):

$$\text{AGE} = N + (GR - PCL - MBW) / MRW$$

where  $N$  is the number of annular rings visible on the core,  $GR$  is the geometric radius of the tree (mm),  $PCL$  is partial core length (mm),  $MBW$  is the width of the bark (mm), and  $MRW$  is the mean ring widths (mm) for the five most inner rings on the core.

#### Statistical methods

For most analyses of RW and BAI growth parameters, I partitioned the dataset into the three geographical regions: Mainland, Mid-coast Islands, and Haida Gwaii. Because 1999 was the first year of obtaining tree cores, on cores obtained in subsequent years (2000–2008), I added the yearly growth ring increments on trees and subtracted this from the measured DBH to provide a corrected DBH value for 1999 for all trees.

Frequency distributions of DBH, AGE, RW, BAI, and SALMBIO for the entire dataset were all significantly right-skewed (Kolmogorov-Smirnov Z [K-S], all  $P < 0.05$ ). For DBH, RW, and SALMBIO, this was normalized with two square root transformations (K-S, all  $P < 0.03$ ). For BAI, a single square root transformation approached normality (K-S = 0.039,  $P = 0.06$ ). Statistical trends were similar with and without transformations. When plotted against year (1950–1999), RW, BAI, and SALMBIO showed significant negative slopes. To examine any potential correlations between the yearly oscillations in these variables, I extracted residuals from linear regressions which removed the longer term trends. DISTFOR and SLOPE were also highly skewed and were categorized (DISTFOR: 0–20 m = 1, >20 m = 2; SLOPE: 0–20 degrees = 1; >20 degrees = 2). For  $\delta^{15}\text{N}$  and TN, I computed means for annual rings of each tree separately for the combined time blocks (1950–1954, 1975–1979) and then compared these for the three geographical regions. Statistical tests (SPSS version 28) included Pearson  $r$ , Spearman rho, K-S Z, linear regression for slope and unstandardized residuals, ANOVA, and general linear model (GLM) with covariates.

I analyzed the data using two approaches. Initially, I used the entire dataset of 502 trees in the 79 watersheds. In 11 of the watersheds, additional trees (10–39) had been cored for more detailed studies (Reimchen and Fox 2013; Reimchen and Arbellay 2018, 2019). To reduce the disproportionate contributions from these 11 watersheds, I limited the data to a maximum of six trees per watershed, three of the largest trees in the carcass zone, and three (if available) of the largest controls. This reduction produced a partial dataset of 282 trees. The majority of trends were similar for the full and partial data sets, although the statistical support was variable. In the current paper,

I use the partial dataset as it provides a more reliable comparison among regions. Yearly trends for BAI are highly correlated with RW for both the full and partial data sets (Mainland,  $r = 0.88$ ,  $P < 0.001$ ,  $n = 157$ ; Mid-coast Islands,  $r = 0.90$ ,  $P < 0.001$ ,  $n = 53$ ; Haida Gwaii,  $r = 0.86$ ,  $P < 0.001$ ,  $n = 72$ ); as such, I present primarily BAI data. Supplementary Materials include companion results from the full dataset (Table S2) and comparison figures (Figures S1–S6).

## Results

### Tree size and age

Within each region, DBH of the focal spruce ranged from one to three metres and was positively correlated with salmon biomass entering the stream, those on Haida Gwaii having about 30% greater diameter than those on the Mainland and Mid-coast Islands (Figure 2). In each region, trees from carcass zones had about a 40% higher DBH relative to adjacent control trees, with the carcass-near category having larger trees than carcass-far trees for the Mainland and Haida Gwaii but not for the Mid-coast Islands (Figure 3). Average age of the trees was 300 years which differed among regions, being higher on Haida Gwaii (Mainland,  $\bar{x}$  (mean) = 247 yr,  $n = 157$ ; Mid-coast Islands,  $\bar{x} = 315$  yr,  $n = 53$ ; Haida Gwaii,  $\bar{x} = 403$  yr,  $n = 72$ ) and which differed among carcass categories, with those in the carcass-far zone being younger ( $\bar{x} \pm \text{SD}$ ; carcass-near  $349 \pm 183$  yr,  $n = 55$ ; carcass-far:  $271 \pm 174$  yr,  $n = 163$ ; control:  $332 \pm 190$  yr,  $n = 64$ ; REGION:  $F_{2,273} = 14.9$ ,  $P < 0.001$ ; CARCASS:  $F_{2,273} = 4.5$ ,  $P < 0.02$ ). Inclusion of AGE as a covariate in a GLM indicates that, relative to control trees, those in the carcass zones were 32% larger on the Mainland ( $F_{1,155} = 20.1$ ,  $P < 0.001$ ), 66% larger on the Mid-coast Islands ( $F_{1,50} = 25.1$ ,  $P < 0.001$ ), and 45% larger on Haida Gwaii ( $F_{1,70} = 28.5$ ,  $P < 0.001$ ).

### Basal Area Increment (BAI)

Relative to control trees, average BAI yearly growth in the carcass zones was 108% higher on the Mainland ( $\bar{x} = 7966 \text{ mm}^2$  versus  $3954 \text{ mm}^2$  with square root transformed BAI,  $F_{1,155} = 20.5$ ,  $P < 0.001$ ), 238% higher on the Mid-coast Islands ( $\bar{x} = 5962 \text{ mm}^2$  versus  $1763 \text{ mm}^2$ ,  $F_{1,51} = 19.5$ ,  $P < 0.001$ ), and 68% higher on Haida Gwaii ( $\bar{x} = 8551 \text{ mm}^2$  versus  $5087 \text{ mm}^2$ ,  $F_{1,70} = 5.6$ ,  $P < 0.03$ ; Figure 4). There were no differences between carcass-near trees and carcass-far trees ( $F_{1,212} = 0.68$ ,  $P = 0.41$ ). Ring width (RW) data (Figure S1) is broadly similar to the BAI data.

Yearly oscillations occurred in BAI. Growth differences between trees in the carcass zone and control trees persisted over five decades, apart from Haida Gwaii that showed greater growth in control trees over time leading to smaller differences with carcass zone trees in more recent years (Figure 5).

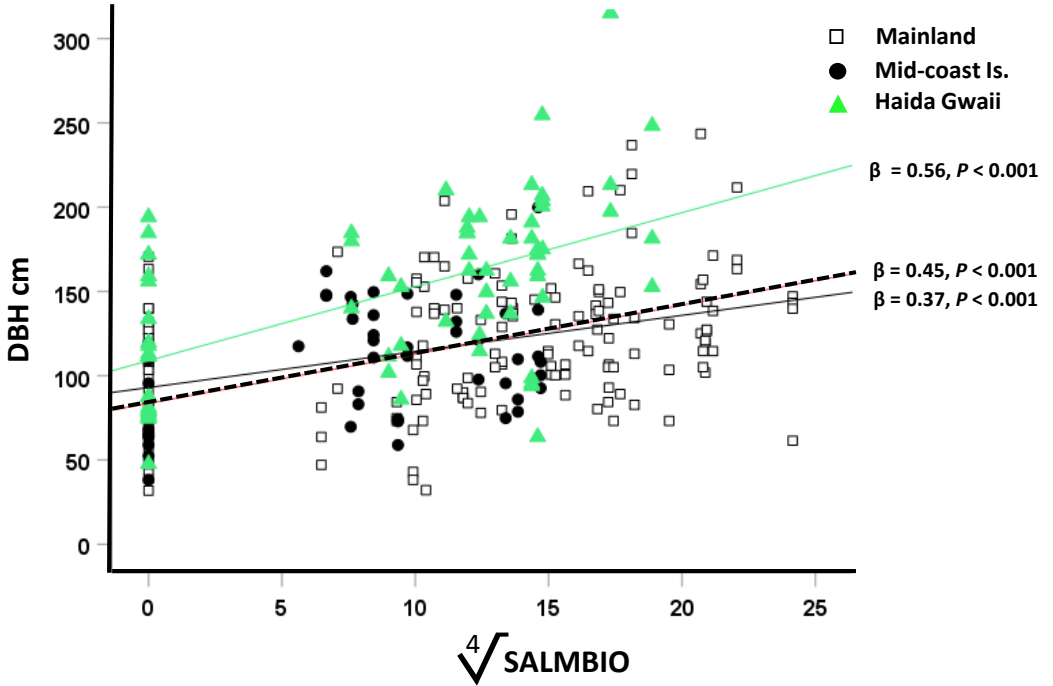


FIGURE 2. Regional trends in diameter at breast height (DBH) of 282 Sitka Spruce (*Picea sitchensis*) trees and salmon biomass (SALMBIO) in each of the 79 British Columbia watersheds. Salmon biomass normalized with the fourth root.

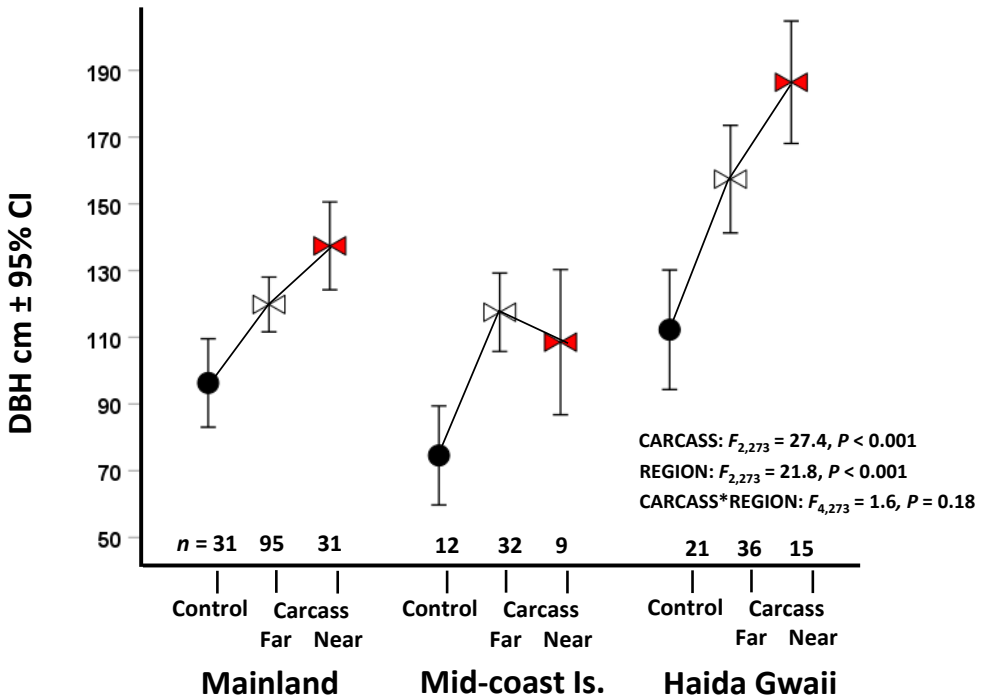


FIGURE 3. Regional trends in average diameter at breast height (DBH) of 282 riparian Sitka Spruce (*Picea sitchensis*) in relation to salmon carcass occurrence in coastal British Columbia.

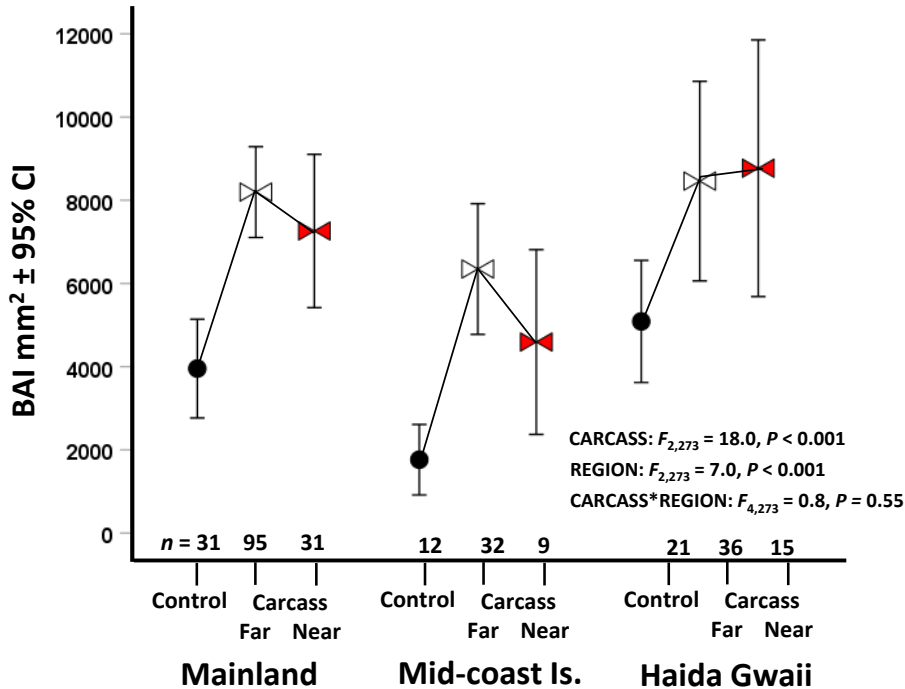


FIGURE 4. Regional trends in average basal area increment (BAI) of 282 riparian Sitka Spruce (*Picea sitchensis*) in relation to salmon carcass occurrence in coastal British Columbia.

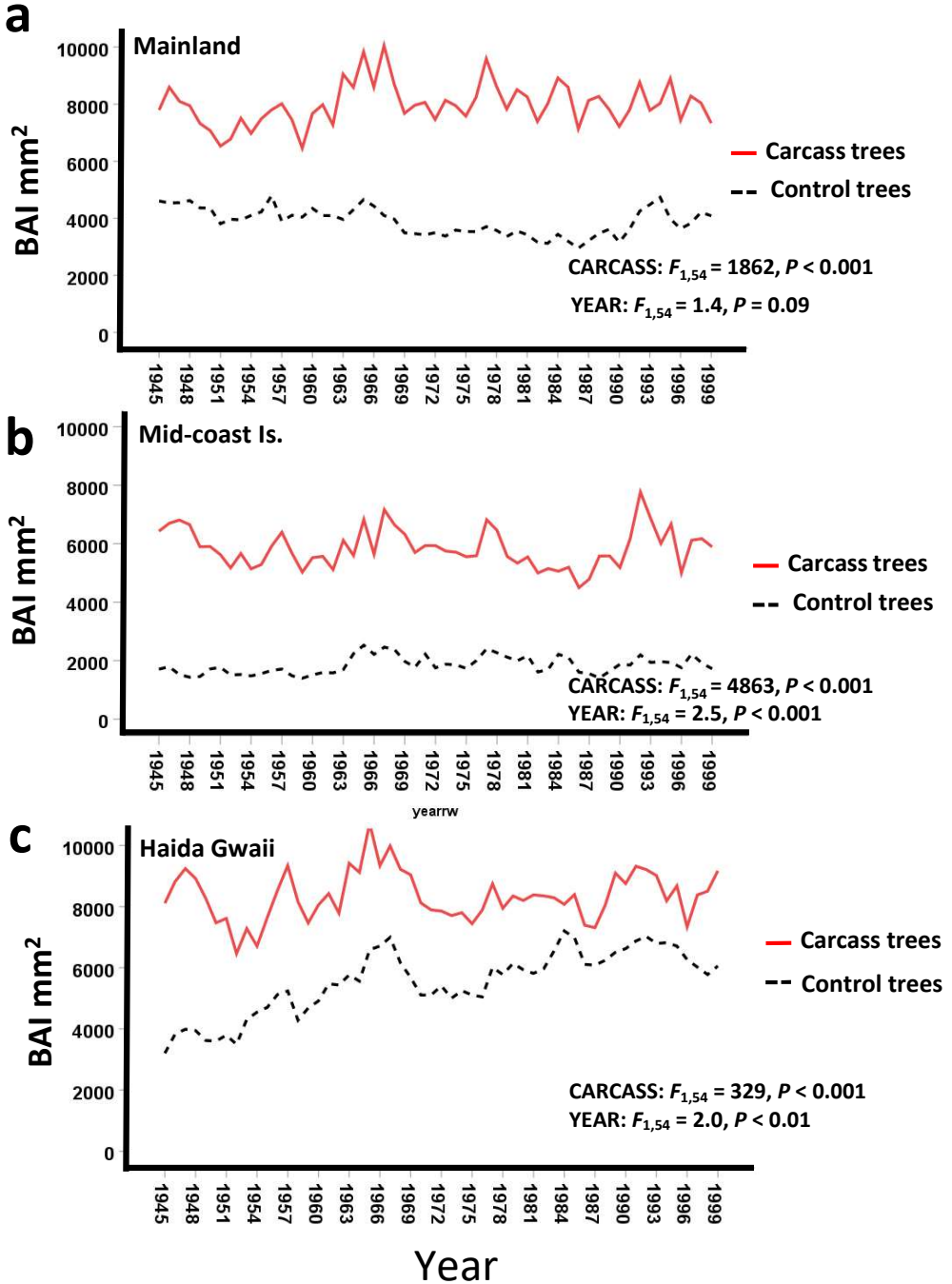
These trends were also present in the full dataset (Figure S2). In analyzing the tree ring data, it appeared that there might be more yearly variability in BAI in the carcass zone relative to adjacent control sites. This was present in larger trees for the Mainland and Mid-coast Islands but not for Haida Gwaii and did not occur in smaller trees (Figure 6).

Are there other biophysical factors that might inflate the apparent importance of carcasses to annular spruce growth? BAI was inversely correlated with tree AGE ( $r_s = -0.40$ ,  $P < 0.01$ ), with DISTFOR ( $r_s = -0.12$ ,  $P < 0.05$ ), and with riparian SLOPE ( $r_s = -0.34$ ,  $P < 0.01$ ). The GLM with square-root transformed BAI as dependent, CARCASS, SLOPE, and DISTFOR as independents, square root transformed AGE as a covariate and all two-way interactions produced a significant model ( $F_{8,275} = 13.3$ ,  $P < 0.001$ ). All two-way interactions as well as DISTFOR were statistically insignificant in each region and removed from the model. The reduced model was significant ( $P < 0.001$ ), accounting for 30%, 60%, and 30% of the variance in BAI for the Mainland, Mid-coast Islands, and Haida Gwaii, respectively (Table 1). Although SLOPE and AGE were significant predictors of BAI in each region, when controlling for these independents, CARCASS remained a significant contribution to BAI on the Mainland and the Mid-coast

Islands but had only a marginal contribution on Haida Gwaii. Relative to control trees, estimated marginal means of BAI for carcass trees were 78% larger on the Mainland, 148% larger on the Mid-coast Islands, and 55% larger on Haida Gwaii. Bivariate plots of BAI and AGE indicate that carcass trees had on average, elevated BAI across a broad range of tree ages for the Mainland and the Mid-coast Islands but had limited effects for Haida Gwaii (Figure 7). The full dataset (Figure S3) showed similar trends.

#### Salmon biomass (SALMBIO)

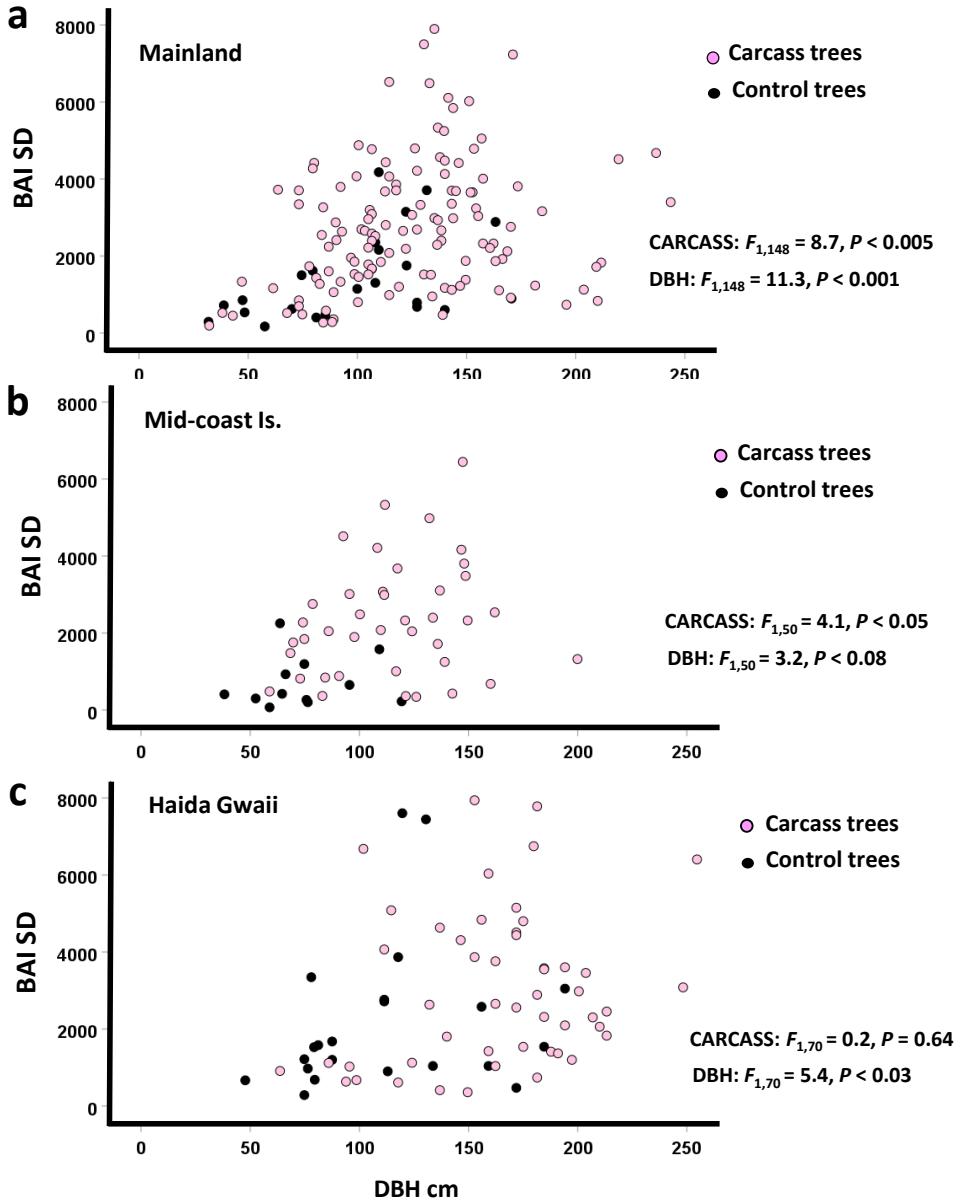
I examined whether the extent of yearly (1950–1998) fluctuations of SALMBIO were associated with yearly fluctuations on BAI. Average SALMBIO oscillated over the five decades with general concordance of oscillations among regions (Mainland versus Mid-coast Islands,  $r = 0.59$ ,  $P < 0.001$ ; Mainland versus Haida Gwaii,  $r = 0.52$ ,  $P < 0.001$ ; Mid-coast Islands versus Haida Gwaii,  $r = 0.36$ ,  $P < 0.02$ ). Apart from an increase in the late 1990s, there was a marginal reduction in SALMBIO over this interval, the effects being larger on the Mainland and Haida Gwaii (Mainland:  $\beta = -0.07$ ,  $t = 3.1$ ,  $P < 0.003$ ; Mid-coast Islands,  $\beta = -0.05$ ,  $t = 1.1$ ,  $P = 0.29$ ; Haida Gwaii,  $\beta = -0.25$ ,  $t = 6.9$ ,  $P < 0.001$ ). Bivariate plots indicate that the major peaks and lows of SALMBIO corresponded



**FIGURE 5.** Regional and temporal (1945–1999) comparisons of 282 Sitka Spruce (*Picea sitchensis*) basal area increment (BAI) in relation to salmon carcass occurrence against adjacent control sites.

to the major peaks and lows for BAI with a lag time of one to four years (derived from computation [ $r$ ] and not from visual assessment); these effects were

most pronounced during the first two decades (Figure 8a). Shorter lags were more prevalent on the Mainland than on Haida Gwaii (Figure 8b).



**FIGURE 6.** Yearly variability (SD) in basal area increment (BAI) of rings (1945–1999) in relation to size of 282 spruce (*Picea sitchensis*) diameter at breast height (DBH) separated for region and salmon carcass occurrence.

#### *Nitrogen isotopes and total nitrogen*

The coast-wide average  $\delta^{15}\text{N}$  signature in tree rings was  $-0.87\text{‰}$  and was highly variable over the study area (range  $-8.6\text{‰}$  to  $7.3\text{‰}$ ,  $n = 147$  trees). These isotopic signatures were positively correlated with SALMBIO on the Mainland ( $r = 0.30$ ,  $P < 0.003$ ,  $n = 89$ ), on the Mid-coast Islands ( $r = 0.54$ ,  $P < 0.004$ ,  $n = 29$ ), but not on Haida Gwaii ( $r = 0.17$ ,  $P = 0.39$ ,  $n = 29$ ). I found no significant differences

between time periods (1950–1954 versus 1975–1979; Mainland,  $Z = 0.01$ ,  $P = 0.99$ ; Mid-coast Islands,  $Z = 1.22$ ,  $P = 0.22$ ; Haida Gwaii,  $Z = 0.36$ ,  $P = 0.77$ ). In the Mainland and Mid-coast Islands watersheds,  $\delta^{15}\text{N}$  was about  $3\text{‰}$  higher in carcass-near trees than adjacent control trees but there was minimal difference on Haida Gwaii (Figure 9). The full dataset (Figure S4) shows in each region highest  $\delta^{15}\text{N}$  signatures in carcass-near trees and lowest values in adjacent control

**TABLE 1.** General linear model analyses (partial dataset) of basal area increment (BAI; 1945–1999) of old-growth Sitka Spruce (*Picea sitchensis*) against tree age (AGE), riparian slope (SLOPE), and salmon carcass condition (CARCASS) for three geographical regions (Mainland, Mid-coast Islands, Haida Gwaii), British Columbia. Distance to the stream (DISTFOR) and all two-way interactions were non-significant and removed from the model. Degrees of freedom (df), *F*-ratio (*F*), probability (*P*), partial eta squared ( $\eta$ ), BAI normalized with a single square root.

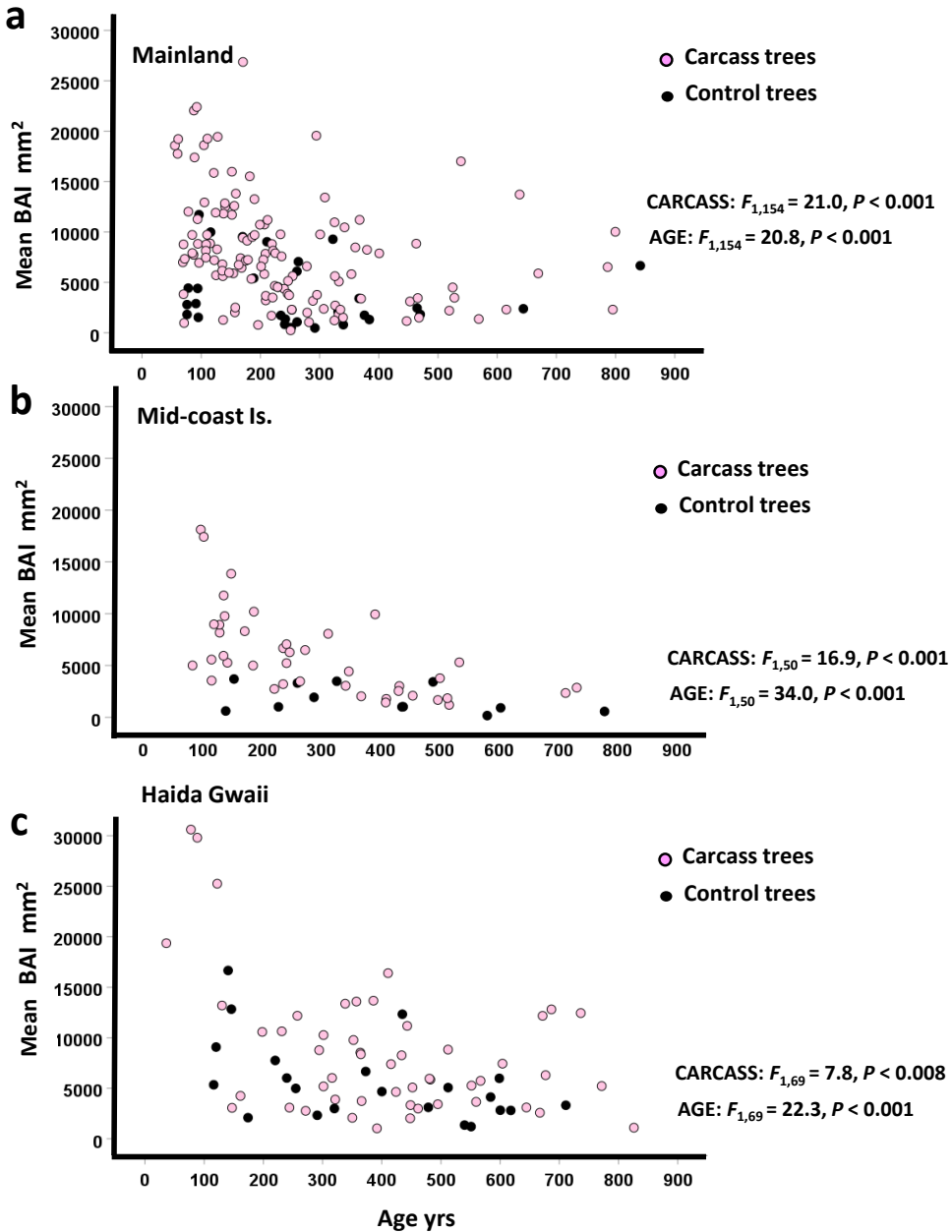
Region	Parameters	BAI			
		df	<i>F</i>	<i>P</i>	$\eta$
Mainland, 157 trees, 47 rivers	Model	3	21.0	<0.001	0.29
	AGE	1	15.1	<0.001	0.09
	SLOPE	1	15.0	<0.001	0.09
	CARCASS	1	12.6	<0.001	0.08
	Error	153			
Mid-coast, 53 trees, 16 rivers	Model	3	24.8	<0.001	0.60
	AGE	1	23.8	<0.001	0.33
	SLOPE	1	4.1	<0.050	0.08
	CARCASS	1	17.5	<0.001	0.26
	Error	49			
Haida Gwaii, 72 trees, 16 rivers	Model	3	9.8	<0.001	0.30
	AGE	1	22.1	<0.001	0.25
	SLOPE	1	0.1	0.890	0.00
	CARCASS	1	6.9	<0.020	0.09
	Error	68			

sites. The GLM with  $\delta^{15}\text{N}$  as the dependent variable and REGION, CARCASS, DISTFOR, and SLOPE as independents, and AGE as a covariate accounts for 18% of the variance ( $F_{1,135} = 2.6$ ,  $P < 0.006$ ) with the highest positive effects for CARCASS ( $F_{2,135} = 6.6$ ,  $P < 0.003$ ) and inverse associations for SLOPE ( $F_{1,135} = 5.5$ ,  $P < 0.03$ ) and no effects for DISTFOR ( $P = 0.66$ ) or for REGION ( $P = 0.22$ ). The GLM with BAI as dependent and REGION as independent and  $\delta^{15}\text{N}$  and AGE as covariates showed a significant effect for AGE ( $F_{1,142} = 18.8$ ,  $P < 0.001$ ) and no effect for REGION ( $F_{2,142} = 1.9$ ,  $P = 0.16$ ) or  $\delta^{15}\text{N}$  ( $F_{1,142} = 0.07$ ,  $P = 0.79$ ).

Coast-wide TN of tree rings averaged 0.07% (range 0.03% to 0.14%) and was highest on Haida Gwaii ( $\bar{x} \pm \text{SE } 0.091 \pm 0.03\%$ ,  $n = 29$ ), lower on the Mainland ( $0.067 \pm 0.03\%$ ,  $n = 89$ ), and lowest on the Mid-coast Islands ( $0.055 \pm 0.02\%$ ,  $n = 29$ ). There were inconsistent associations with carcass categories, TN being higher in control trees on the Mainland but higher in carcass-near trees on Haida Gwaii (Figure 10). There was a significant excess of TN in the more recent period (1975–1979) compared to the older period (1950–1954) for the Mainland ( $Z = 3.1$ ,  $P < 0.001$ ) and for the Mid-coast Islands ( $Z = 3.8$ ,  $P < 0.001$ ) but not for Haida Gwaii ( $Z = 1.12$ ,  $P = 0.26$ ). Total nitrogen was not related to SALMBIO (Mainland,  $r_s = -0.15$ ,  $P = 0.18$ ,  $n = 89$ ; Mid-coast Islands,  $r_s = -0.17$ ,  $P = 0.38$ ,  $n = 29$ ; Haida Gwaii,  $r_s = 0.24$ ,  $P = 0.20$ ,  $n = 29$ ). The full dataset (Figure

S5) differed from the partial dataset in that each of the regions exhibited marginally greater TN values in control trees relative to trees in carcass zones.

There were no overall correlations between  $\delta^{15}\text{N}$  and TN within carcass zone forests for each region (Mainland,  $r = 0.07$ ,  $P = 0.58$ ,  $n = 76$ ; Mid-coast Islands,  $r = 0.22$ ,  $P = 0.28$ ,  $n = 26$ ; Haida Gwaii,  $r = -0.13$ ,  $P = 0.63$ ,  $n = 17$ ). However, regional differences as well as watershed specific trends were evident (Figure 11). For Haida Gwaii, 15/17 carcass trees had greater TN values than the coastal averages while for the Mid-coast Islands, 22/26 carcass trees had lower TN values than the coastal average ( $\chi^2_1 = 11.6$ ,  $P < 0.001$ ). Log-linear analysis (three regions  $\times$  four quadrats) yielded a significant difference in the frequency distribution of trees among the four quadrats (two-way interaction  $\chi^2_{11} = 83.8$ ,  $P < 0.001$ ), the largest contribution being the excess of Mid-coast Islands trees in the low  $\delta^{15}\text{N}$  and low TN quadrat ( $Z = 2.6$ ,  $P < 0.01$ ). Similar results were evident in the full dataset (Figure S6) including comparable statistical trends (two-way interaction  $\chi^2_{11} = 104.2$ ,  $P < 0.001$ ). While  $\delta^{15}\text{N}$  and TN were not correlated overall within and among regions, the three watersheds with the highest combined  $\delta^{15}\text{N}$  and TN were Neekas River on the Mainland and Salmon River and Bag Harbour on Haida Gwaii (Figure S6).



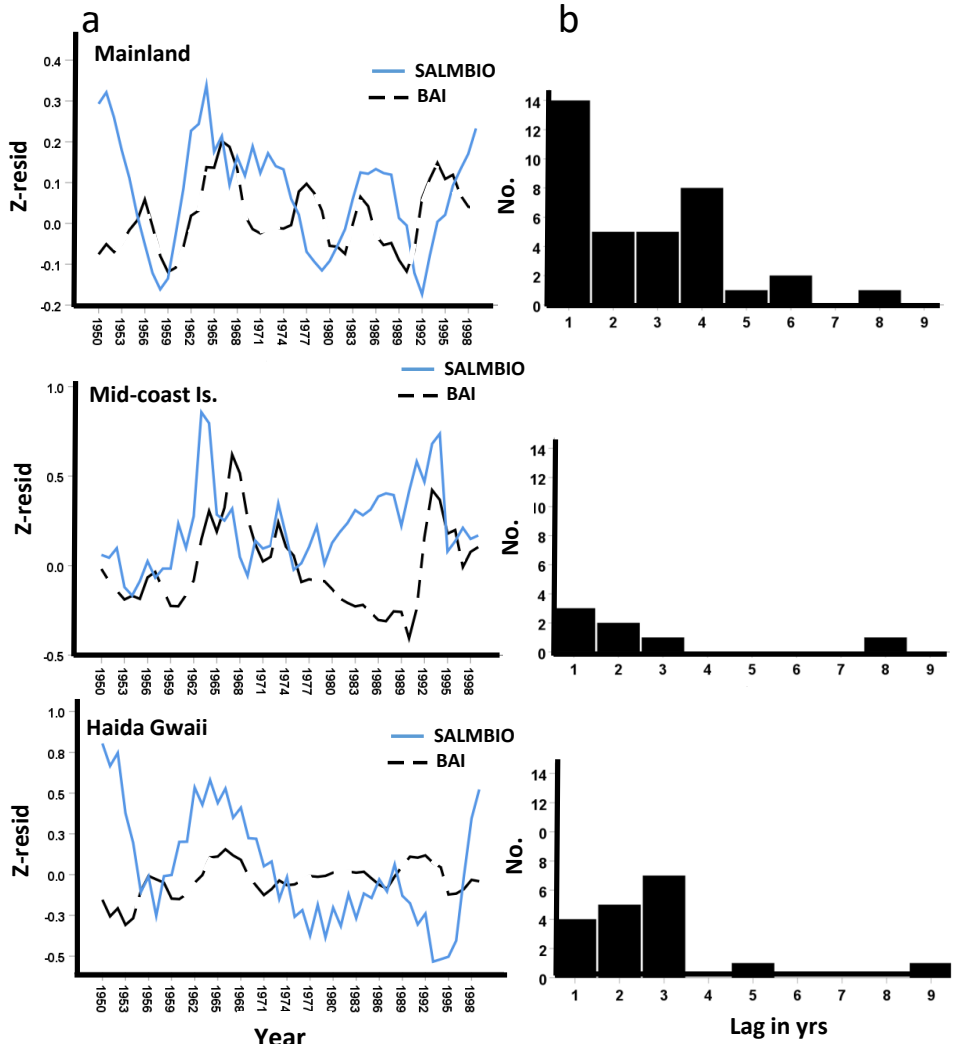
**FIGURE 7.** Relationship between mean basal area increment (BAI; 1945–1999) for each of 282 cores in relation to tree age of Sitka Spruce (*Picea sitchensis*) separated for region and carcass occurrence.

## Discussion

I undertook a coastal survey in British Columbia to evaluate radial growth (RW and BAI) of the largest Sitka Spruce from riparian zones with and without access to salmon-derived nutrients. My results are broad at both regional (Mainland, Mid-coast Islands, Haida Gwaii) and local scales and suggest a much

greater contribution to primary production in conifers than estimated in previous tree-ring studies (Drake *et al.* 2002; Reimchen *et al.* 2003; Reimchen and Fox 2013; Reimchen and Arbellay 2018, 2019).

Deficiency of soil nitrogen constrains productivity in many plant communities (LeBauer and Treseder 2008) and as such, it is not unexpected that the



**FIGURE 8.** a. Relationship between yearly oscillations of average salmon biomass and average growth (basal area increment [BAI]) of 282 Sitka Spruce (*Picea sitchensis*) for 1945 to 1998. Salmon biomass and BAI each scaled to a mean of zero based on residuals from linear regression. b. Frequency of the yearly lags (LAG) for the major oscillation on salmon biomass and BAI based on each core.

salmon spawning migrations in the north Pacific and their predator-mediated transfer into riparian zones positively influences conifer size and growth (Ben-David *et al.* 1998; Cederholm *et al.* 1999; Hilderbrand *et al.* 1999; Reimchen and Fox 2013). Alder (*Alnus* spp.), a recognized nitrogen-fixer that is often common in riparian zones, was rare or absent in the areas with old growth spruce that I sampled. The spruce trees I surveyed adjacent to salmon-spawning gravels averaged 1.2 m DBH and 300 years in age (range 60–842 yr), those on Haida Gwaii being marginally larger and older than those on the Mainland and the Mid-coast Islands. Within each region, DBH

increased in watersheds with more salmon entering the streams. Larger watersheds, usually with more salmon, often have wide non-sloping riparian zones, deeper soils, and potentially greater retention of nutrients from reduced hyporheic flow (O’Keefe and Edward 2003; Wondzell 2011), each of which may facilitate increased size and longevity of old growth trees. Yet, there remains ambiguity in these associations as multiple biophysical attributes can differ among these geographically diverse watersheds such as precipitation and temperature that are independent of salmon nutrients. However, my data address much of this ambiguity as the DBH was about 50% larger

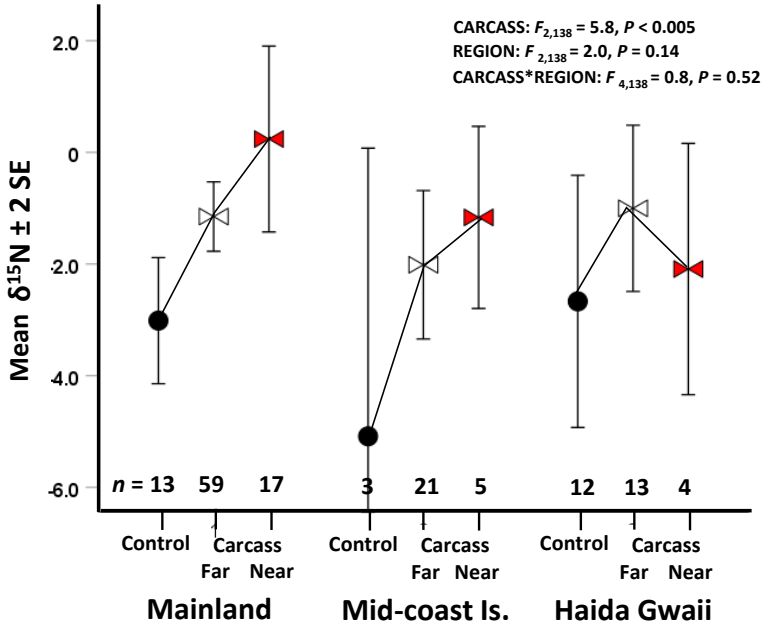


FIGURE 9. Average  $\delta^{15}\text{N}$  signatures for tree rings of riparian Sitka Spruce (*Picea sitchensis*) heartwood (1950–1954, 1975–1979) among regions in relation to salmon carcass occurrence.  $n$  = number of trees.

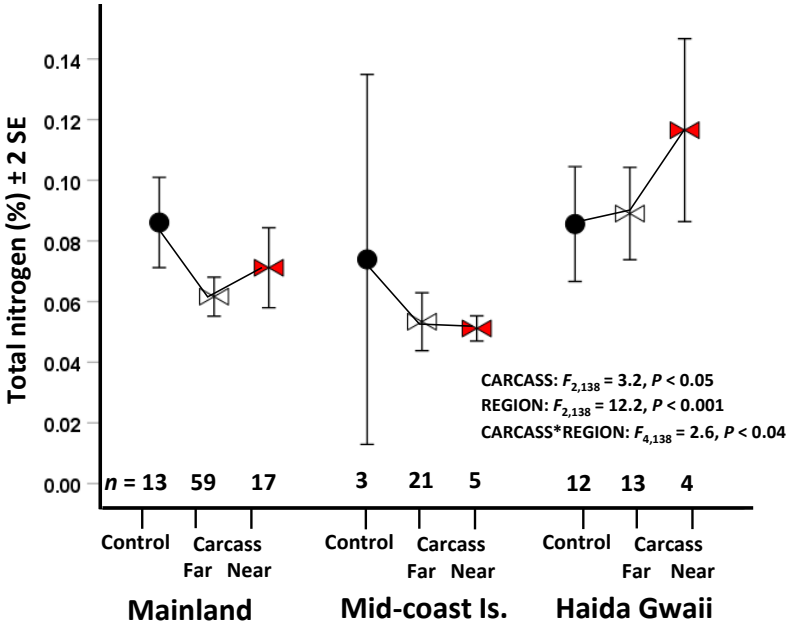
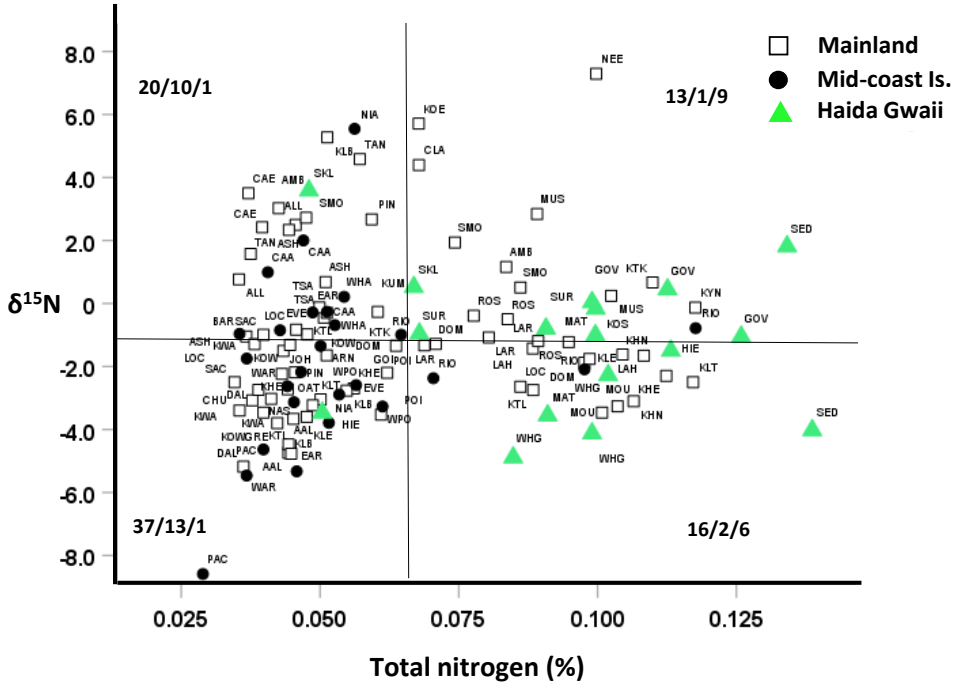


FIGURE 10. Total nitrogen for tree rings of riparian Sitka Spruce (*Picea sitchensis*) heartwood (1950–1954, 1975–1979) among regions in relation to salmon carcass occurrence.  $n$  = number of trees.

in carcass zones relative to adjacent control trees and in two of three regions, DBH was higher in carcass-near trees as opposed to carcass-far trees. Furthermore, while the close proximity of the control trees

to the carcass trees does not remove the microspatial edaphic conditions that occur in these riparian zones, they greatly minimize the differences compared to the 2–25 km distances that have been used in previous



**FIGURE 11.** Bivariate plot of  $\delta^{15}\text{N}$  data against total nitrogen (TN) for each Sitka Spruce (*Picea sitchensis*) tree from the salmon carcass zones, separated by region. Stream labels shown adjacent to each value (see Table S1 for full names). Sets of three values in each quadrat indicate total number of trees from that quadrat for each region. Note the disproportionate number of Mid-coast Islands trees in the low  $\delta^{15}\text{N}$  and low TN quadrat.

studies (e.g., Drake and Naiman 2007).

Quantifying radial growth was my primary interest and I found that BAI did not differ between carcass-near trees and carcass-far trees. These trees averaged 100% greater growth than adjacent control trees and ranged from 70% greater on Haida Gwaii to 240% greater on the Mid-coast Islands. These differences persisted over much of the five decades of yearly data. Although less informative, I also examined RW which was also similar between carcass-near and carcass-far trees with both averaging about 60% greater growth than adjacent control trees, ranging from 10% greater on Haida Gwaii to 125% greater on the Mid-coast Islands. Other biophysical factors covaried with the presence or absence of carcasses and may have contributed to the observed differences in growth. For example, I found that annular growth was lower on older trees (see Cherubini *et al.* 1998; Peters *et al.* 2014), lower on those from steeper slopes, and lower on those further from the stream. However, when I statistically corrected for these effects, the relative BAI growth enhancement (marginal means) for presence/absence of carcasses ranged from 55% to 150% dependent on region. These estimates, derived from 282 trees in 79 watersheds, are much larger than

previously reported (Reimchen and Arbellay 2019) from 13 trees in five watersheds where there was an average 19% greater growth in carcass trees. Four of these five watersheds, including Salmon River, had unusually high carcass density and bear activity (T.E.R. pers. obs.) and I suspected that even ‘control’ sites in these watersheds could be positively influenced by nutrient uploading. This would reduce the growth differential between carcass and control trees. Elevated isotopic signatures in control trees in one of these watersheds (Salmon River, Haida Gwaii) are consistent with this interpretation. Previous tree ring studies have also identified positive responses to nutrient loading and salmon abundance in comparisons with control sites (Helfield and Naiman 2001; Drake and Naiman 2007). However, the distances between salmon sites and control sites were large, averaging 6 km (maximum 25 km). Tree age and distance from the stream were not compared and as such, the differences between these may involve multiple habitat differences unrelated to salmon abundance and cannot provide a reliable proxy for historical signatures of salmon.

I found that over the five decades, there were major yearly oscillations in BAI that were often concordant

among geographical regions, including reduced growth in the 1950s and higher growth in the mid-1960s, in 1978, and in 1993. These common coast wide responses presumably indicate common climatic effects and/or nutrient pulses. Spruce growth is optimal on moist sites with rich soil nutrient regimes (Farr and Harris 1979; Farrelly *et al.* 2011), environmental conditions that largely characterize salmon watersheds of the Pacific Northwest. However, globally climatic variables tend to be poorly associated with Sitka Spruce growth (Blyth and MacLeod 1981; Worrell and Malcolm 1990; Feliksik and Wilczyński 2008; Hadley and Knapp 2011). That the major growth oscillations I observed in carcass forests were positively correlated with those from adjacent control sites suggest broader climatic influences largely independent of salmon numbers entering the streams.

If annular tree growth is responding directly to salmon abundance, then one predicts that the extensive yearly variability in abundance of salmon in British Columbia (NuSEDS 2019) should result in higher variability in annular tree growth relative to adjacent control trees of similar size. My data are consistent with this prediction for the Mainland and the Mid-coast Islands but not for Haida Gwaii, although for the latter the major exceptions are 2/19 control trees that have elevated variance. Longer term trends in growth have been used to estimate salmon abundance in past centuries (Starheim *et al.* 2013).

Positive correlations between salmon abundance and radial growth with a time lag from one to six years were initially reported for conifers in Alaska and Oregon (Drake and Naiman 2007) and in British Columbia (Reimchen and Fox 2013). In experimental fertilization studies, uptake of enriched nitrogen occurred one year after application (Hart and Classen 2003). In the current study, there were multiple oscillations in BAI over 50 years that were associated with salmon biomass that lagged from one to eight years; shorter lags (1–3 years) were the most common, consistent with more detailed studies at several of these watersheds (Reimchen and Arbellay 2019). Longer lags might reflect a more complex cycling of nutrients in the soils prior to uptake by old-growth trees (Simard *et al.* 2012).

Quantification of  $\delta^{15}\text{N}$  signatures in annular growth rings was initially reported by Poulson *et al.* (1997) using full ring mass of felled trees and subsequently by Drake *et al.* (2002, 2011), Reimchen *et al.* (2003), and Saurer *et al.* (2004) using increment cores. Further investigations allowed historical insight into nutrient cycling using isotopic signatures of tree rings in salmon watersheds (Drake and Naiman 2007; Reimchen and Fox 2013; Reimchen and Arbellay 2018, 2019) and in seabird colonies

(Holdaway *et al.* 2007; Reimchen *et al.* 2013). Holdaway *et al.* (2007) found marine nutrients did not influence conifers, presumably because enriched nutrients do not by themselves translate to elevated growth when other parameters (moisture, phosphorus, etc.) are limiting in seabird colonies. I found that the presence/absence of carcasses were better predictors of  $\delta^{15}\text{N}$  in tree rings than salmon spawning biomass. Trees with carcasses near their base had about 3‰ isotopic enrichment relative to adjacent control trees, indicative of highly localized spatial heterogeneity in nutrient uptake in these riparian zones. These sharp gradients in marine-derived nutrients and corresponding large differences in tree ring  $\delta^{15}\text{N}$  are inconsistent with conclusions and predictions (Handley *et al.* 1999; Amundson *et al.* 2003) that precipitation and temperature will be the major predictors of  $\delta^{15}\text{N}$  in temperate latitudes, at least with respect to rainforests of western North America.

I observed multiple exceptions to these isotopic associations with salmon carcasses including marked deficiency of tree ring  $\delta^{15}\text{N}$  in some watersheds where salmon spawning migrations were large as well as occasional high isotopic signatures in control sites. At least some of these exceptions are associated with differences in activity of the major predators. Black Bear (*Ursus americanus*) and Grizzly Bear (*Ursus arctos*) are dominant transfer vectors of salmon carcasses from the stream to the forests in western North America (Reimchen 1994, 2000, 2017; Hilderbrand *et al.* 1999) but are absent from multiple watersheds. For example, on the Mid-coast Islands and Haida Gwaii, smaller islands with salmon streams commonly have no evidence of carcass transfer due to the absence or very low density of bears or other transfer vectors. As well, high stream banks and deep channels on some of the larger salmon rivers on the Mainland limit or exclude movement of bears from the stream channel into the riparian zone also resulting in low isotopic signatures. I cannot account for why control sites occasionally had enriched isotopic signatures. Diverse mechanisms are probably involved as isotopic nitrogen is an integrator of nutrient cycling in the complex edaphic interactions occurring in forests (Robinson 2001; Craine *et al.* 2009). Transfer vectors, other than bears, such as canopy-roosting seabirds (Christie and Reimchen 2008) or nesting raptors (Anthony *et al.* 1982), may also contribute. Furthermore the extended historical use of these riparian forests by Indigenous Peoples, whose cultures were based on marine resources, may account for such elevated signatures in what I classified as ‘control’ sites.

I also evaluated the TN in the rings predicting that this could give insight to the general availability of soil nutrients. Total nitrogen in conifer heartwood is

characteristically low relative to sapwood or foliar tissues and has thus received limited attention in tree-ring studies. Heartwood TN values averaged 0.03% in Red Spruce (*Picea rubens* Sargent) from eastern North America (Doucet *et al.* 2011), 0.05% in Norway Spruce (*Picea abies* (L.) H. Karsten) in Switzerland (Saurer *et al.* 2004), and 0.01% in hybrids between Black Spruce (*Picea mariana* (Miller) Britton, Sterns & Poggenburgh) and Red Spruce (Martin *et al.* 2015). In my study of Sitka Spruce, coast-wide average TN value was about 0.07% in carcass zones and about 0.08% in adjacent control trees, approximately double that observed in other geographical regions. These results differ from those of Reimchen and Arbella (2019) who reported an average 0.02% increase in TN in five control trees relative to eight adjacent carcass trees, data also included in the current analyses of 282 trees, and suggestive of the asymmetric number of trees.

There were regional differences in the extent of co-variation between TN and  $\delta^{15}\text{N}$ . When partitioning the data into quadrats separated by coast-wide averages for TN and  $\delta^{15}\text{N}$ , the majority of carcass trees from Haida Gwaii had greater TN values, but average  $\delta^{15}\text{N}$  values, while the Mid-coast Islands watersheds had both low TN and low  $\delta^{15}\text{N}$ . These trends occurred in both partial and full datasets. The Mid-coast Islands also had the lowest average salmon biomass, the lowest BAI growth throughout the five decades, the largest differences in BAI between control trees and carcass zone trees as well as a substantial number of positive lags between salmon biomass and BAI. This might indicate that the control sites on the Mid-coast Islands are particularly nutrient-deficient, possibly from limited soil depth, emphasizing the particular importance of salmon spawning migration to the riparian zones in these small watersheds.

### Conclusions

I show that across a broad geographical region of coastal British Columbia, bear-mediated transfer of salmon carcasses to riparian zones results in an approximate doubling of annual radial growth of mature Sitka Spruce relative to adjacent control trees. Enrichment of nitrogen isotope signatures in growth rings among trees with salmon carcasses at their base confirm the uptake of these marine-derived sources. Major yearly fluctuations in radial growth over five decades (1945–1999) are concordant among geographical regions and within watersheds between carcass trees and adjacent control trees indicative of broad climatic influences. However, the yearly growth variance is greater in carcass trees and is associated with a one to four year lag in the major yearly oscillations in salmon biomass entering the streams. My data confirm and greatly extend previous studies

of the ‘salmon forest’ and emphasize the substantive contribution of vectors such as bears to riparian primary productivity.

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## SUPPLEMENTARY MATERIALS:

**TABLE S1.** Watersheds surveyed in coastal British Columbia to examine the relationship between salmon carcasses and Sitka Spruce (*Picea sitchensis*) growth.

**TABLE S2.** General linear model analyses (full dataset) of basal area increment (BAI; 1945–1999) of old-growth Sitka Spruce (*Picea sitchensis*) against tree age (AGE), riparian slope (SLOPE), and carcass condition (CARCASS) for three geographical regions.

**FIGURE S1.** Partial data set ( $n = 282$  trees). Regional and temporal (1945–1999) trends of Sitka Spruce (*Picea sitchensis*) ring width (RW) in relation to salmon carcass trees against adjacent control trees.

**FIGURE S2.** Full data set ( $n = 502$  trees) of regional and temporal (1945–1999) trends for basal area increment (BAI) on Sitka Spruce (*Picea sitchensis*) in relation to salmon carcass trees against adjacent control trees.

**FIGURE S3.** Full dataset ( $n = 502$  trees) of relationship between mean basal area increment (BAI; 1945–1999) for each core in relation to tree age of Sitka Spruce (*Picea sitchensis*) separated for region and carcass occurrence.

**FIGURE S4.** Full dataset ( $n = 247$ ) of average  $\delta^{15}\text{N}$  signatures for tree rings of riparian Sitka Spruce (*Picea sitchensis*) heartwood (1950–1954, 1975–1979) among regions in relation to salmon carcass occurrence.

**FIGURE S5.** Full dataset ( $n = 247$ ) of average total nitrogen for tree rings of riparian Sitka Spruce (*Picea sitchensis*) heartwood (1950–1954, 1975–1979) among regions in relation to salmon carcass occurrence.

**FIGURE S6.** Full dataset ( $n = 247$ ) of bivariate plot of  $\delta^{15}\text{N}$  data against total nitrogen (TN) for each Sitka Spruce (*Picea sitchensis*) tree and separated by region.

## Wood Frog (*Lithobates sylvaticus*) skeletogenic plasticity in anthropogenic habitats

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### Abstract

Habitat loss and landscape fragmentation are major causes of numerous amphibian population declines. Although logging activities have been related to serious effects on growth rate and size at metamorphosis in several species, less is known about skeletal developmental modifications associated with disturbed habitats. We studied the effects of forest canopy modifications caused by logging activities on the skeletal development of a pond-breeding anuran, Wood Frog (*Lithobates sylvaticus*). Biotic and abiotic factors were collected for 30 semi-permanent ponds located in three habitat categories (regenerated forest, along skidding trails, and logged areas). A sample of 58 cleared and double-stained tadpoles were analyzed to compare developmental trajectories among habitats. Water temperature and pond morphometric characteristics, which were correlated with logging-related habitat alteration, had a major impact on tadpole developmental differences among pond categories. Developmental plasticity was evident in both absolute and relative timing of chondrification and ossification between regenerated forest ponds and disturbed ponds (i.e., along skidding trails and in logged areas). Ossification and chondrification patterns had a different response to environmental factors. Notably, we observed the early onset of skeletogenesis in the disturbed ponds, which may result in deleterious effects on the fitness of post-metamorphosed juveniles.

Key words: Logging activities; developmental plasticity; pond-breeding amphibians; skeletogenesis; Wood Frog; *Lithobates sylvaticus*

### Introduction

Vertebrates can be critically affected by abiotic factors throughout their lifespan (Noble *et al.* 2018; Singh *et al.* 2020). Among these factors, temperature and humidity are known to affect phenology and the timing of breeding activities of several amphibian and reptile species (Bachmann 1969; Beebee 1995; Reading 1998; Lannoo and Stiles 2017; Noble *et al.* 2018; Singh *et al.* 2020). In aquatic environments, water temperature is known to influence the development of cartilage (chondrification) and bone (ossification) in fishes and amphibians (Fuiman *et al.* 1998; Haas 1999; Mabee *et al.* 2000; Gomez-Mestre *et al.* 2010). Skeletal elements that form later in the development have been shown to be more strongly influenced by environmental constraints and were therefore more

susceptible to express a plastic response (Hallgrímsson *et al.* 2007; Cardini and Elton 2008; Young and Badyaev 2010; Grünbaum *et al.* 2012). Ossification patterns have also been suggested to be more sensitive to functional requirements during development in comparison to chondrification (Grünbaum *et al.* 2003; Campinho *et al.* 2004). However, abiotic factors in breeding ponds that affect skeletal development in amphibians remain poorly documented (Hanken and Hall 1984; Gomez-Mestre *et al.* 2010).

Logging activities can tremendously change the habitat characteristics, such as soil properties and plant species distribution and abundance within a forest (Krag *et al.* 1986; Aust *et al.* 1993; Kariuki *et al.* 2006). These changes can also have significant effects on animal populations that use these habitats (Potvin

1999). Impacts on the abundance, diversity, and distribution of species, species interactions (e.g., predation), and habitat selection have been documented for numerous animal species (Ganey and Balda 1994; Darveau *et al.* 1997; Potvin 1999; Werner and Glennemeier 1999; Trottier 2006). By removing the forest canopy near aquatic habitats, logging activities contribute to increasing exposure to sun radiation leading to higher water temperature and modifying the duration a pond holds water (hydroperiod; DeMaynadier and Hunter 1995; Waldick *et al.* 1999).

Characteristics of both aquatic and terrestrial microhabitats that are modified by logging activities can influence the distribution and growth of amphibians (DiMauro and Hunter 2002; Houlahan and Findlay 2003; Trottier 2006; Beauchamp 2007). Amphibians are particularly sensitive to habitat modifications that can be linked to some of their physiological and ecological characteristics (such as skin permeability, low dispersal capacity, small home-range size, philopatry; Blaustein 1994; Duellman and Trueb 1994; Demaynadier and Hunter 1998). Such abiotic modifications of ponds can change the availability of tadpole food resources (Skelly *et al.* 2002; Skelly and Golon 2003; Baldwin *et al.* 2006), which can affect the reproductive effort and distribution of pond-breeding amphibians. The creation of temporary ponds along skidding trails and in cutover areas because of logging activity can also negatively affect amphibian development (Waldick *et al.* 1999; DiMauro and Hunter 2002). These temporary ponds are likely to dry out before tadpoles can reach metamorphosis and consequently induce high mortality (DiMauro and Hunter 2002), potentially reducing population fitness. Thus, multiple factors interact with amphibian survival, and logging effects can differ greatly among life stages within conspecifics (Semlitsch *et al.* 2009).

Amphibians can demonstrate phenotypic plasticity during their development in response to different environmental pressures (Newman 1992; Dahl *et al.* 2012). Developmental plasticity in anurans has been observed in several tissues and morphological traits (Udin and Keating 1981; Dieringer 1995; Touchon and Warkentin 2008). For example, the length and thickness of tail muscles of Wood Frog (*Lithobates sylvaticus*) increase in size when predators are present (Relyea 2002). Gomez-Mestre *et al.* (2010) showed that for both Red-eyed Tree Frog (*Agalychnis callidryas*) and African Clawed Frog (*Xenopus laevis*), low temperatures induced a lower degree of ossification and longer legs when compared to those that developed at higher temperatures. Habitat modifications can have observable effects not only on external morphology of pond-breeding amphibians, but also on internal anatomy during development.

The development of the amphibian skeleton is sensitive to pollution and habitat degradation (Ouellet *et al.* 1997; Lajmanovich *et al.* 2003; Taylor *et al.* 2005). Here, we provide an innovative approach to address the effects of logging activities on the skeletogenetic plasticity of amphibians. Our objective was to evaluate the impact of forest canopy modifications from logging activities on the skeletal development of Wood Frog in semi-permanent ponds in eastern Canada. Ponds in anthropogenically disturbed habitats (i.e., near skidding trails and in logged areas) were compared with ponds in regenerated forests. The most discriminating factor among pond categories is expected to be water temperature. Because of the absence of the forest canopy, higher water temperature in disturbed ponds should promote faster Wood Frog development compared to regenerated forest ponds. Environmental contrasts among pond categories are also likely to influence the absolute and relative timing of chondrification and ossification during development. While there is obvious coordination between cartilage and bone formation, the magnitude of their response to environmental constraints may differ. Given the results from previous studies in fishes (Grünbaum *et al.* 2003; Campinho *et al.* 2004), we predict that environmental conditions will have a greater effect on ossification than chondrification patterns.

## Methods

### Study area

Surveys were conducted in the Eastern Balsam Fir - Yellow Birch bioclimatic domain (Saucier 1998) at the interface between the northern hardwood and boreal biomes of eastern Canada. This region has 88% forest cover that has been exploited by logging companies since 1901 (Boucher *et al.* 2009). Thirty ponds in the Duchénier Wildlife Reserve (eastern Quebec, Canada; Figure S1) were sampled in recently cut and regenerated forests. The area is dominated by coniferous species and is a transition area between the boreal and deciduous forest ecosystems (Rowe 1972).

We selected 30 ponds that: (1) contained at least one amphibian species, (2) had a semi-permanent hydroperiod, (3) were <0.2 ha, (4) lacked a stream connection, (5) were devoid of fishes, and (6) were <500 m from a road. We sampled 10 ponds for each habitat category: logged areas, skidding trails, and regenerated forest areas (Figure S1).

### Biotic and abiotic environmental characteristics

Global positioning system coordinates for each pond and distances from the nearest skidding trails, logged area, and regenerated forest were recorded at the beginning of summer 2004. Pond length and width, aquatic substrate composition, vegetation cover

around the pond, and vegetal water coverage were recorded on three separate occasions between May and August 2004.

Nine morphometric (length, width, maximum depth, and surface area) and physicochemical parameters (water temperature, transparency, dissolved oxygen concentration, pH, and conductivity) were measured in each pond. The maximum depth and physicochemical characteristics were measured weekly. Physicochemical characteristics were measured between 0800 and 1700 with a YSI 650 MDS portable terminal (Yellow Springs, Ohio, USA) equipped with a YSI 600QS probe. These measurements were made 10 cm below the water surface at the deepest point of each pond. Water transparency was visually estimated using three categories (1 = clear, 2 = semi-opaque, 3 = opaque).

#### *Developmental plasticity*

Between 10 May and 19 August 2004, 100 Wood Frog tadpoles and transforming froglets per pond were collected, one pond per habitat category ( $n = 300$ ). The specimens were euthanized in MS-222 (Fisher Scientific, Ottawa, Ontario, Canada), fixed in neutrally buffered formalin (5–10%), and preserved in 70% ethanol.

A sample of 58 Wood Frog tadpoles provided a fairly comprehensive sequence of skeletogenic development for all the pond categories: 20 specimens from a skidding trail pond (D01), 18 from a logged area pond (D101), and 20 from a regenerated forest pond (D57). The developmental stage of each specimen was determined using methods described by Gosner (1960) that refers to a simplified staging table based on external anatomy. Tadpole soft tissues were digested with 1% trypsin in a saturated sodium borate solution (Dingerkus and Uhler 1977). Acid-free double staining protocol (Walker and Kimmel 2007) was used. Cartilaginous structures were stained using acid-free Alcian blue and bones were stained with ethanol/Alizarin red S solution.

Cleared and stained specimens (Figure 1) were observed using a Leica MZ16A stereomicroscope (Heerbrugg, Wahlkreis Rheintal, Switzerland). A skeletal element was considered to be chondrified when the Alcian blue stain was observed. Alizarin red S stain indicated that an element was ossified. A total of 126 skeletal (cranial and postcranial) elements were scored for three possible developmental states: absent (0), chondrified (1), and ossified (2). Cranial nomenclature follow Cannatella (1999) and Duellman and Trueb (1986). Postcranial nomenclature largely follows Duellman and Trueb (1986). The absolute timing (number of days post-hatching [dph]) of the first appearance of cartilage and bone was compared among pond categories. In some

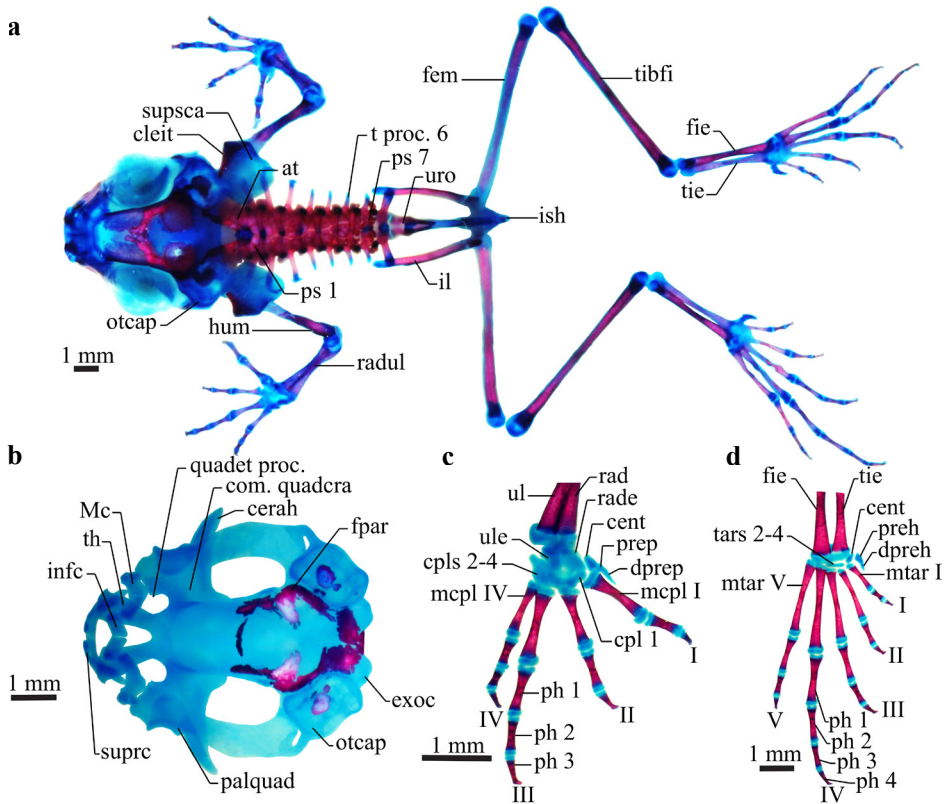
analyses, endochondral elements were further separated into six anatomical systems: skull, vertebral column, forelimbs, pectoral girdle, pelvic girdle, and hindlimbs. We define the mean onset as the average number of dph for the onset of all endochondral elements belonging to an anatomical system.

Gosner stage classification is useful to visually establish a relative developmental stage (Gosner 1960), but the time to reach each stage can vary among individuals. Gosner stages were not used as a comparative proxy because they were considered insufficiently accurate to compare development among three pond categories with different developmental durations. Furthermore, because Gosner stages are based on external morphology (Gosner 1960), they are too coarse to describe internal anatomy. Morphometric measurements, including snout-vent length (SVL), head length, and head width, are inappropriate as a size proxy because of the parabolic relationship between developmental duration and all the morphometric measurements considered (Figure S2). We developed a novel age proxy to compare specimens within and among pond categories. An approximate dph was estimated from the mean hatching period in the three ponds from where the specimens were collected. Zero dph was considered the sampling date when the first specimen reached Gosner stage 25 in each pond, the first tadpole stage after hatching.

#### *Statistical analyses*

For the 30 surveyed ponds and, individually for the three ponds from where frogs were collected, we used permutation one-way analyses of variance (ANOVA, 10000 permutations) to describe biotic and abiotic factors among pond categories (Herve 2018). We performed a canonical discriminant analysis (CDA) using the 30 studied ponds to validate the morphometric and physicochemical characteristics responsible for differences among pond categories. Pond lengths and widths were excluded from the CDA to avoid redundancy with surface area. Data were not transformed. The multivariate normality assumption was validated by Mardia's test (Mardia 1985), homoscedasticity was validated using Box's M test (Morrison 1976), and multicollinearity was tested using Pearson correlations (Becker *et al.* 1988). The accuracy of the classification rule was tested by the division of the sum of unconfused predictions on the prediction total, which was 30 (one per pond).

As an indicator of the absolute timing of chondrification and ossification, we compared the onset of all skeletal elements among pond categories (Figures S3 to S7). Permutation one-way ANOVAs (10000 permutations) complemented by permutation *t*-tests (10000 permutations) were performed to compare the mean onset of chondrification and ossification events



**FIGURE 1.** a. Dorsal view of the entire skeleton of a fully metamorphosed (Gosner stage 46) Wood Frog (*Lithobates sylvaticus*). b. Skull of a tadpole (Gosner stage 35) and the forelimb (c) and hindlimb (d) of the individual in a. Abbreviations are as follows: otcap = otic capsule; supsca = suprascapular; cleit = cleithrum; at = atlas; ps = presacral vertebra; t proc. = transversal process; uro = urostyle; il = ilium; ish = ishium; hum = humerus; radul = radio-ulna; fem = femur; tibfi = tibiofibular; fie = fibulare; tie = tibiale; suprc = suprarostril cartilage; infc = infrarostral cartilage; Mc = Meckel's cartilage; th = trabecular horn; quadet proc. = quadratoethmoidal process; com. quadra = commissura quadrato cranialis; cerah = ceratohyal; palquad = palatoquadrate; fpar = frontoparietal; exoc = exoccipital; ul = ulna; rad = radius; ule = ulnare; rade = radiale; cent = centrale; cpl(s) = carpal(s); prep = prepollex; dprep = distal prepollex; mcpl = metacarpal; ph = phalanx; tars = tarsals; preh = prehallux; dpreh = distal prehallux; mtar = metatarsal. Photos: Laurent Houle.

of endochondral bones within anatomical systems (i.e., skull, vertebral column, forelimb and hindlimb, and pectoral and pelvic girdles; Herve 2018). Almost all skeletogenic event onsets were identified using their first appearance. We used logistic regressions to estimate the onset of six skeletogenic events, considering the cutting point ( $dph_{50}$ ) as their onset (Grünbaum *et al.* 2012). Considering one skeletogenic event for a given element, the cutting point is defined as the dph when 50% of the individuals had a state of absence of the event and 50% had a state of presence. Logistic model suitability was tested using receiver operating characteristic (ROC) curves (Wright 2005) determined by calculating the area under the curves (AUC). The AUC represents a measure of overall accuracy for a diagnostic test and can be used as a test

for a ROC curve (Park *et al.* 2004). Area under the curve values under 0.5 are not considered to be accurate while values of one are perfectly accurate (Park *et al.* 2004).

As an indicator of the relative timing of chondrification and ossification, we compared trajectories of a cumulative number of formed skeletal elements among pond categories. Congruence tests were performed using permutation Spearman's rank correlation tests (10000 permutations; Dagnelie 1973), conducted using 64 endochondral bones (Table S1). A rank value was given to each chondrification and ossification event using Dagnelie's method to adjust equal ranks and to calculate Spearman's rank coefficient ( $r_s$ ; Dagnelie 1973). The appendicular endochondral bones were also tested separately using the

same method. Multiple comparisons of the  $r_s$  were calculated by bootstrapping (10000 iterations).

It was not possible to use a multiple regression/general linear model to compare the onset of skeletal element chondrification or ossification with the pond characteristics from where the frogs were collected because collections were only made in three ponds, one per category.

## Results

### *Biotic and abiotic environmental characteristics*

The canopy cover at the 30 ponds studied differed significantly among the three pond categories ( $F_{2,27} = 77.3$ ,  $P < 0.001$ ; Table S2). All pond morphometric factors differed significantly between disturbed and regenerated forest ponds. Regenerated forest ponds were the largest (length, width, and surface area) and deepest. Water temperature was significantly higher in disturbed ponds ( $F_{2,27} = 6.9$ ,  $P = 0.004$ ; Table S2). The substrate composition differed among pond categories. A higher proportion of dead leaves was found in regenerated forest ponds ( $F_{2,27} = 13.3$ ,  $P < 0.001$ ; Table S2). Skidding trail ponds contained a smaller proportion of humus ( $F_{2,27} = 8.9$ ,  $P = 0.001$ ; Table S2) and mosses ( $F_{2,27} = 4.6$ ,  $P = 0.011$ ; Table S2) and a higher proportion of fine sediments (i.e., fine sand and silt;  $F_{2,27} = 14.7$ ,  $P < 0.001$ ; Table S2). Water temperature ( $F_{2,33} = 10.8$ ,  $P = 0.01$ ; Table S3) and surface area ( $F_{2,6} = 10.0$ ,  $P = 0.003$ ; Table S3) were significantly different among the pond categories from where the frogs were collected.

Pond categories were used as the grouping factor to determine which morphometric and physicochemical parameters were the most discriminating to differentiate ponds. The first dimension of the CDA estimated 86.6% of the optimal linear combination of the seven variables, whereas the second dimension estimated 13.4%. Water temperature, surface area, depth, and transparency have the greatest impact on pond discrimination (Figure 2). The three pond categories were well separated, despite a slight overlap. The classification rule has an accuracy of 89.3%.

### *Absolute and relative timing of chondrification and ossification*

The complete sequences of chondrification and ossification for the 126 Wood Frog skeletal elements (Figures S3–S7) showed congruence and differences in terms of absolute and relative timing among pond categories. The general sequence of formation (chondrification and ossification) for the six anatomical systems was fairly conservative independent of pond categories (Table S4).

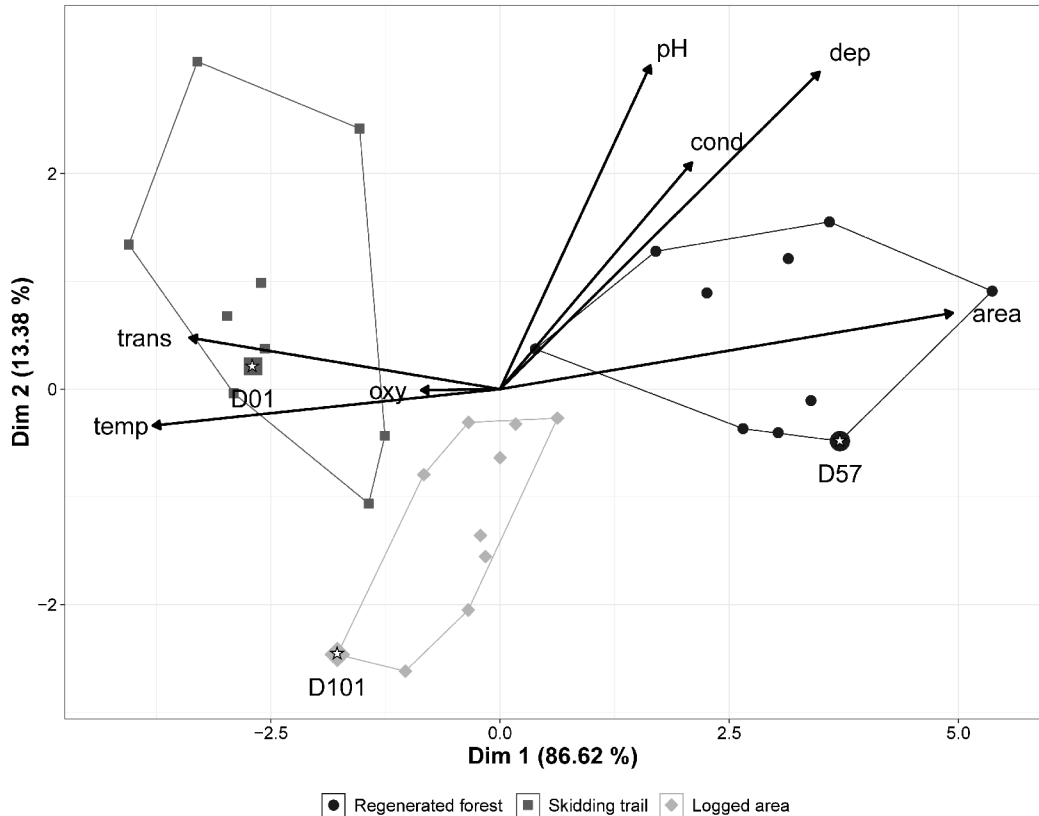
The onset of chondrification and ossification varied minimally among individuals for an element within a pond category. The only inter-individual

differences were observed for (1) the onset of chondrification for the transversal processes of vertebrae 1 and 2 in both logged area and skidding trail ponds; (2) the ossification of the atlas in the logged area ponds; and (3) the chondrification of the urostyle in skidding trail ponds (Table S5).

Within all anatomical systems, we found similarities in the observed pattern of the mean chondrification and ossification onsets among pond categories (Figure 3a). There was at least one significant difference among pond categories for all the anatomical systems except the skull and pelvic girdle (Table S6, Figure 3a). Chondrification and ossification of vertebral elements were delayed (i.e., longer dph) in regenerated forest ponds (Table S6, Figure 3a). Mean onsets of chondrification of forelimbs and hindlimbs were significantly longer in regenerated forest ponds (Table S6, Figure 3a). Intragroup variation associated with the mean onset of limbs was higher for chondrification than ossification. Mean onset of limb ossification differed significantly among the three pond categories (Table S6, Figure 3a). The mean onset of pectoral girdle chondrification in regenerated forest was longer than in logged area ponds. The mean onset of pectoral girdle ossification in regenerated forest pond was longer than in disturbed ponds (Table S6, Figure 3a). Mean onsets of chondrification and ossification of skull and pelvic girdle did not differ significantly among pond categories.

Wood Frog cartilaginous trajectories were separated into three phases (Figure 3b): (1) an initial phase between 10 and 20 dph, (2) a gradual increase between 20 and 50 dph, and (3) a final phase after 50 dph, indicating its completion. Ossified trajectories were also separated into three phases (Figure 3c): (1) an initial phase between 10 and 30 dph, (2) a threshold between 30 and 55 dph, and (3) a final phase after 55 dph. Both cartilaginous and ossified trajectories differed among pond categories and occurred faster in disturbed ponds compared to regenerated forest. The cartilaginous trajectory for the regenerated forest differed significantly (25–50 dph) from that of disturbed ponds, indicated by non-overlapping CI. Ossified trajectories showed a similar pattern between disturbed and regenerated forest ponds from 35 to 50 dph.

The correlation between chondrification and ossification of 64 endochondral bones did not differ significantly within and among pond categories ( $r_s = 0.89–0.92$ ; Table S7). Comparison among pond categories showed slightly higher  $r_s$  for the chondrification patterns compared to the ossification between regenerated forest ponds and disturbed ponds. The direction of the correlation between the chondrification and ossification in the skidding trail and logged area apparently reversed, although the difference



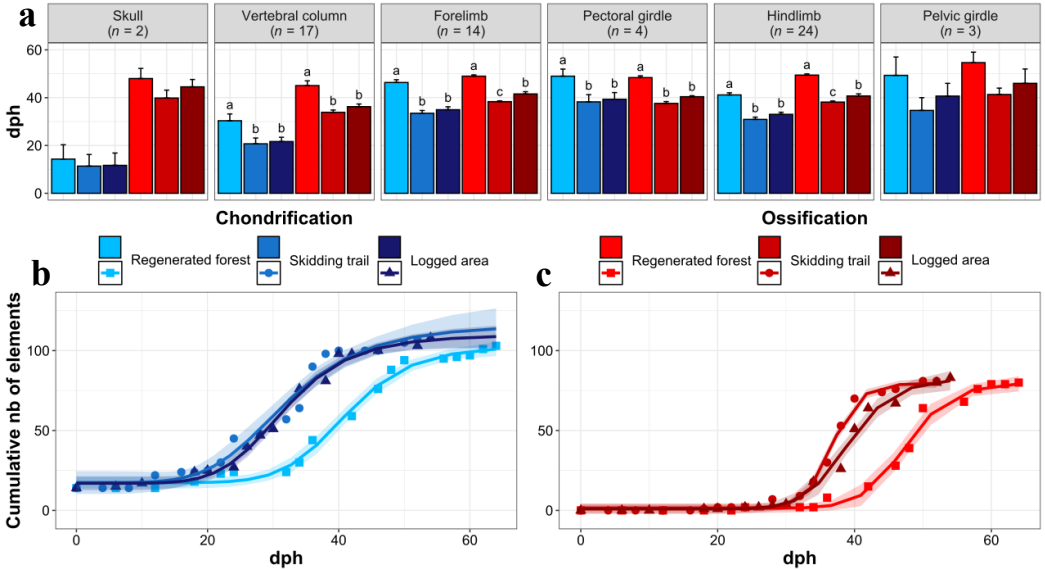
**FIGURE 2.** Canonical discriminant analysis showing environmental factors explaining differences among pond categories in the 30 studied ponds, Duch n r Wildlife Reserve, eastern Quebec, Canada. Vector lines represent discriminant coefficients for the first (Dim 1) and second (Dim 2) dimensions. The stars identify the ponds from which Wood Frog (*Lithobates sylvaticus*) specimens were sampled. Cond: conductivity; area: surface area; dep: depth; oxy: dissolved oxygen; temp: water temperature; trans: transparency.

was not significant. The appendicular endochondral bones (representing 59.4% of the total number of elements; Table S1) were tested separately. Significant differences in  $r_s$  were found in ossification patterns of limbs among pond categories (Table S8). Ossification  $r_s$  in both forelimb and hindlimb between the two disturbed ponds were highly congruent and also significantly different from the  $r_s$  comparing regenerated forest ponds to skidding trail ponds and  $r_s$  comparing regenerated forest ponds to logged area ponds (Table S8). This difference is because of small shifts in the order of the sequences for seven elements in forelimbs and for 11 elements in hindlimbs (mainly distal elements in both anatomical systems) between disturbed and regenerated forest ponds.

## Discussion

Amphibians that reproduce in ponds can exhibit plasticity in developmental and growth rates induced

by the environment (Amburgey *et al.* 2016; Orizola and Laurila 2016; Sz kely *et al.* 2017). To our knowledge, our study is the first to describe amphibian developmental plasticity of skeletogenesis in a field study using absolute and relative timing of skeletogenic (chondrification and ossification) events and developmental trajectories. In our investigation, (1) two canopy-related (water temperature and transparency) and two pond morphometric (surface area and depth) variables were found to be the most important factors explaining differences among pond categories, (2) changes were observed in absolute and relative timing of skeletogenic events, and (3) limb ossification was more responsive to environmental conditions than chondrification. We considered these results indicators of developmental plasticity in Wood Frogs among pond categories. Forest canopy removal by logging accelerates the timing of skeletogenesis



**FIGURE 3.** a. Mean onset of chondrification (blue bars) and ossification (red bars) of Wood Frog (*Lithobates sylvaticus*) endochondral bones among pond categories in the Duch enier Wildlife Reserve, eastern Quebec, Canada. Letters indicate grouping results of permutation *t*-tests. Wood Frog b. cartilaginous and c. ossified developmental trajectories among pond categories. Non-linear regressions are from dose-response models that use four parameters log-logistic function. Shaded areas correspond to 95% CI associated with each curve.

and seems to have a larger effect on processes that occur later during development than those that occur earlier. Furthermore, we provide the first detailed sequence of Wood Frog chondrification and ossification.

Amphibian growth rate has previously been related to several biotic and abiotic factors in breeding ponds (Amburgey *et al.* 2016; Freidenburg 2017). One such important factor is the forest canopy (Skelly *et al.* 1999; Renken *et al.* 2004; Semlitsch *et al.* 2008). Closed canopy ponds are normally associated with slower growth of anurans than open canopy ponds because of the lack of light, cooler water temperature, lower dissolved oxygen concentration, lower primary productivity, lower periphyton abundance, and different types of food resources (Skelly *et al.* 1999, 2002; Werner and Glennemeier 1999). Because all selected ponds in our study had a semi-permanent hydroperiod, hydroperiod was assumed to be relatively constant among pond categories. For this reason, we did not intensively monitor water level variation. However, Sz ekely *et al.* (2017) showed that Pacific Horned Frog (*Ceratophrys stolzmanni*) can exhibit plastic reactions, such as an accelerated developmental rate and a reduced duration of some metamorphic stages, because of a declining water level. Gomez-Mestre *et al.* (2013) also showed similar results for Western Spadefoot (*Pelobates cultripes*) using a

different method. In our study, the greater depth found in regenerated forest ponds is likely to have slowed Wood Frog developmental rate. Significant differences observed in developmental trajectories between disturbed and regenerated forest ponds provide some evidence of a shift in developmental rate. Based on previous studies (Skelly *et al.* 2002; Gomez-Mestre *et al.* 2013; Dittrich *et al.* 2016; Sz ekely *et al.* 2017), we strongly suspected that water temperature and depth had an impact on developmental rates we observed among pond categories.

*Development and growth differences can affect survival*

Wood Frog is known to breed in open and closed canopy ponds (Werner and Glennemeier 1999). Growth has been reported to be faster in open canopy ponds (Skelly *et al.* 1999; Werner and Glennemeier 1999; Halverson *et al.* 2003), but Skelly *et al.* (2002) reported that some biotic factors (such as food availability) can partially mitigate depressed growth rate in closed canopy ponds.

Faster development in disturbed ponds in comparison to regenerated forest ponds could be a fitness advantage. In North America, an early metamorphosis means a longer terrestrial feeding and growing period before winter (Semlitsch *et al.* 1988). Berven (1990) noted that Wood Frog juveniles that metamorphosed early and were larger at metamorphosis,

had a higher adult survival, and could reach sexual maturity earlier. For many ranids, at least 80% of the growth that leads to adult size occurs during the terrestrial phase (Werner 1986). However, as shown in our study, the entire skeletogenesis occurs during the aquatic growth period; it is known that the pre-metamorphic period affects the morphology and performance of juveniles (Álvarez and Nicieza 2002; Relyea and Hoverman 2003; Richter-Boix *et al.* 2006). Álvarez and Nicieza (2002) showed that a faster growth rate (from high water temperature) can negatively affect the jumping performance and the amount of energy reserves of juvenile Iberian Painted Frog (*Discoglossus galganoi*). A fluctuating water level, a characteristic associated with open canopy ponds, can lead to faster growth rate in Common Parsley Frog (*Pelodytes punctatus*), but also to juveniles with shorter and less muscular hind limbs (Richter-Boix *et al.* 2006). Logging activities are also known to alter terrestrial habitat characteristics in such ways that they can become highly unsuitable for many amphibian species (DeMaynadier and Hunter 1995; Waldick *et al.* 1999). This leads us to conclude that the faster development in disturbed ponds in response to higher water temperature and lower (and more fluctuating) water level could lead to poorer juvenile fitness. This, associated with a harsh terrestrial habitat, could reduce Wood Frog survival rates.

#### *Developmental plasticity*

We found that the frogs had a plastic response in the absolute and relative timing of chondrification and ossification between disturbed and regenerated forest ponds. The observed differences among ponds seem to be related to water temperature, transparency, and morphometric characteristics (i.e., surface area and depth). Acceleration of developmental rate associated with higher temperature has also been reported in fishes (Fuiman *et al.* 1998) and birds (Hosseini and Hogg 1991). Developmental plasticity in skeletal anatomy has been studied in fishes exposed to different experimental constraints (Campinho *et al.* 2004; Cloutier *et al.* 2010). Some authors concluded that there was a small impact of plasticity on the order of events within the sequences of chondrification and ossification in Arctic Char (*Salvelinus alpinus*; Cloutier *et al.* 2010; Grünbaum *et al.* 2012).

In our study, we found significant changes in the order of limb ossification between disturbed and regenerated forest ponds. Limb chondrification patterns are very similar when comparing pond categories, but ossification patterns are more congruent between both disturbed pond types than between disturbed ponds and regenerated forest ponds. This suggests that the sequence of bone formation of the appendicular skeleton might be slightly more responsive

to environmental differences observed between disturbed and regenerated forest ponds. Although there is coordination between chondrocyte and osteoblast differentiation in the formation of endochondral bone (Cloutier *et al.* 2010), some authors have reported a different response between chondrification and ossification in fishes exposed to temperature treatments (Mabee *et al.* 2000; Campinho *et al.* 2004). Cloutier *et al.* (2010) concluded that the effects of environmental constraints on patterns of chondrification and ossification could be partially independent in fishes. As suggested by our study, this pattern is likely to be similar in amphibians. The ossification pattern of the appendicular skeleton reacts more sensitively than the chondrification pattern. This could be because ossification mostly occurs after chondrification; the accumulation of variant phenotypes during earlier developmental stages leads to a greater likelihood to observe larger scale variation in ossification patterns.

Environmental characteristics (such as canopy-related factors) are well known to influence amphibian richness, distribution, reproduction effort, and the survival of tadpoles (Hecnar and M'Closkey 1998; Kolozsvary and Swihart 1999; Lehtinen *et al.* 1999; Marsh and Trenham 2001). Developmental plasticity is also suggested to affect tadpole and adult survival and reproduction which can have important repercussions on population dynamics. The absolute and relative timing of chondrification and ossification in the frogs in our study showed a plastic response to different environmental conditions.

#### **Author Contributions**

Writing – Original draft: L.H.; Writing – Review & Editing: L.H., L.S., O.L., A.C., and R.C.; Conceptualization: L.H., J.B., J.T., L.S., and R.C.; Investigation: J.B. and J.T.; Methodology: L.H., J.B., and K.S.; Formal analysis: L.H., A.C., and R.C.; Funding Acquisition: R.C.

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care and sampling protocols followed the instructions of the Comité de protection des animaux (CPA), associated to the Ministère de l'Agriculture, des Pêcheries et de l'Alimentation du Québec (MAPAQ) and the Société de la Faune et des Parcs (ref. 20020604-005-01-S-F). Three permits were obtained for this study: Comité de protection des animaux (CPA), Ministère de l'Agriculture, des Pêcheries et de l'Alimentation du Québec (MAPAQ), and Société de la Faune et des Parcs (SFP; ref. 20020604-005-01-S-F). We also thank the reviewers who provided useful comments on the manuscript.

### Raw data repository and voucher specimens

Raw data are available freely from the following GitHub repository [https://github.com/LaurentHoule03/Raw\\_data\\_Lithobates\\_sylvaticus\\_skeletogenesis.git](https://github.com/LaurentHoule03/Raw_data_Lithobates_sylvaticus_skeletogenesis.git). The specimens will be donated to the herpetological collection of the Canadian Museum of Nature.

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#### SUPPLEMENTARY MATERIALS:

**FIGURE S1.** Location of the 30 studied ponds in the Duchénier Wildlife Reserve, Quebec, Canada.

**FIGURE S2.** Snout–vent length, head width, and head length non-linear relationships during larval period for 45 of the 58 cleared and stained Wood Frog (*Lithobates sylvaticus*) tadpoles and froglets from the Duchénier Wildlife Reserve, Quebec, Canada.

**FIGURE S3.** Sequence of Wood Frog (*Lithobates sylvaticus*) chondrification and ossification for cranial elements from a regenerated forest, a skidding trail, and a logged area pond in the Duchénier Wildlife Reserve, Quebec, Canada.

**FIGURE S4.** Sequence of Wood Frog (*Lithobates sylvaticus*) chondrification and ossification for the vertebral column from a regenerated forest, a skidding trail, and a logged area pond in the Duchénier Wildlife Reserve, Quebec, Canada.

**FIGURE S5.** Sequence of Wood Frog (*Lithobates sylvaticus*) chondrification and ossification for forelimb elements from a regenerated forest, a skidding trail, and a logged area pond in the Duchénier Wildlife Reserve, Quebec, Canada.

**FIGURE S6.** Sequence of Wood Frog (*Lithobates sylvaticus*) chondrification and ossification for pectoral and pelvic girdle elements from a regenerated forest, a skidding trail, and a logged area pond in the Duchénier Wildlife Reserve, Quebec, Canada.

**FIGURE S7.** Sequence of Wood Frog (*Lithobates sylvaticus*) chondrification and ossification for hind limb elements from a regenerated forest, a skidding trail, and a logged area pond in the Duchénier Wildlife Reserve, Quebec, Canada.

**TABLE S1.** List of endochondral bones of Wood Frog (*Lithobates sylvaticus*) from the Duchénier Wildlife Reserve, Quebec, Canada.

**TABLE S2.** Mean and 95% CI values of 24 biotic and abiotic parameters among pond categories from 30 ponds in the Duchénier Wildlife Reserve, Quebec, Canada where chondrification and ossification sequences of Wood Frog (*Lithobates sylvaticus*) were studied.

**TABLE S3.** Mean and 95% CI values of 24 biotic and abiotic parameters among pond categories from the three ponds in the Duchénier Wildlife Reserve, Quebec, Canada where the Wood Frog (*Lithobates sylvaticus*) specimens were collected.

**TABLE S4.** Chronology of formation for the six anatomical systems of Wood Frog (*Lithobates sylvaticus*) from all three pond categories pooled from the Duchénier Wildlife Reserve, Quebec, Canada.

**TABLE S5.** Logistic models output used to determine onset of chondrification or ossification for six skeletal elements of Wood Frog (*Lithobates sylvaticus*) from the Duchénier Wildlife Reserve, Quebec, Canada.

**TABLE S6.** Permutation ANOVAs and permutation *t*-tests for the mean onsets of chondrification and ossification of 64 cartilage bones of Wood Frog (*Lithobates sylvaticus*) from the Duchénier Wildlife Reserve, Quebec, Canada.

**TABLE S7.** Test of congruence within and among pond categories between cartilaginous and ossified trajectories of 64 cartilage bones of Wood Frog (*Lithobates sylvaticus*) from the Duchénier Wildlife Reserve, Quebec, Canada.

**TABLE S8.** Test of congruence among and within pond categories between cartilaginous and ossified trajectories of cartilage bones from the appendicular skeleton of Wood Frog (*Lithobates sylvaticus*) from the Duchénier Wildlife Reserve, Quebec, Canada.

## Note

### First known observations of migratory Army Cutworm Moth (*Euxoa auxiliaris*) in the southern Canadian Rocky Mountains

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#### Abstract

Army Cutworm Moth (*Euxoa auxiliaris*) migrates long distances to mountain talus slopes where they aggregate in prodigious numbers over summer. Composed of ~70% lipid and ~25% protein at the height of summer, the moths attract Grizzly Bear (*Ursus arctos horribilis*) to talus slopes in certain mountain ranges in the contiguous United States to forage at aggregations. We present the first known observations of migratory Army Cutworm Moths aggregating on talus slopes in the southern Canadian Rocky Mountains of British Columbia and Alberta. Because this is a potential food resource for the bears, managers may wish to evaluate suitable moth habitat.

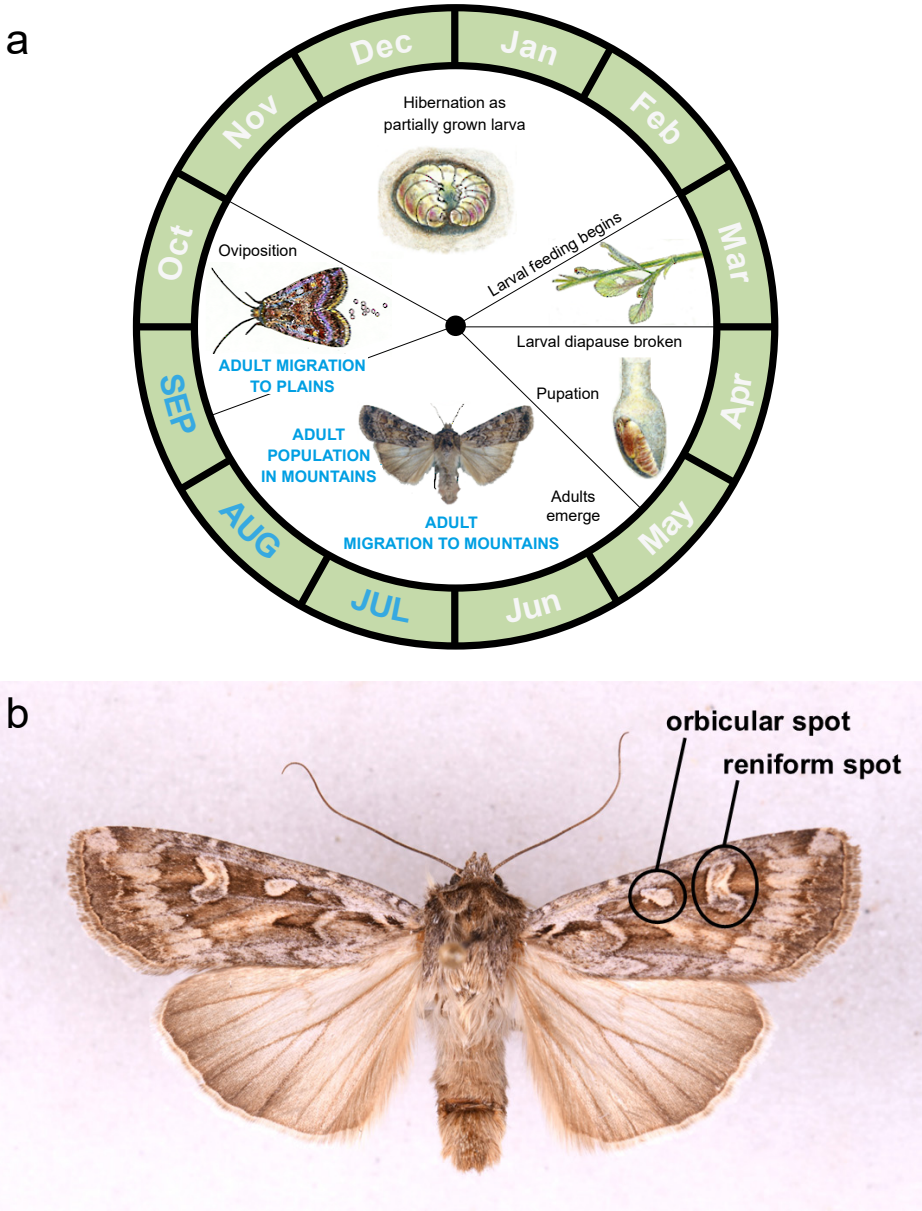
Key words: Army Cutworm Moth; *Euxoa auxiliaris*; lipid; protein; aggregation; talus slope; food resource; Grizzly Bear; *Ursus arctos horribilis*

Army Cutworm Moth (*Euxoa auxiliaris* (Grote, 1873), Lepidoptera: Noctuidae) is known for its aggregating behaviour (Powell and Opler 2009). The moths are migratory, splitting their one-year life cycle (Figure 1a) between lower elevation agriculture-dominated habitats of North America's Great Plains and Intermountain West, where they may be considered a pest (Strickland 1916; Pruess 1967; Hardwick and Lefkovich 1971; Burton *et al.* 1980; Blodgett *et al.* 2010; Floate 2017), and high elevation talus slopes of the Rocky Mountains, often hundreds of kilometres away, where they are potential food for Grizzly Bear (*Ursus arctos horribilis*) in the contiguous United States (Chapman *et al.* 1955; Klaver *et al.* 1986; Mattson *et al.* 1991; French *et al.* 1994; O'Brien and Lindzey 1998; White *et al.* 1998a; Robison 2009; Bjornlie and Haroldson 2021; Peterson 2022a). In their mountain habitat, the moths aggregate by day in prodigious numbers in the subsurface interstitial space (air pockets) of talus matrices and forage at night on

wildflower nectar (French *et al.* 1994; White *et al.* 1998b; Robison 2009; Peterson 2022a). Over summer, the moths increase their mass and change body composition from ~15–20% lipid to ~65–70%, while their protein content remains stable but proportionally declines from ~70% to ~25% of their mass because of the surge in their lipid content (Pruess 1967; Kevan and Kendall 1997; White *et al.* 1998b).

In certain areas of the Rocky Mountains, Grizzly Bears ascend to talus slopes to feed on aggregating Army Cutworm Moths during July–September (White 1998b; Robison 2009; Peterson 2022a). With a gross energy content of nearly 8 kcal/g dry weight in late summer, the moths are one of the richest foods available to mountain-dwelling Grizzly Bears (Pritchard and Robbins 1990; French *et al.* 1994; White *et al.* 1998b; Gunther *et al.* 2014).

Despite their well-documented premigration natal presence on the plains of Alberta (Strickland 1916; Floate 2017), the presence of migratory Army



**FIGURE 1.** a. The Army Cutworm Moth’s (*Euxoa auxiliaris*) one-year life cycle begins and ends in low elevation, agriculture-dominated areas. From July into September the moths are found in distant mountain talus slopes. b. The orbicular and reniform spots are diagnostic markings for identifying Army Cutworm Moth (Powell and Opler 2009). Diagram a: Don White, Jr. Photo b: M.T. James Entomological Collection, Washington State University.

Cutworm Moths in the southern Canadian Rockies of Alberta and British Columbia (BC) was previously undocumented. Oku (1983) proposed that the moths may lose the impetus to migrate north of 50° latitude. However, Dittmore *et al.* (2023) suggested that the moths may originate substantially further north. To

date, Grizzly Bears have not been documented foraging on moths in Canada (Hamer *et al.* 1991; McLellan and Hovey 1995; Munro *et al.* 2006; Nielsen *et al.* 2017).

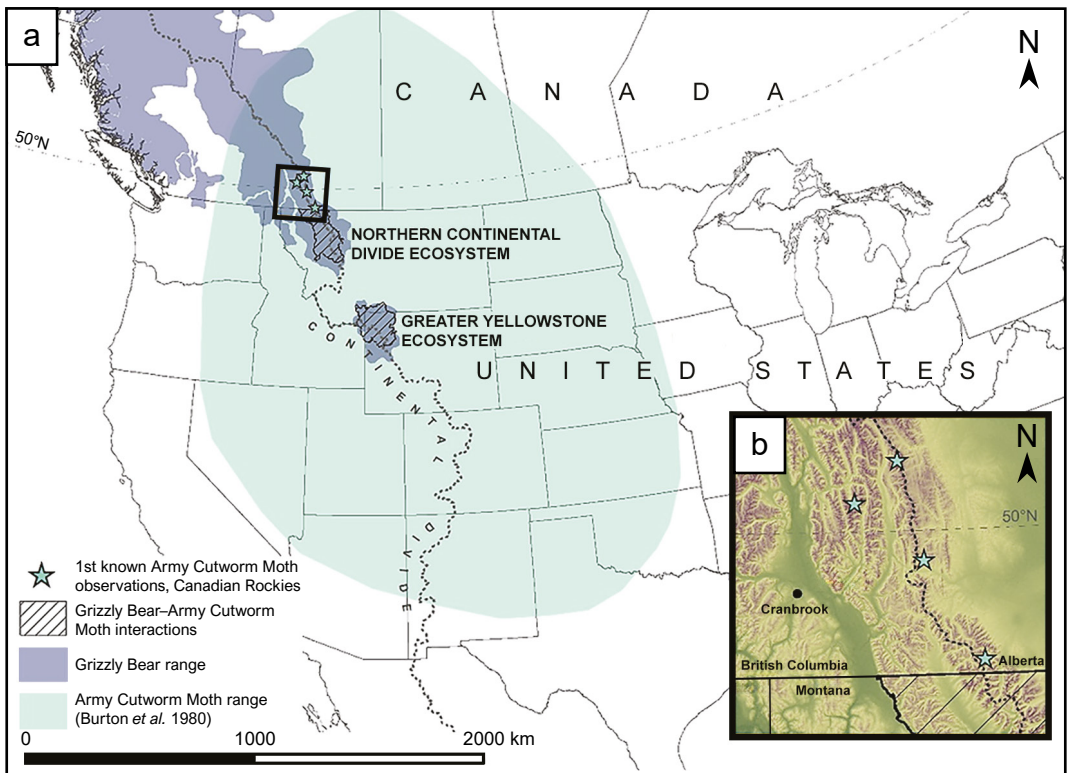
In summer 2022 and 2023, during recreational hikes in the southern Canadian Rockies, we oppor-

tunistically examined probable talus slopes for Army Cutworm Moths. These trips followed an initial modelling exercise of probable Army Cutworm Moth habitat and a cluster analysis of Grizzly Bear telemetry data (Peterson 2022b). We documented Army Cutworm Moths in two ways: by observing moths flying out from talus underfoot in response to our travel across a talus slope and by excavating rocks from talus slopes (Figure S1, Video S1) that possessed characteristics consistent with suitable moth habitat (Peterson 2022a). We identified Army Cutworm Moths at talus slopes by their aggregating nature within talus matrices and their diagnostic forewing reniform and orbicular spots (Figure 1b; Powell and Opler 2009).

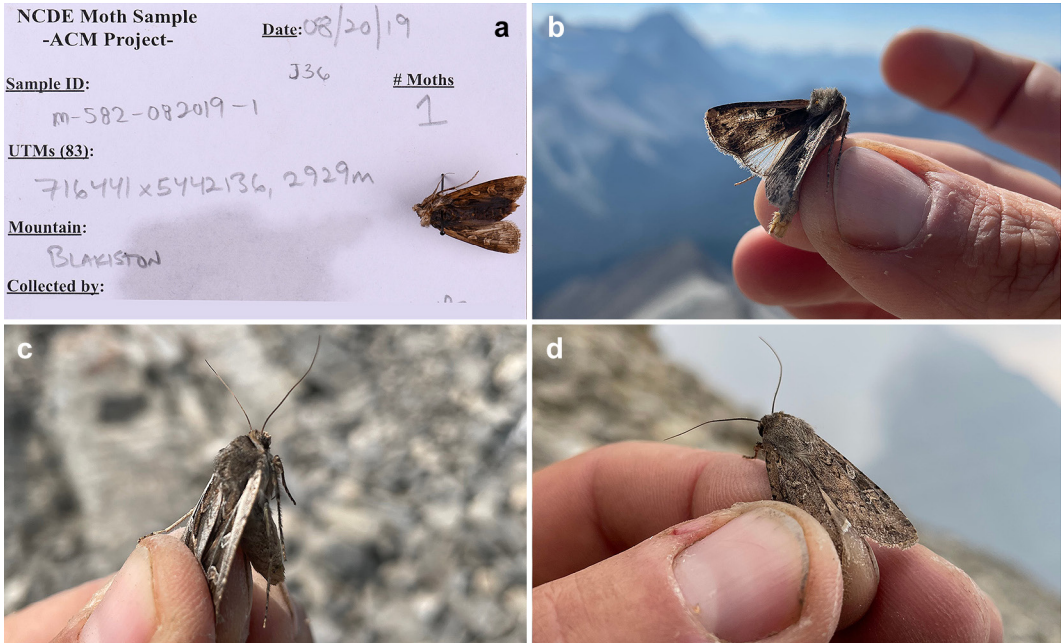
Army Cutworm Moths were initially observed in Canada on 20 August 2019 on a talus slope in Waterton Lakes National Park, Alberta (49.0935°N, 114.0365°W), during transboundary graduate field research (Figure 2; Peterson 2022a). Photographs were taken (Figure 3a) and specimens were collected and provided to Dittmore *et al.* (2023) for analysis.

On 1 September 2022, we observed migratory

Army Cutworm Moths aggregating at three locations between 3000 m and 3300 m elevation on a talus slope near the headwaters of the Bull River (50.0587°N, 115.2145°W), northeast of Cranbrook, BC (Figures 2, 3b, S2a). We searched this site because of its potential for finding the moths. We next observed aggregating moths at two locations between 2600 m and 2785 m elevation on 16 August 2023 on a talus slope near the headwaters of the Crownsnest River (49.7042°N, 114.5736°W), northwest of Coleman, Alberta (Figures 2, 3c, S2b), during recreational travel. Then, on 19 August 2023, we observed aggregating Army Cutworm Moths during travel and excavated numerous locations between 2900 m and 3000 m elevation on a talus slope near the headwaters of the Fording River (50.3153°N, 114.8014°W), northeast of Elkford, BC (Figures 2, 3d, S2c). We investigated this area based on previously identified Grizzly Bear telemetry data clusters that were consistent with moth foraging. We documented all 2022–2023 moth observations with photographs that showed their diagnostic traits but did not collect vouchers.



**FIGURE 2.** a. Approximate annual ranges of Army Cutworm Moth (*Euxoa auxiliaris*) and Grizzly Bear (*Ursus arctos horribilis*; from McLellan *et al.* 2017) showing possible overlap and areas where bears are known to feed on these moths in the contiguous United States. b. Close-up of observed Army Cutworm Moth locations in the southern Canadian Rockies of Alberta and British Columbia.



**FIGURE 3.** Photo evidence of Army Cutworm Moth (*Euxoa auxiliaris*) on talus slopes in: a. Waterton Lakes National Park, Alberta (49.0935°N, 114.0365°W), on 20 August 2019, Washington State University Collection Catalogue #WSUC00018396 (<https://ecdysis.org/collections/individual/index.php?occid=5216140&clid=0>); b. near the headwaters of the Bull River, British Columbia (50.0587°N, 115.2145°W), on 1 September 2022; c. Crowsnest River, Alberta (49.7042°N, 114.5736°W), on 16 August 2023; and d. Fording River, British Columbia (50.3153°N, 114.8014°W), on 19 August 2023. Photos: Erik Peterson.

Our observations indicate Army Cutworm Moths do in fact migrate into the southern Canadian Rockies as far north as 50° and that their aggregations are generally consistent with occupied moth habitats in the Northern Continental Divide (White *et al.* 1998b; Peterson 2022a) and Greater Yellowstone Grizzly Bear Recovery Ecosystems (French *et al.* 1994; Robison 2009) in the contiguous United States. The presence of the moths north of the international border at 49° also suggests they may be a summer food for Grizzly Bears in the southern Canadian Rockies. Other animals observed feeding on aggregations of migratory Army Cutworm Moths include Raven (*Corvus corax*), Clark's Nutcracker (*Nucifraga columbiana*), Gray-crowned Rosy Finch (*Leucosticte tephrocotis*), Black Rosy Finch (*Leucosticte atrata*), Black Swift (*Cypseloides niger*), American Pipit (*Anthus rubescens*), Mountain Bluebird (*Sialia currucoides*), owls (unknown spp.), bats (unknown spp.), Black Bear (*Ursus americanus*), Coyote (*Canis latrans*), mustelids (unknown spp.), and Wolf Spider (Lycosidae; French *et al.* 1994; White 1996; Coop *et al.* 2005; Robison 2009; pers. obs. E.P.). Regardless of whether bears in Canada currently forage for Army Cutworm Moths, the expected northward range shift of mobile species

because of climate change (Parmesan and Yohe 2003) may mean the moths will become increasingly available as a food for Grizzly Bears in Canada.

Given the potential for human disturbance at sites where Grizzly Bears forage for Army Cutworm Moths (White *et al.* 1999), there is value in determining the moth's occurrence in the southern Canadian Rockies. Thus, we suggest a systematic survey for Army Cutworm Moth occurrence across talus slopes in the southern Canadian Rockies to inform managers. Potential moth aggregations with high human use, such as climbing or hiking areas in national and provincial parks, may be highest priority for survey. The research could be guided by recently established methods for assessing moth occurrence (Peterson 2022a) and archived location data from Grizzly Bear radiotelemetry studies in the region (Boulanger and Stenhouse 2014; Lamb *et al.* 2020), which could reveal past moth-feeding sites used by bears.

#### Author Contributions

Writing – Original Draft: E.P.; Writing – Review & Editing: E.P. and G.M.; Conceptualization: E.P.; Investigation: E.P.; Methodology: E.P.; Funding Acquisition: G.M.

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#### SUPPLEMENTARY MATERIAL:

**FIGURE S1.** Screenshot from video of our 1 September 2022 observation of Army Cutworm Moth (*Euxoa auxiliaris*) aggregating in a mountain talus slope near the headwaters of the Bull River, British Columbia (50.0587°N, 115.2145°W).

**FIGURE S2.** Army Cutworm Moth (*Euxoa auxiliaris*) observations from 2022 to 2023 showing their aggregating behaviour near the headwaters of: a. Bull River, British Columbia (50.0587°N, 115.2145°W), on 1 September 2022; b. Crowsnest River, Alberta (49.7042°N, 114.5736°W), on 16 August 2023; and c. Fording River, British Columbia (50.3153°N, 114.8014°W), on 19 August 2023.

**VIDEO S1.** Video from our 1 September 2022 observation of Army Cutworm Moth (*Euxoa auxiliaris*) aggregating in a mountain talus slope near the headwaters of the Bull River, British Columbia (50.0587°N, 115.2145°W), posted at <https://youtu.be/D98pK-QspL0>.

# The Canadian Field-Naturalist

## Book Reviews

**Book Review Editor’s Note:** The Canadian Field-Naturalist is a peer-reviewed scientific journal publishing papers on ecology, behaviour, taxonomy, conservation, and other topics relevant to Canadian natural history. In line with this mandate, we review books with a Canadian connection, including those on any species (native or non-native) that inhabits Canada, as well as books covering topics of global relevance, including climate change, biodiversity, species extinction, habitat loss, evolution, and field research experiences.

**Currency Codes:** CAD Canadian Dollars, USD United States Dollars, EUR Euros, AUD Australian Dollars, GBP British Pounds.

### CONSERVATION AND CLIMATE CHANGE

#### **Ignition: Lighting Fires in a Burning World**

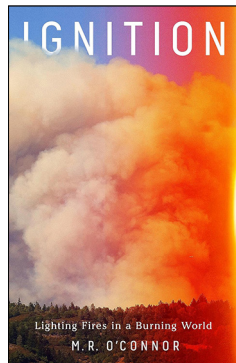
By M.R. O’Connor. 2023. Bold Type Books. 384 pages, 39.00 CAD, Hardcover, 22.99 CAD, E-book.

#### **The Summer Canada Burned: the Wildfire Season that Shocked the World**

By Monica Zurowski and Postmedia. 2023. Greystone Books. 192 pages, 34.95 CAD, Hardcover, 27.99 CAD, E-book.

Wildfires are increasing globally (Koudenoukpo 2023). Reporting on fires, like many ongoing events, is subject to gaps created by news cycles, and it can be difficult for people to obtain an overall view on the extent of wildfire impacts and risks. Two recent books, *Ignition* by M.R. O’Connor and *The Summer Canada Burned* by Monica Zurowski, address these issues from different perspectives, but when read together they provide valuable insights on wildfire causes, costs, and solutions.

Both books begin with succinct descriptions of unprecedented and devastating wildfires. Zurowski, an editor and writer at the *Calgary Herald*, opens *The Summer Canada Burned* with statistics from the 6236 individual fires (18% above the 10-year average) that burned an area of 165 000 km<sup>2</sup> (six times the national average) in Canada



during the summer of 2023 (p. 5). In *Ignition*, science journalist O’Connor begins with a description of Australia’s 2019 to 2020 fires that burned 185 000 km<sup>2</sup>, an area larger than New Brunswick, Prince Edward Island, and Nova Scotia combined (p. 3). From this common beginning the two books diverge in focus. Zurowski concentrates on fire’s impacts on communities and individuals and the resources that were required to fight the 2023 summer fires. O’Connor focusses on wildfire strategies in the United States by obtaining wildfire fighting training. She then joins teams that fight wildfires and also set intentional fires as ecosystem management strategies. Using these experiences, O’Connor explores the paradox between fire as a creative force (directed by humans shaping the environment to promote diverse ecosystems and community well-being) versus the destructive force of increasingly powerful fires. Together these books challenge the reader to examine current wildfire fighting and management practices.

In the early 2000s, scientists began to use the term megafire to describe the “large, complex, and intense fires” that open both books (p. 100 *Ignition*). O’Connor explains that megafires are characterized by aerosols that enter the atmospheric boundary between the troposphere and the stratosphere. This boundary, labelled the tropopause, varies in its distance above the Earth, from 18 km above the equator to six km above the polar regions (SKYbrary 2024).

Michael Fromm, a U.S. Naval Research Laboratory meteorologist and physicist, told O'Connor he refers to clouds generated from these fires as pyrocumulonimbus or pyroCBs. PyroCBs are important because they are the precursors to the fire tornados that make megafires so dangerous. Fromm's team began investigating this phenomenon in 1998 after tracing aerosols observed over Sweden back to a fire in Canada's boreal forest. The first pyroCB in Australia was observed in 2003 and was accompanied by fire tornados with winds over 181 km/h. PyroCBs were subsequently viewed in western Russia in 2010 and South America and Africa in 2018. In *The Summer Canada Burned*, Mohammad Reza Alizadeh, a climate scientist at Massachusetts Institute of Technology and McGill University, explains to author Zurowski that climate change contributes to the common characteristics preceding megafires, including drought, high temperatures, low humidity, and strong winds.

Zurowski points out that the resources needed to fight megafires are unprecedented. For example, as early as 12 May 2023, the extent of the year's fires had already exceeded the ability of Canada's domestic firefighters and military personnel to contain them. Fortunately, Canada was able to call on firefighters from the United States, Spain, Mexico, South Africa, France, Australia, New Zealand, Portugal, Brazil, and South Korea. The costs of fighting these fires included evacuations for more than 120 000 Canadian homes, sheltering sites for evacuees, management of automobile traffic in areas with few exit routes, helicopters for remote community evacuations, and resources to handle the needs of farm animals and pets. Commercial and personal financial losses came from the destruction of businesses and homes, but also from interruptions—often lasting more than a month—in business and personal incomes caused by the evacuations. O'Connor emphasizes that wildfires that become megafires are amorphous and have unpredictable behaviours that differ from structural fires. Therefore, additional training for firefighters is required that focusses on handling situations where fires burn faster than expected, turn back, and restart. Firefighters need to learn how to set backfires and build individual safety zones. Implementing these strategies requires preparation and leaders with scientific knowledge and experience who can interpret and predict changes in weather and how it will affect fire behaviour.

Wildfires, particularly megafires, have not only financial costs, but also physical and mental health impacts. *The Summer Canada Burned* includes the toll that air quality degradation has on health, noting that New York City and Montréal had at various times the worst air quality in the world in 2023 because of

the Canadian fires (pp. 50 and 78). In Ottawa, the fine particulate matter index reached a high of 260 micrograms per cubic metre compared to its average of four to 11 micrograms (p. 68 *The Summer Canada Burned*). *Ignition* delves into the psychology of wildfire fighting, from the highs of beating a fire to the post-traumatic stress disorder (PTSD) that can come from being caught in unpredictable fire events. These events can quickly overtake a firefighter and require sheltering in a personal fireproof tent to wait for rescue. As one firefighter explained, "In the dark, smoky shelter with the heat bearing down, the urge to look outside to see if you should run is almost inexpressible" (p. 124 *Ignition*). Sometimes multiple flame fronts pass before rescue crews arrive. O'Connor explores the symptoms of PTSD resulting from these near-death incidents through interviews with survivors, colleagues, and family members. Both books emphasize that the economic and health consequences of megafires are creating unsustainable pressures on public resources and urge that solutions be explored.

Exploring these solutions in-depth is beyond the stated objective of *The Summer Canada Burned*; they are covered in a cursory manner using quotes from firefighting organizations, politicians, scientists, and the public. *Ignition*, in contrast, has a specific objective to explore how humans have and are using fire as a constructive solution for shaping the environment. Drawing on examples from the Jemez Mountains in northern New Mexico, Hecate Island in British Columbia, and the pine barrens in the eastern United States, O'Connor describes tree-ring fire scarring studies that indicate Indigenous communities across diverse environments altered landscapes for centuries using small and patchy fires. These fires created habitats to support the growth of the specific plants and animals they harvested. Learning from these Indigenous community practices, early settlers often adopted fire as a constructive force. These types of Indigenous practices form the basis for scientific studies conducted today by the Indigenous Ecology Lab at the University of British Columbia (<https://www.indigenousecology.com>).

Stephen J. Pyne, Arizona State University emeritus professor and author of several publications on fire management, explains to O'Connor that viewing fire as a destructive, rather than creative force began with harvesting timber for profit and the displacement of Indigenous communities from traditional lands. Pyne explains that fire suppression regulations, designed to eliminate all fires regardless of origin, intent, or danger, began to be codified in the mid-1800s as the British developed scientific forestry principles to maximize yields for the lumber industry

in the colonial territories of India, Canada, and Australia. Only in Burma, where locals went on strike, was fire suppression officially renounced.

In the United States, two main proponents of fire suppression were the U.S. Forest Service's first head, Gifford Pinchot, and John Muir, a founder of America's conservation movement. Pinchot adopted objectives to maximize high yields and lumber board feet rather than conserve the diverse forests of Western Larch, Giant Sequoia, Pitch Pine, and Lodgepole Pine that were the results of cultural burning. Yosemite National Park, an area where Indigenous communities had used fire to create a diverse ecosystem over centuries, entered a fire suppression regime under Muir's guidance. Pyne explains, "Muir understands fire, but he doesn't see it as necessary or useful, he thought it was something that you could remove from the landscape to make it better" (p. 90 *Ignition*). In the 1940s, the U.S. Forest Service hired psychologist John Shea to investigate the use of fire in the southern United States where cultural controlled burning was legal. He subsequently characterized the belief in controlled burning as the "defensive beliefs of a disadvantaged culture group" (p. 93 *Ignition*). Studies like these coincided with advertising campaigns using Smokey Bear to highlight the importance of fire suppression in reducing wildfires and conserving healthy forests.

O'Connor identifies 1962 as a turning point in the use of fire suppression as the dominant method of controlling fires and managing forests. A sequence of papers, citizen action plans, and reports supporting active fire intervention to restore national park forests to pre-colonial conditions were circulated at scientific and public conferences. As a result, the 1970s became a decade when fire as a constructive force was practiced and researched.

However, during the 1980s fire suppression policies began to dominate again as urban residents near rural areas demanded fire protection, as *Ignition* explains. Two notable prescribed burns that got out of control set back the use of controlled fires for management. A burn in Yellowstone National Park in 1988 and then on Cerro Grande, a mountain in New Mexico, in 2000 led to cuts in fire programs throughout the United States. Nevertheless, isolated cases of controlled fires for ecological management continued in Gila National Forest (southwestern United States), Flint Hills (Kansas), and Yosemite (California). Cur-

rently, fire suppression as a fire management policy is beginning to wane as researchers investigate links between climate change and megafires and the use of fire as a constructive force by Indigenous communities becomes better understood.

The legacy of fire suppression is in the background of *The Summer Canada Burned* but very much in the foreground of *Ignition*. However, each book describes recognition among members of the public, conservation groups, and others that controlled burns have a place in fire management and that the role of intentional burning in controlling megafires will be an ongoing process that will vary among ecosystems. Readers interested in a record of the extent and costs of the 2023 fires in Canada will find *The Summer Canada Burned* an important reference. However, the lack of an index hinders the reader in finding their way back to specific topics of interest. *Ignition*, in contrast, is well indexed with an extensive Bibliography and Notes. It presents an in-depth look at the individual, societal, and ecological relationships that humans have with fire while challenging readers to consider how societal objectives influence the definition, direction, and interpretation of science.

Additional perspectives and work on these issues can be found in:

- An article on the North American tree-ring fire-scar network: [https://www.fs.usda.gov/rm/pubs\\_journals/2022/rmrs\\_2022\\_margolis\\_e001.pdf](https://www.fs.usda.gov/rm/pubs_journals/2022/rmrs_2022_margolis_e001.pdf).
- *CBC Ideas*'s two-part podcast series called "Healing the Land": <https://www.cbc.ca/player/play/audio/1.7126114> (Part 1) and <https://www.cbc.ca/player/play/audio/1.7127150> (Part 2).
- *Hakai Magazine*'s story in May 2024 called "Not Too Wet to Burn": <https://hakaimagazine.com/features/not-too-wet-to-burn/>.

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## ENTOMOLOGY

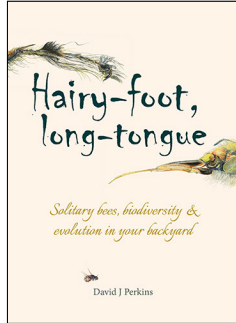
**Hairy-foot, Long-tongue: Solitary Bees, Biodiversity & Evolution in Your Backyard**

By David J. Perkins. 2024. Whittles Publishing. 200 pages, 31.95 CAD, Paper.

The title of this book does nothing to grab the appropriate reader's attention; could it be about ogres in the fantasy genre, or perhaps it alludes to something more in the realm of horror? Thankfully, the subtitle (which is not always included in online search results when it's needed) does clear it up. The title reflects the physical qualities of the central character in this book, *Anthophora plumipes*, or Hairy-footed Flower Bee (HFFB), which has a widespread distribution across Europe. Throughout this book, many other species of solitary bees are mentioned, often in the context of HFFB.

The illustrations in the book include photographs, diagrams, and drawings. Many of these illustrations were done by the author. The photographs are adequate; sometimes they're a bit dark or fuzzy, sometimes they're great. The diagrams are well-drawn, clear, and easy to interpret. However, the drawings are stunning, and they alone make it worth picking up a copy of the book. Considerable time with a microscope must have been invested to translate the colours and impressive detail onto these pages! The illustrations included that are not by the author are credited, often with considerable notation, in 30 pages toward the back of the book.

Page 1 is on the lefthand side. I don't believe I've ever seen that before. There is a publisher's note explaining the anomaly: "This highly illustrated book utilises double paged spreads to present images and



text. To enable the reader to get the most from this style, we have strayed from convention and page 1 appears as the first left-handed page" (p. viii). I have read this over and over and don't get it ... how could the page number (which I rarely look at anyway) alter my appreciation of the images and text?

The bulk of the book comprises short segments (they're not delineated as chapters, *per se*) of discrete topics. As expected, there are sections on anatomy, feeding, nesting, and other classic topics. Because the book's author is a city dweller, there are many references to urban bee diversity and habitats. There are segments with multiple entries but the writing typically returns to the HFFB. Parasitism, kleptoparasitism, and parasitoidism on these bees are fascinating topics that are perhaps too briefly covered.

There are a few errors, unexpected in a book of such otherwise high quality. On the last paragraph of page 87: "Megachilidae is the only other genus of bees ..."; however, Megachilidae is a family of bees. At the top of page 114: "Males hatch from puparia ..."; eggs hatch, adults eclose from puparia. There are some others, but these suffice to illustrate the point.

An eight-page glossary towards the end of the book is thorough and appreciated.

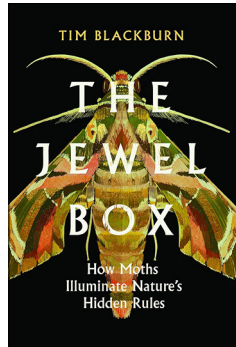
Overall, this is a great book that is sure to inspire readers to be more observant of these lesser-known bees and perhaps entice them to create gardens or build nesting structures for the bees' benefit.

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## The Jewel Box: How Moths Illuminate Nature's Hidden Rules

By Tim Blackburn. 2023. Island Press. 288 pages, 37.95 CAD, Hardcover, 29.99 CAD, E-book.

Tim Blackburn is a professor of invasion biology at University College London and an accomplished ecologist; this book is a clear reflection of that expertise. It is essentially an ecology text with a moth narrative, complete with equations for population size (mainly in Chapter 1). Using the contents of the author's moth trap as the context, the book delves into fundamental tenets of ecology in each chapter. There are a few black and white photos, including one at the start of each chapter. The sections are divided by charming moth symbols, but the book does not contain colour images.



As a note, although the entomological societies of America and Canada adopted the common name Spongy Moth for the species *Lymantria dispar* in March 2022, the author uses the older common name (considered by some to be derogatory, still in use in the United Kingdom [UK]) for the species—this is briefly acknowledged in a footnote.

The Introduction provides an overview of the field of ecology, and topics covered in the book include: population growth models (Chapter 1); interspecific competition (Chapter 2); predation and parasitism (Chapter 3); reproduction and growth strategies (Chapter 4); ecological communities (Chapter 5); migration, metapopulations, and habitat patches (Chapter 6); species richness and diversification (Chapter 7); and species declines and human influences (Chapter 8).

This book will teach readers about moths, and the explanations of ecological concepts are well executed and grounded in moth-y examples. Because the examples are pulled from a moth trap set in the UK, most of the moth-specific focus is on those species, although the links to broader concepts increase the book's relevance beyond the UK.

I would assign this book as an ecology primer to my students, and as moths are a love of mine, indoctrinating students to moth ecology would be an excellent bonus. Depending on your background in academic ecology, this book could be an excellent review, a solid introduction, a bridge to more learning, or a wonderful connection between your current knowledge of insects and ecology, building on both and clarifying concepts with well-grounded examples. If you have not had the opportunity to study ecology or population biology and you've at least a passing interest in insects, this book will teach you the fundamentals better than most expensive textbooks. It is also eminently more fun to read. However, if you mainly seek moth facts and your eyes glaze over at the thought of Lotka and Volterra's predator-prey model, this may not be the book for you. Moth-focussed readers could skim over the ecological theory sections, but the academic and moth content is interwoven. Overall, the author has created a moth-centred ecology text that delivers on its promise of 'illuminating nature's hidden rules'; providing you do not pick it up expecting the glossy colour moth photos of a coffee-table book or the prose and scope of a travelogue, this book may be just what you are looking for.

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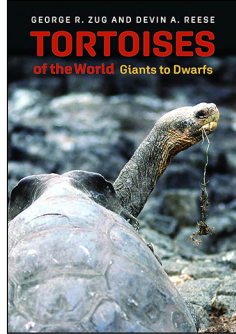
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## HERPETOLOGY

**Tortoises of the World: Giants to Dwarfs**

By George R. Zug and Devin A. Reese. 2024. Johns Hopkins University Press. 256 pages, 25 colour photos, 15 black and white photos, and 51 black and white illustrations, 64.95 CAD, Hardcover, 55.99 CAD, E-book.

I think most people know the children's story of the tortoise and the hare. Zug and Reese use this old, familiar fable as an excellent way to introduce their book on tortoises by illustrating the biological differences between tortoises and hares (mammals). Focussed completely on the chelonian (turtle and tortoise) family Testudinidae (tortoises), this work is intended as a semi-technical overview of the biology and diversity of all tortoise species worldwide. The first chapter sets the stage with brief summaries of all subsequent chapters. Topics covered include tortoise anatomy, physiology and behaviour, mating and reproduction, life cycles, ecology, global diversity, evolutionary history, human exploitation, and conservation. The book highlights the range of diversity in tortoises, from the smallest species you can hold in the palm of your hand to the giants occurring on islands such as the Galápagos.



Each chapter of the book has excellent illustrations and black and white photographs depicting tortoise anatomy, behaviour, and general geographic distribution, as well as figures and tables presenting summary data on various aspects of their biology. There is also a series of 25 excellent colour plates consisting of photographs of various species of tortoises doing all the activities described in the book, such as foraging on vegetation, mating, laying eggs in excavated nests, burrowing, seeking shelter as a 'herd' under limited shade, and encountering predators. Particularly, I enjoyed the colour plate of female Aldabra Giant Tortoise coming onshore in Tanzania covered in barnacles after surviving a six-week accidental floating journey at sea (and apparently not much the worse for wear!).

I personally enjoyed reading this book very much, and it reminded me of C. Kenneth Dodd's similar semi-technical work on the genus *Terrapene*, *North American Box Turtles: a Natural History* (University of Oklahoma Press, 2001). There is something in *Tortoises of the World* for both the focussed academic researcher and the more casual reader. In order to make this book approachable to a broader audience, the authors did not include in-text citations or a comprehensive bibliography (however, the latter is available

in an online source document for interested parties; <https://repository.si.edu/handle/10088/117719>). The authors use plain language throughout the book, with more technical terms in parentheses, to make the text digestible for the non-technical reader. I think the authors did a great job in formatting the book to accommodate both audiences.

Even as someone with a professional background in herpetology and turtles (although not tortoises, specifically), I learned quite a lot from this book. My favourite chapters were the last two regarding tortoise exploitation by humans and tortoise conservation, respectively. However, my engagement in these final chapters was greatly enhanced by reading all the content on tortoise biology and diversity in the preceding chapters of the book. Gaining a better appreciation for all the fascinating things tortoises do (and how they evolved and survived over millions of years) made me all the more upset upon learning about their mistreatment by humans through overharvesting (historically and in the present), as well as the spread of disease among tortoises facilitated by humans, and the habitat loss due to human encroachment and climate change. The book culminates in what is (in my opinion) the most important chapter focussing on the success stories, challenges, and complexities of tortoise conservation. Reading this book not only increases one's understanding of tortoise biology but also serves to bolster an understanding of the need to protect tortoises from extinction, especially given that they are one of the most imperilled groups of vertebrates globally.

One important note about this book is that it's intended to be a semi-technical and more general text about tortoise biology. While skimming through the book prior to my cover to cover read for this review, I was initially (mildly) disappointed that the section on tortoise species diversity (Chapter 7) was limited to only a paragraph for each of the world's extant (and recently extinct) species. However, the book highlights many examples of the biology of many individual tortoise species throughout its other chapters. So, in reading the book fully I don't see this as a major limitation. Additionally, this book serves as a great introduction to the species group as a whole, and one could consult other texts for a deeper dive into any focal tortoise species of interest. For example, Carl H. Ernst and Jeffrey E. Lovich's *Turtles of the United States and Canada, Second Edition* (Johns Hopkins University Press, 2009), which is included as

a suggestion at the end of the book for further reading, contains in-depth technical accounts and exhaustive literature reviews on North American tortoise species.

Overall, I greatly enjoyed this book and would highly recommend it for the reading list of anyone

interested in natural history—from the professional herpetologist to the casual naturalist.

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## ORNITHOLOGY

**Birds of the Mesozoic: an Illustrated Field Guide**

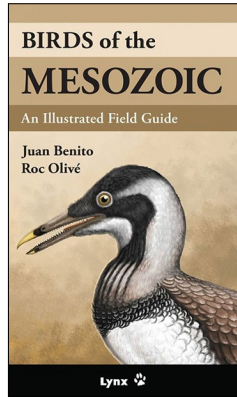
By Juan Benito. Illustrations by Roc Olivé. 2022. Lynx Edicions. 272 pages, 250 colour illustrations, 6 photos, and 16 figures, 35.00 CAD, Paper.

Exactly as the title suggests, this book is structured like a field guide, with species accounts facing plates of reconstructed birds in stereotypical poses. A 48-page Introduction deals with Phylogeny, Taxonomy, Osteology, Plumage, Biology, and the avian Fossil Record. It is followed by 189 pages of species descriptions, providing, in addition to the colour plates, details on morphology, plumage, biology (where available), and notes on the specimens, their measurements, and the locations of fossil sites. The authors include 208 fossil species, all but three coming from Mesozoic sediments.

Before I elaborate on this bare-bones description, a little digression: when I first saw the subtitle on Benito and Olivé's book, I thought it was a joke. Surely, we did not have enough material to reconstruct the appearance of Mesozoic birds or, if we did, it could only be a handful. But I had forgotten *Archaeopteryx*. This remarkable Jurassic fossil—found in Solnhofen, Bavaria, in 1861—was discovered two years after the publication of Charles Darwin's *On the Origin of Species* (John Murray, First Edition 1859). Darwin, when he became aware of it, derived considerable satisfaction at the discovery of this 'missing link'. It was in a perfect state of preservation.

Although several more specimens of *Archaeopteryx* were obtained in the 19th century, the trail of Mesozoic birds mostly went cold until the 1980s when researchers began discovering well-preserved Mesozoic bird fossils in South America and eastern Asia. Since then, the initial trickle of new fossils has become a torrent, with hundreds of new species, mostly from China, being named in the 21st century. Not only has the diversity of material been remarkable, but the preservation of many of the specimens in soft, fine-grained mudstones is outstanding, allowing not only complete bones, positioned as in life, but also feathers to be preserved with minute detail. Even feather colour can sometimes be determined. Consequently, the field guide plates are far less fanciful than I had anticipated at the outset.

The Introduction provides a brilliant summary of avian evolution. An explanation of the classification



of Mesozoic birds is very necessary because only four of the species described here belong to Neornithes, the clade that includes all modern birds. The boundary between dinosaurs and birds is not much dealt with here. Rather, the book provides a diagram of the branching clades from theropod dinosaurs to the basal bird (or bird-like) clade—here termed Avialae—through Pygostylia to Ornithothoraces. The latter divides into Enantiornithes (100 species figured) and Euornithes (36 species), giving rise, via Ornithurae, to Neornithes. Representatives of both major modern clades, Palaeognathae (ostriches, etc.) and Neognathae (the rest), were present in the Late Cretaceous period and hence survived the asteroid strike that probably finished the dinosaurs. All other clades vanished in that cataclysm, if not earlier. To my eye, it is only with Pygostylia (Early Cretaceous) that we have something unequivocally a bird, having a beak without teeth and a fused pygostyle for the tail. The earlier groups look like nothing we can currently relate to—call them dino-birds, perhaps?

Personally, I found the diversity of Mesozoic birds extraordinarily impressive. Suitable bird-preserving sediments have been found from only a short period during the Middle Jurassic. Otherwise, sediments have been discovered from a period of a few million years in the Late Jurassic, 10 million years in the Early Cretaceous, and another 10 million years in the Late Cretaceous. Given that every shape and size of reptile, including many flighted ones, provided competition during those periods and that only small areas of the world have yielded fossils, the discovery of 200+ species of birds seems to indicate a very diverse avifauna during the Mesozoic.

Only 16 of the species figured come from Jurassic sediments, and all but one of those are thought to have been pigeon-sized or larger. The remainder come from the Cretaceous and include many species sparrow-sized or smaller, of which Enantiornithes were the most diverse. This group comprised many species that were either tail-less or had very short tails. Some species had very long tails comprising two or four feathers, all of which consisted of a long vane-less rachis tipped by a short vaned section, making them look like canoe paddles. The latter design includes *Confuciusornis sanctus*, of which thousands of fossils have been found in Liaoning, China, many beautifully preserved.

For those who, like me, were largely ignorant of Mesozoic birds, this is a very thought-provoking

book. It is well written and beautifully illustrated. I enjoyed it immensely. Overall, the message of avian Mesozoic fossils is that, long before the demise of their close relatives, the great dinosaurs, birds had become common and diverse, occupying a wide range of habitats and exhibiting a great diversity of

behaviours. A modern birder, transported back to the Cretaceous, could expect to develop a respectable life list (while keeping a sharp eye out for *Velociraptor*, of course).

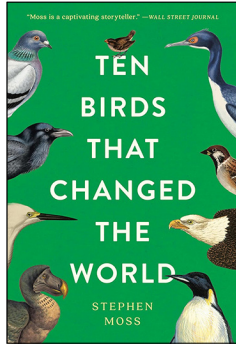
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## Ten Birds that Changed the World

By Stephen Moss. 2023. Basic Books. 416 pages and 10 black and white illustrations, 38.00 CAD, Hardcover, 29.99 CAD, Paper, 22.99 CAD, E-book.

How does one determine which 10 birds changed the world out of around 11 000 known species (IOC 2024)? In the Introduction, Moss states that each species he chose relates to “a fundamental aspect of our humanity” that changed the course of human history (p. 4). In the order that the species appear in the book, these themes are: mythology, communication, food and family, extinction, evolution, agriculture, conservation, politics, hubris, and the climate emergency.



Common Raven (*Corvus corax*; Chapter 1) is prominent in the mythologies of many cultures around the world because of its intelligence, behaviour, and ability to adapt to a wide range of climatic conditions, habitats, and elevations. This species is so adaptable that the concept of it having native habitat hardly applies. Raven is ambivalent in many myths, playing both benevolent and malevolent roles, signifying vital connections between birds, people, and history.

The domestication of wild doves for food and feathers occurred between 5000 and 10 000 years before present (YBP) in the area of present-day Iraq. While there are more than 300 species in the family Columbidae, it is the ubiquitous Rock Pigeon (*Columba livia*; Chapter 2) that rose to importance because of its homing instinct. Tens of thousands of pigeons were used to send life-or-death messages during the two world wars of the 20th century, often trumping other methods of communication. Their advantages are many during wartime: they fly rapidly and so are difficult to shoot down; they return quickly; they have no radio signal to intercept; they cannot be interrogated by the enemy, nor betray their government by acting as double agents.

Wild Turkey (*Meleagris gallopavo*; Chapter 3) is the largest game bird in the world and was an early and welcome source of food for Indigenous peoples and settlers. It has become part of the founding myth of the United States and Thanksgiving celebrations. It is the only significant avian species to be domesticated in the Americas, which occurred between 2000 and 2300 YBP.

Moss says that Dodo (*Raphus cucullatus*; Chapter 4) “has become the definitive emblem of extinction” (p. 113). The first written description of the bird

was in 1598 of a specimen from Mauritius—and by 1662 the species was extinct. It wasn’t predation by humans that did Dodo in, but predators introduced by humans, which ate eggs and chicks from their ground nests. Moss laments that we know less about the biology of Dodo than we do of famous dinosaurs.

Moss’s icon for evolution is not a single species, but the group known as Darwin’s Finches (subfamily Geospizinae; Chapter 5) found in the Galápagos Islands of Ecuador. The ancestral species was likely blown over from the mainland two to three million years ago and then evolved into 17 species (depending on the taxonomic authority) through adaptive radiation. The size and shape of their beaks reflects differences in food and feeding methods. While these finches did not actually inspire Charles Darwin’s theories of natural selection, they are still one of the best demonstrations of those developed by his successors, such as David Lack, who is considered by some to be “the father of evolutionary biology” (p. 153).

The Pacific coast of South America—hot and dry with virtually no rainfall—has a rich marine environment because the Humboldt Current produces constant upwelling of cold water, which creates ideal conditions for fish. The fish, in turn, attract many seabirds, such as Guanay Cormorant (*Leucocarbo bougainvillii*; Chapter 6). Over centuries the birds’ droppings, known as guano, formed a thick crust (up to 50 m deep) on their nesting islands. It was harvested and sold for fertilizer—from 1840 to 1879 some 12.7 million tonnes of guano were shipped from Peru to Europe and North America. This gruelling work was done by tens of thousands of indentured Chinese labourers in “a tale of greed and profit, horror and hardship, vast riches and almost unimaginable suffering” (p. 181). In the first 15 years of the industry, labourer mortality was 35 to 40%! Cormorant populations plummeted by 90% from the long-term damage to breeding habitats, daily disturbance by labourers, and the taking of birds and eggs to eat by the starving men. Guano is still harvested in some areas, although it has mostly been replaced by synthetic products.

Starting in the late 1700s, it became very fashionable for high-society women in Europe to wear bird feathers in their hats. This led to a very profitable plume, or millinery, trade, which was also very cruel and destructive—by the mid-1880s as many as five million waterbirds, including Snowy Egret (*Egretta thula*; Chapter 7), were being killed annually for their skins and breeding feathers. But it was also women in the United Kingdom who began lobbying to stop

this practice, culminating in the formation of the Society for the Protection of Birds (SPB, later becoming the Royal SPB) in 1891. In North America a similar effort led to the formation of the Massachusetts Audubon Society in 1896. While women were vilified for wearing the hats, it was a long time before anger was turned on the men doing the killing and profiting. It wasn't until significant laws such as the *Lacey Act*, the *Weeks-McLean Act*, and the *Migratory Bird Treaty Act* were passed that the trade began to decline.

While Bald Eagle (*Haliaeetus leucocephalus*; Chapter 8) is commonly used in iconography, marketing, and politics, and is the national bird of more countries and nation states than any other species, it was never officially adopted as the national bird of the USA (it is on both the Great Seal of the United States and the Seal of the President, though). The eagle is a symbol of strength, longevity, and freedom, but has also been used to justify power and authority from the Roman Empire to Nazi Germany.

Destructive authority was behind the slaughter of hundreds of millions (perhaps one billion) Eurasian Tree Sparrow (*Passer montanus*; Chapter 9) in 1958 after Mao Zedong, former chairman of the People's Republic of China, declared them pests in the name of preventing famine. Unsurprisingly, the following summer the rice harvest was a disaster as millions of insects, now not being eaten by sparrows, stripped the crops bare. While this was not the sole cause of the crop failure, the Great Sparrow Campaign showed "the danger of a society losing touch

with fundamental ecological truths" (p. 291). Many other bird species also died during this campaign.

In the final chapter Moss uses Emperor Penguin (*Aptenodytes forsteri*) as "the poster bird of the impending catastrophe" of climate change (p. 300). Warming oceans are causing their food resources to decline or move farther away, and warming air temperatures are reducing the amount and extent of sea ice, impacting breeding colonies when the ice breaks up earlier and drowning chicks.

Moss does discuss many other species throughout the book, and readers can find more information in numerous footnotes and 58 pages of chapter notes. The 20-page index is thorough, including illustrations and footnotes. The leading page of each chapter includes a beautiful pen-and-ink illustration by Nicole Heidaripour of the relevant species. My one quibble is with the publisher, who bulked up the paper and used increased leading (the space between adjacent lines of text, in this case 27 lines per page rather than a more normal 37), which makes the book thicker than it needs to be and thus costs more than it needs to.

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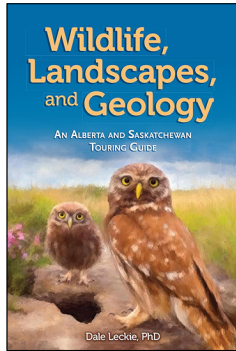
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## OTHER

**Wildlife, Landscapes, and Geology: an Alberta and Saskatchewan Touring Guide**

By Dale Leckie. 2024. Broken Poplars Publishing. 216 pages, 29.95 CAD, Paper.

This book is a lovely field guide for travellers interested in the wildlife of southern and central Alberta and Saskatchewan. The book explores the landscapes and underlying geology of the region through the lens of nearly 30 species, some common and iconic, and others rare and obscure. The introduction describes the ecozones of the region and provides maps to five suggested driving routes. Following this there are sections devoted to mountains, post-glacial landscapes, grasslands, and river valleys; within each section several species are profiled. The book is filled with beautiful photography and stunning artwork. The author has partnered with two accomplished artists, Dean Francis and Sergio Gaytán, to accompany each species description with artwork highlighting either that species or an aspect of that species' landscape.



The author, Dale Leckie, is a geologist with extensive knowledge of the geology of western Canada. He has previously published two popular field guides to the geology of Alberta and the Rocky Mountain parks. In this book he expands on these themes by linking each species to their physical habitat. For each species described, the author includes aspects of ecology, the landscapes inhabited, and specific sites where the species can be viewed. Central to each of these descriptions is the geological 'why'—the features of the landscape that drive each species' presence at a particular place and time of year.

The unique focus on geology is the chief value of

this book. I'm familiar with many of the species and places highlighted but found myself eagerly turning the pages to learn more. On the practical side, there are many valuable tips for those planning a road trip. These include suggestions on accessible places to visit, the best times of year to look for a particular species, and how to search for the species when on-site. The suggestions on how to spot some of the more cryptic and obscure species, such as Mountain Plover and Greater Short-horned Lizard, are particularly valuable.

While I enjoyed the book and highly recommend it, there are some flaws. Some are minor, such as poor page layouts that leave large blank areas or figures with incomplete legends or missing data sources. For me the largest negative was that, while the conservation status of each species is mentioned, the reasons underlying that conservation status are not discussed. This is a missed opportunity to highlight conservation challenges. More importantly, in a book facilitating the viewing of rare and threatened species, it is important to highlight that for some of these species human activity is a significant threat. Any time we encourage people to seek out potentially vulnerable species, it is critical that we educate readers on how to avoid unintentional harm. A few lines outlining the threats and suggestions on sensitive observation would have been welcome.

Overall, this is an excellent book that I would highly recommend to any naturalist interested in the fauna and landscapes of southern and central Alberta and Saskatchewan.

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## ZOOLOGY

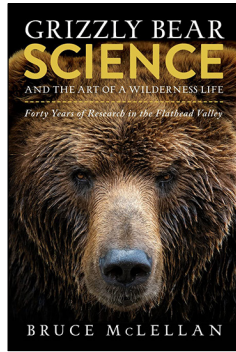
**Grizzly Bear Science and the Art of a Wilderness Life: Forty Years of Research in the Flathead Valley**

By Bruce McLellan. 2023. Rocky Mountain Books (RMB). 336 pages and 16 colour plates, 32.00 CAD, Paper, 15.99 CAD, E-book.

This book is a fascinating account of Grizzly Bears (*Ursus arctos horribilis*) that inhabit the Flathead region of southern British Columbia, just north of the Montana state line. The author describes his research in-depth, combining fascinating anecdotes with important science in an easy-to-read tome. The book is over 300 pages long, but I found it a relatively quick read. I greatly enjoyed the personal narratives of McLellan's field experiences intertwined with his stories of raising two children with his wife Celine without many modern amenities, like running water. The couple lived in a small, remote cabin next to the Flathead River and endured floods that washed away some of their camp and forest fires that burned areas around them. Their children grew up immersed in nature and both ultimately obtained graduate degrees related to bear ecology.

McLellan writes with authority and a deep knowledge of his study subjects. Readers get close to many of the bears that he captures in foot snares to radio-collar. He then tracks them in the spring when they wake from hibernation to feed on animal carcasses that died during the winter, as well as greens (i.e., grasses, clovers, horsetails, Cow Parsnip) and roots (i.e., sweet vetch roots, Glacier Lily bulbs; pp. 63–68). McLellan follows his study subjects in the summer as they seek huckleberry patches at higher elevations that have been impacted by wildfires—the fires help facilitate growth of the berries. This high-energy fruit allows the bruins to pack on fat to make it through winter hibernation (pp. 70–74).

This book is the author's life work on bears. He even reminisces on the first grizzly he saw in 1958 when he was four years old in Banff National Park (p. xii). Childhood sightings aside, the book really begins in 1978 when he captures Rushes (pp. 5–6, 12), a big male bruin and the first of 170 collared grizzlies (and over 200 captured bears) in his 42 years of research (pp. xiii, 22). That first male, estimated to be 291 kg, is difficult to sedate—the bear charges the author, although his movement is limited by the length of the chain attached to the snare. Once successfully radio-collared, Rushes and the other study subjects are an



important portal into a new world of understanding about bears. Radiotelemetry provides a revolutionary amount of data for McLellan to analyse (pp. 9, 11, 57).

One thing that is very apparent throughout this book is the individual nature of bears. The author names and follows them for years, sometimes even for the duration of their lives. His team focusses on monitoring females over males, because males have huge home ranges, are more difficult to follow, and don't tell as much about the population ecology of bears as do females (pp. 136, 186). Plus, keeping a collar on males is difficult because they have huge necks, often over 76 cm in diameter, which is on par with the size of their heads (p. 136). In his targetting of female bears, we learn about Blanche, Melissa, Elspeth, Aggie, Jennie, and Maggie, among other individual bears living in the Flathead Valley (e.g., pp. 285–286, and throughout the book). Those radio-collared bears teach McLellan about Grizzly Bear ecology in his study area. For example, we learn that both sexes are not territorial like most carnivores (p. 138), and that females do not disperse over long distances, which slows the range expansion of this species (pp. 143–144). Incredibly, he follows two females for >27 years and another one for 32 years (pp. 22, 142).

Using up-close observations, the author describes how females are mostly vegan, while males eat more meat—it makes up 38% of their diets (p. 61). When huckleberries are ripe in the late summer, bears eat 26 to 36 kg of them each day (pp. 82–83). Female grizzlies can go from an average of 97 kg before berry season to 129 kg afterward. Males go from 161 kg to 192 kg during that same timeframe (p. 82). Bears are active for 15 hours a day when feeding on fruit (p. 106). This gorging is important as they need enough fat to make it through hibernation, which is an amazing adaptation given that bears are the only large mammals that hibernate (p. 86). McLellan has also studied American Black Bears (*Ursus americanus*) in the Flathead Valley and has observed some of those bruins doubling their weight while eating blackberries over a roughly three-week period; one was so fat it looked like a “bloated tick” (p. 81)!

Bears roam tremendous distances, especially males (p. 137), and this inevitably leads them into conflicts with humans. McLellan, a hunter of ungulates (i.e., deer, Elk), finds it difficult to stay objective after Rushes, that first bear he captured, is shot and

killed from a roadway (pp. 21–22). Over time, he captures hundreds of grizzlies and never has to shoot one out of fear for his safety (pp. 180, 202), yet he documents many bears shot near roads, even yearlings (pp. 184–186). This angers him as it isn't ethical hunting and is often done illegally, serving no purpose. He eventually deduces that roads equal dead bears (p. 191), so by protecting relatively pristine areas bears—especially females—can survive longer, even though they don't necessarily need wilderness areas to survive. Most bears (82%) in his study are killed by people (p. 189), and there is a high rate of unreported kills (p. 190).

The book is easy to understand, even when the author presents more technical information, such as graphs of his findings (e.g., pp. 80, 84, 109, 113, 117, 263–264). However, I liked his stories the most as they provide snapshots of a bear biologist in action and what it's like to study these magnificent animals. There are times when he gets within one metre of a young grizzly (p. 113) and three metres of a large male (p. 120); wild grizzlies in wild places make him feel so “amazingly alive” (p. 120). His most memorable encounter is when a Golden Eagle lands on a ridgeline one metre from him as he watches Grizzly Bears foraging below (p. 195). The two sit side by side for a few seconds before the bird flies off. I found it interesting that he most values that sighting, given that he has been within literal ‘spitting distance’ of all the large animals in the Flathead Valley, including within five metres of a wild wolf (p. 193).

I enjoyed the description of McLellan darting a big male grizzly and the adventure that he has after that, which involves him following and finally finding the

bear in a forest not knowing if he is sedated (pp. 233–239). Once the bear is discovered asleep, the author then has to hold the large bruin's head out of a frigid stream so the bear won't drown. There is another riveting story of a darted female that gets within three metres of him, and he debates whether he will have to shoot her if she attacks (pp. 280–282). I wondered why all team members aren't required to carry bear spray in situations like that. That would seem to be an obvious solution to avoid a potentially lethal encounter.

I really enjoyed *Grizzly Bear Science and the Art of a Wilderness Life*. McLellan writes with perspective and candour. He summarizes much of the major findings from his study, including the bears' vital need for high-energy foods like berries (which is the best predictor of grizzly densities in his study area), and the importance of coexistence to protect bears—especially females—because most bears die from human causes, even in populations not hunted by people (pp. 222, 254, 257). I appreciated the author's positivity at the end of the book when he states that he is amazed (and never thought it would be possible) that there would now be 1000 grizzlies in northern Montana and >700 in the Yellowstone area. Both populations are also spreading to the Great Plains (p. 268). At the end of the book, he notes how lucky he is to have spent a life studying grizzlies (p. 275). He also states that it is easy to coexist with bears with a little bit of money and much human effort and caring (p. 276).

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EDITOR'S COMMENT: Also see this Note in the same *Canadian Field-Naturalist* issue about Army Cutworm Moths being potential food for Grizzly Bears. That study was done in an area of southeastern British Columbia (BC) that includes the Flathead River Valley; it's the non-mountainous finger extending into BC from the United States just west of the Alberta–BC border on Figure 2b.

Peterson, E., and G. Mowat. 2024. First known observations of migratory Army Cutworm Moth (*Euxoa auxiliaris*) in the southern Canadian Rocky Mountains. *Canadian Field-Naturalist* 138(2): 175–180. <https://doi.org/10.22621/cfn.v138i2.3141>

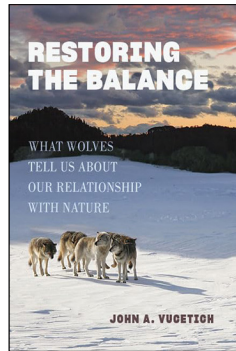
## Restoring the Balance: What Wolves Tell Us about Our Relationship with Nature

By John A. Vucetich. 2024. Johns Hopkins University Press. 416 pages, 38.95 CAD, Paper. Also available as an E-book. Hardcover edition published in 2021.

*Restoring the Balance* is a detailed account of the wolves (*Canis lupus*) of Isle Royale National Park in Michigan. The author states early on that this is not a wolf book because of its “prominence of introspection” (p. xvii). Nor is it a science book because there is too much triumph and heartbreak. And neither is it a philosophical tome. Yet all three facets weave throughout this book, making it unique and incredibly comprehensive. Due to this interesting combination of disciplines, it was an exhausting, slow read for me. There are over 400 pages of text (including 25 pages of Notes and 17 pages of References) and, because of the relatively small font, many words per page. In addition, I had to look up quite a few words to see what they meant (e.g., Coda, the title of the last chapter in the book), which slowed my pace. Altogether, it took me nearly two months to read it from cover to cover, while I was engaged with other professional and personal duties during that timeframe. I, by far, enjoyed the field aspects the most and breezed through those sections where wolves and Moose are the focus (i.e., most of Chapters 6 and 7). It was most interesting reading the descriptions of the wolves as they travelled through their territories and encountered their main prey, Moose, as well as rival wolves. Conversely, when introspection and philosophy appeared, my reading pace slowed considerably, as I tried to deeply understand what the author was discussing, such as in Chapter 4, Balance of Nature, and regarding island biogeography (pp. 261–268). Studying the mathematical formulas and graphs that the author presents was more like reading a college textbook than a wolf book, but that is part of the charm and breadth that Vucetich covers in this volume, making the book a unique contribution to the study of wolves.

Readers who enjoy books about nature, wolves, carnivores, wildlife, and national parks—especially remote wilderness ones like Isle Royale—will appreciate this book. Vucetich writes with authority and perspective that is unparalleled in the 60+ years that research on wolves and Moose has taken place on Isle Royale.

Wolves colonized Isle Royale via an ice bridge from the mainland between 1948 and 1949 (pp.



67–68). Research on wolves on the island began in 1958 (p. 69). The first three years of work found a stable population of 20 wolves and 600 Moose (pp. 88, 90), leading to the belief that the population was balanced, a.k.a. Vucetich’s reference to the “balance of nature”, whereby animal populations are stable and don’t fluctuate much. Over time, researchers found that the population fluctuated greatly, peaking at 50 wolves in 1980 (pp. 146–147). Yet after widespread starvation from lack of Moose, the population dropped to just 14 wolves two years later in 1982 (p. 149). Vucetich writes extensively about the balance of nature and the problematic simplicity of making that claim without researchers conducting long-term research on a given ecosystem.

Research on the island has found anything but a balance over the years. For instance, during the 1990s there were low wolf numbers and a large Moose population, and the wolves acted more like scavengers than predators (p. 160). Following an eruption in the Moose population and then a severe winter, more than 1500 of the large herbivores died in the first five months of 1996, an event which was thought to be the highest all-time density of Moose carcasses found anywhere (pp. 161–162). Wolves, as well as foxes, ravens, and eagles, couldn’t take full advantage of the offering due to the huge surplus. Therefore, maggots and carrion beetle populations erupted (p. 162).

I enjoyed the stories of individual wolves and packs the most. There is the amazing story of survival about two different females attacked by packs; both wolves escaped by entering frigid Lake Superior (pp. 166–167, 224–226). It was fascinating reading about the wolf Old Gray Guy and how he led the Middle Pack for six years, eventually taking over the entire island (starting at p. 168). Vucetich gives intricate details of how Old Gray Guy’s family patrolled their territory and killed Moose and other wolves (Chapters 6 and 7). Old Gray Guy (radio-collared and given the scientific number M93) was an immigrant, arriving via ice bridge sometime in 1997 or 1998. He was so successful that he fathered 34 offspring, yet this caused the population to become inbred because all the wolves on the island eventually shared his genes (pp. 187–189). So, while this “cryptic immigration” (i.e., the researchers didn’t know that an immigrant wolf had reached Isle Royale until performing genetic analysis) infused new genes into the population, long-term studies showed that within a decade Old Gray Guy’s DNA was so dominant on the island that the

population became too related and faltered (pp. 191–193).

My favourite chapter (Chapter 7, *The Unraveling*) provides awesome details from Vucetich's field notes on individual wolves and how the population crashed. He starts by mentioning that all individual animals have a story to tell, just like people do (p. 211). That quote sets up the rest of the chapter very well. In it, he discusses the alpha female of the Middle Pack, which lived to be 12 years old and was one of the oldest wolves to have ever lived on Isle Royale (pp. 205, 215). There are fascinating accounts of how the researchers followed her pack for two weeks without the pack making a kill or eating; the wolves encountered Moose but couldn't successfully kill one, despite great efforts to do so (pp. 203–206). However, the old female was resilient and had 27 to 28 offspring in her lifetime. Interestingly, she had two different mates during that time, her son and her father, Old Gray Guy, which reveals just how inbred the population was (p. 219). Chapter 7 also includes the riveting trials and tribulations of Romeo of the Chippewa Harbor Pack (p. 218). He killed the alpha male of the Middle Pack, and then later drowned in a copper-mining well along with two other siblings (pp. 221, 223). These deaths caused the population to decline to just nine wolves across the entire island in 2012 (p. 224). By March 2011, the wolves were already functionally extinct. The Moose population doubled without effective predation, growing at a rate of 22% per year (p. 233). With the declining frequency of ice bridges each season, there was little hope that an immigrant wolf would arrive from the mainland (p. 192).

Toward the end of the book, Vucetich discusses the politics of the National Park Service (NPS) and their resentment of him (p. 234). He advocated for genetic rescue of the wolf population beginning in 2009 when he predicted (accurately) that the population would crash without new genetic infusion (pp. 236–237). He describes the history of national parks as places of overabundant herbivores due to lack of predators, which were killed from many areas before they became protective places (p. 296). To prevent that from happening on Isle Royale, Vucetich recommended bringing one or two new wolves to the island and documenting their reproduction to ensure that their genes were represented in the population (p. 324). But, despite his decades of research on Isle

Royale, Vucetich was excluded from the population restoration process when ultimately 20 wolves were released on the island in 2018 and 2019 (p. 325). He found out about the releases and obtained most of his information from the NPS's press releases and media accounts of the reintroduction (p. 325). Despite the successful establishment of the new population, there was a high level of inbreeding that occurred just a few years into the program because a related family had done most of the breeding in the nascent years of the restoration process (pp. 328–329). Thus, genetic rescue (by translocating a single individual who successfully reproduces) might still be needed in the near future as a proactive approach to maintaining genetic diversity within the population (p. 332).

Toward the end of the book, Vucetich does an admirable job of advocating for wolves and stressing our obligation to right past wrongs and support recovery programs where feasible (pp. 313–314). He discusses the Golden Rule of fair treatment to all beings—which includes predators like wolves (p. 306)—and goes into the philosophy behind this. It is a dense read, but it is important as he lays the foundation for why predators like wolves should be recovered. He also points out that there is still a sustained hatred against wolves by a minority of the public, and this hatred is enabled by state and federal government policies (p. 308). Vucetich maintains that a dignified life consists of food, space, and freedom from persecution (pp. 308, 357). He concludes the book in the same way he started it, by asking the question, why wolves? His answer: “because they remind us to think” (pp. 32, 323).

This is an important book, adding to the sizable body of work already published on the species. Vucetich writes with great perspective and summarizes 60+ years of research studying Moose–wolf relations on Isle Royale. While I stated at the outset of this review that it took me a long time to read it, don't take that as a negative assessment and avoid purchasing this book. On the contrary, it combines important facets of wolf biology, theoretical modelling (i.e., science), and philosophy, which makes it a good reference. Vucetich acknowledges the moral obligations humans have to protect all forms of life, including predators like wolves.

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## NEW TITLES

Prepared by Jessica Sims

If you are interested in reviewing a book on this list, please contact Jessica Sims (bookrevieweditor@canadianfieldnaturalist.ca). This list covers a range of upcoming and new releases in field biology, ecology, and natural history. We also welcome your suggestions for new titles and offers to review unlisted books with a Canadian connection, including those on any species (native or non-native) that inhabits Canada, or books covering topics of global relevance, including climate change, biodiversity, species extinction, habitat loss, evolution, and field research experiences.

**Please note:** Books marked with a \* have already been assigned to a *Canadian Field-Naturalist* reviewer. All other books are available for review and review copies of books marked with a † have been explicitly offered by publishers.

**Currency Codes:** CAD Canadian Dollars, AUD Australian Dollars, USD United States Dollars, EUR Euros, GBP British Pounds.

## BIOLOGY

**The Amateur Plankton Researcher's Practical Guide: How to Study Plankton at Home.** By Albert Calbet. 2025. Springer. 142 pages and 91 colour photos, 36.50 CAD, Hardcover, 27.99 CAD, E-book.

**The Color of North: the Molecular Language of Proteins and the Future of Life.** By Shahir S. Rizk and Maggie M. Fink. 2025. Belknap Press. 288 pages, 36.95 CAD, Hardcover. Also available as an E-book.

**Doctors by Nature: How Ants, Apes, and Other Animals Heal Themselves.** By Jaap de Roode. 2025. Princeton University Press. 264 pages and 25 black and white illustrations, 38.00 CAD, Hardcover, 31.99 CAD, E-book.

**The Game of Species: an Introduction to Biodiversity.** By Julián Simón López-Villalta. 2025. Pelagic Publishing. 152 pages, 42.00 CAD, Paper.

**To Have or To Hold: Nature's Hidden Relationships.** By Sophie Pavelle. 2025. Bloomsbury. 336 pages, 40.00 CAD, Hardcover, 28.00 CAD, E-book.

**Intraterrestrials: Discovering the Strangest Life on Earth.** By Karen G. Lloyd. 2025. Princeton University Press. 248 pages and 11 colour illustrations, 38.00 CAD, Hardcover. Also available as an E-book.

**Life's Devices: the Physical World of Animals and Plants.** Princeton Science Library. By Steven Vogel. Foreword by Rob Dunn. 2025. Princeton University Press. 384 pages, 29.99 CAD, Paper. Also available as an E-book.

**Living Night: on the Secret Wonders of Wildlife After Dark.** By Sophia Kimmig. 2025. The Experiment. 272 pages, 24.95 CAD, Hardcover, 18.99 CAD, E-book.

**The Neck: a Natural and Cultural History.** By Kent Dunlap. 2025. University of California Press.

336 pages and 25 black and white images, 33.95 CAD, Hardcover.

**Nonadaptive Selection: an Evolutionary Source of Ecological Laws.** By John Damuth and Lev R. Ginzburg. 2025. University of Chicago Press. 240 pages, 149.50 CAD, Hardcover, 45.50 CAD, Paper. Also available as an E-book.

## BOTANY

**Aroids: Plants of the Arum Family. Third Edition.** By Deni Brown. 2025. Royal Botanic Gardens, Kew. Distributed by University of Chicago Press. 456 pages, 450 colour plates, and 40 line drawings, 97.50 CAD, Paper.

**Berries of Labrador.** By Ellen Bryan Obed. Illustrations by Valerie Powell. 2024. Memorial University Press. 116 pages, 26.95 CAD, Paper.

**Evolution of the Arborescent Gymnosperms: Pattern, Process and Diversity, Volume 1—Northern Hemisphere Focus.** By Christopher N. Page. 2025. Cambridge University Press. 730 pages, 344.95 CAD, Hardcover.

**Evolution of the Arborescent Gymnosperms: Pattern, Process and Diversity, Volume 2—Southern Hemisphere Focus.** By Christopher N. Page. 2025. Cambridge University Press. 686 pages, 344.95 CAD, Hardcover.

**Flower Day: a Story of 24 Hours and 24 Floral Lives.** By Sandra Knapp. Illustrations by Katie Scott. 2025. University of Chicago Press. 208 pages and 26 halftones, 23.50 CAD, Hardcover.

**International Code of Nomenclature for Algae, Fungi, and Plants. 2025 Edition (Madrid Code, Twentieth International Botanical Congress).** By the Editorial Committee of the Madrid Code. 2025.

University of Chicago Press. 288 pages, 175.50 CAD, Hardcover, 58.50 CAD, Paper.

**Kew Pocketbooks: Medicinal Plants.** By Melanie-Jayne Howes and Eliot Jan-Smith. 2025. Royal Botanic Gardens, Kew. Distributed by University of Chicago Press. 96 pages and 40 colour plates, 19.50 CAD, Hardcover.

**The Lost Orchid: a Story of Victorian Plunder and Obsession.** By Sarah Bilston. 2025. Harvard University Press. 400 pages, 39.95 CAD, Hardcover. Also available as an E-book.

**Love Them to Death: Turning Invasive Plants into Local Economic Opportunities.** Edited by Wendy L. Applequist. 2025. Missouri Botanical Garden Press. Distributed by University of Chicago Press. 304 pages and 49 colour plates, 39.00 CAD, Paper.

**Mythic Plants: Potions and Poisons from the Gardens of the Gods.** By Ellen Zachos. 2025. Workman Publishing Group. 192 pages, 29.00 CAD, Hardcover, 16.99 CAD, E-book.

**Native Plants of British Columbia's Coastal Dry Belt: a Photographic Guide.** By Hans Roemer and Mary Sanseverino. 2025. Harbour Publishing. 272 pages, 29.95 CAD, Paper.

**Nature's Greatest Success: How Plants Evolved to Exploit Humanity.** By Robert N. Spengler III. 2025. University of California Press. 512 pages and 50 black and white illustrations, 37.95 CAD, Hardcover.

**Peony.** By Gail Harland. 2025. Reaktion Books. Distributed by University of Chicago Press. 216 pages, 96 colour plates, and 10 halftones, 34.99 CAD, Hardcover.

**Plant Ecology in a Changing World. First Edition.** By James R. Ehleringer and Russell Monson. 2025. CRC Press. 602 pages, 56 colour illustrations, and 403 black and white illustrations, 251.95 CAD, Hardcover.

**Silm Da'axk / To Revive and Heal Again: Historical Ecology and Ethnobotany in Laxxyuubm Gitselasu.** By Chelsey Geralda Armstrong in collaboration with Gitselasu knowledge holders. 2025. Athabasca University Press. Distributed by University of Chicago Press. 376 pages and 80 colour plates, 49.99 CAD, Paper.

**Treasured Trees. Edition, Revised and Updated.** By Christina Harrison and Martyn Rix. Illustrations by Masumi Yamanaka. 2025. Royal Botanic Gardens, Kew. Distributed by University of Chicago Press. 128 pages and 40 colour plates, 39.00 CAD, Hardcover.

**Trees of North America, Europe, the UK and Ireland.** By Roger Phillips. 2025. Pan Macmillan. 304 pages and 1000+ colour photos, 35.00 GBP, Hardcover.

**Trees of the Rocky Mountains: Identifying the Region's Prominent Trees.** By Robert Weiss. 2025. Globe Pequot. 200 pages, 31.95 CAD, Paper.

**Victorian Nightshades: How the Solanaceae Shaped the Modern World.** By Elizabeth A. Campbell. 2025. University of Virginia Press. 348 pages and 45 black and white illustrations, 162.95 CAD, Hardcover, 53.95 CAD, Paper.

#### CONSERVATION AND CLIMATE CHANGE

**Arctic Passages: Ice, Exploration, and the Battle for Power at the Top of the World.** By Kieran Mulvaney. 2025. Island Press. 200 pages, 37.95 CAD, Hardcover.

**A Billion Butterflies: a Life in Climate and Chaos Theory.** By Jagadish Shukla. 2025. St. Martin's Press. 288 pages, 40.00 CAD, Hardcover, 16.99 CAD, E-book.

**Climate Injustice: Why We Need to Fight Global Inequality to Combat Climate Change.** By Friederike Otto. Translated by Sarah Pybus. 2025. Greystone Books. 272 pages, 38.95 CAD, Hardcover.

**Conserving Nature in Greater Yellowstone: Controversy and Change in an Iconic Ecosystem.** By Robert B. Keiter. 2025. University of Chicago Press. 376 pages and 15 halftones, 149.50 CAD, Hardcover, 37.95 CAD, Paper. Also available as an E-book.

**The Conversation on Extreme Weather.** Critical Conversations Series. Edited by Jennifer A. Horney. 2025. Johns Hopkins University Press. 320 pages, 25.99 CAD, Paper.

**Entwined: Dispatches from the Intersection of Species.** By Bridget A. Lyons. 2025. Texas A&M University Press. 224 pages, 28.50 CAD, Paper.

**Environmental Governance in the Gulf of St. Lawrence.** Sustainability and the Environment Series. By Peter Clancy and Mario Levesque. 2025. UBC Press. 448 pages, 14 maps, 24 charts, and 7 tables, 49.95 CAD, Paper.

**Following Nature's Lead: Ancient Ways of Living in a Dying World.** By M.D. Usher. 2025. Princeton University Press. 232 pages and 21 black and white illustrations, 38.00 CAD, Hardcover. Also available as an E-book.

**Hope Dies Last: Visionary People Across the World, Fighting to Find Us a Future.** By Alan Weisman. 2025. Penguin Publishing Group. 512 pages, 42.00 CAD, Hardcover, 18.99 CAD, E-book.

**How to Survive: Living with Care in the Climate Crisis.** Edited by Francesca Du Brock and Julie Decker. 2025. Hirmer Publishers. Distributed by University of Chicago Press. 200 pages and 40 colour plates, 54.95 CAD, Paper.

**Jasper on Fire: Five Days of Hell in a Rocky Mountain Paradise.** Sutherland Quarterly No. 8. By Matthew Scace. 2025. Sutherland House Books. 100 pages, 19.95 CAD, Paper.

**Lost Animals, Disappearing Worlds: Stories of Extinction.** By Barbara Allen. 2025. Reaktion Books. 248 pages, 32 colour illustrations, and 7 black and white illustrations, 39.00 CAD, Hardcover.

**Lost Songs of Nature: Nature's Symphony in the Age of Noise Pollution.** By Michel Leboeuf. Translated by Jennifer Strachan. 2025. Great Plains Publications. 216 pages, 28.95 CAD, Paper.

**Marginlands: a Journey into India's Vanishing Landscapes.** By Arati Kumar-Rao. 2025. Milkweed Editions. 280 pages, 33.99 CAD, Hardcover.

**Marketing the Wilderness: Outdoor Recreation, Indigenous Activism, and the Battle over Public Lands.** By Joseph Whitson. 2025. University of Minnesota Press. 240 pages and 37 black and white illustrations, 128.99 CAD, Hardcover, 31.99 CAD, Paper.

**My Head for a Tree: the Extraordinary Story of the Bishnoi, Guardians of Nature.** By Martin Goodman. Preface by Ram Niwas Bishnoi Budhnagar. Foreword by Peter Wohlleben. 2025. Greystone Books. 272 pages, 36.95 CAD, Hardcover.

**Novel Ecologies: Nature Remade and the Illusions of Tech.** By Allison Carruth. 2025. University of Chicago Press. 224 pages, 20 colour plates, and 14 halftones, 149.50 CAD, Hardcover, 35.95 CAD, Paper, 30.99 CAD, E-book.

**In Praise of Floods: the Untamed River and the Life It Brings.** Yale Agrarian Studies Series. By James C. Scott. 2025. Yale University Press. 248 pages and 48 black and white illustrations, 36.50 CAD, Hardcover, 31.99 CAD, E-book.

**Is a River Alive?** By Robert Macfarlane. 2025. Random House Canada. 384 pages, 39.00 CAD, Hardcover, 16.99 CAD, E-book.

**Sea of Grass: the Conquest, Ruin, and Redemption of Nature on the American Prairie.** By Dave

Hage and Josephine Marcotty. 2025. Random House. 384 pages, 42.00 CAD, Hardcover, 18.99 CAD, E-book.

**Transforming the Prairies: Agricultural Rehabilitation and Modern Canada.** By Shannon Stunden Bower. 2025. UBC Press. 316 pages, 15 black and white photos, and 11 maps, 34.95 CAD, Paper.

**Travels Up the Creek: a Biologist's Search for a Paddle.** By Lorne Fitch. 2024. Rocky Mountain Books (RMB). 232 pages, 25.00 CAD, Paper, 10.99 CAD, E-book.

**World War Zoos: Humans and Other Animals in the Deadliest Conflict of the Modern Age.** By John M. Kinder. 2025. University of Chicago Press. 384 pages and 51 halftones, 45.50 CAD, Hardcover. Also available as an E-book.

#### ECOLOGY

**Bad Nature: How Rat Control Shapes Human and Nonhuman Worlds.** By Andrew McCumber. 2025. University of Chicago Press. 224 pages, 149.50 CAD, Hardcover, 35.95 CAD, Paper. Also available as an E-book.

**Carion Ecology, Evolution, and Their Applications. Second Edition.** Edited by M. Eric Benbow, Jeffery K. Tomberlin, and Aaron M. Tarone. 2025. CRC Press. 704 pages, 67 colour illustrations, and 124 black and white illustrations, 220.00 USD, Hardcover.

**Spatial Analysis: a Guide for Ecologists. Third Edition.** By Mark R.T. Dale and Marie-Josée Fortin. 2025. Cambridge University Press. 350 pages, 64.99 CAD, Paper.

#### ENTOMOLOGY

**Aphids Unveiled: the Saga of Nature's Most Irritating Insects.** By Amanda Rose Newton. 2025. CRC Press. 112 pages and 71 colour illustrations, 281.50 CAD, Hardcover, 99.50 CAD, Paper. Also available as an E-book.

**Arthropods of Canadian Grasslands, Volume 5: Beetle Diversity of a Canadian Prairie Homestead.** Biological Survey of Canada Monograph Series No. 9. By David Larson. 2024. The Biological Survey of Canada. 128 pages and colour photos, Open Access URL at [https://drive.google.com/file/d/1AX0Aa7cWTUjoaP\\_f4oxLL6JHfM2ns8/view](https://drive.google.com/file/d/1AX0Aa7cWTUjoaP_f4oxLL6JHfM2ns8/view).

**Beepedia: a Brief Compendium of Bee Curiosities.** Pedia Books Series. By Laurence Packer. Illustrations by Ann Sanderson. 2025. Princeton University Press.

176 pages and 51 black and white illustrations, 24.99 CAD, Hardcover. Also available as an E-book.

**Bugwatching: the Art, Joy, and Importance of Observing Insects.** By Eric R. Eaton. Illustrations by Samantha Gallagher. 2025. Princeton University Press. 208 pages, 100+ colour photos, and 40 colour illustrations, 32.00 CAD, Paper. Also available as an E-book.

**Dragonflies and Damselflies of the World: a Guide to Their Diversity.** A Guide to Every Family Series. By Klaas-Douwe B. Dijkstra. 2025. Princeton University Press. 256 pages and 250 colour illustrations, 44.00 CAD, Hardcover. Also available as an E-book.

**Honeybee Ecology: a Study of Adaptation in Social Life.** Monographs in Behavior and Ecology. By Thomas D. Seeley. 2025. Princeton University Press. 212 pages, 199.50 CAD, Hardcover, 60.50 CAD, Paper. Also available as an E-book. First published in 1985.

**Insect Anatomy: Structure and Function. First Edition.** Edited by Bernard Moussian. 2025. Academic Press. 701 pages, 370.50 CAD, Hardcover.

**Rise of the Zombie Bugs: the Surprising Science of Parasitic Mind-Control.** By Mindy Weisberger. 2025. Johns Hopkins University Press. 296 pages and 13 black and white illustrations, 38.95 CAD, Hardcover. Also available as an E-book.

**Three Mosquitoes: the Biology of Deadly Insects.** By Jeffrey R. Powell. 2025. Johns Hopkins University Press. 264 pages, 28 colour illustrations, and 22 black and white illustrations, 45.95 CAD, Paper. Also available as an E-book.

**The Wonder Cabinet of Fabulous Insects: Secrets of the World's Rarest and Strangest Insects.** By Denis Richard and Pierre-Olivier Maquart. 2025. Cernunnos. 240 pages, 50.00 CAD, Hardcover.

#### HERPETOLOGY

**The Book of the Frog.** By Sally Coulthard. 2025. Apollo. 176 pages and 25 black and white illustrations, 28.00 CAD, Hardcover, 15.99 CAD, E-book.

**California Amphibians and Reptiles.** Princeton Field Guides. By Robert Hansen and Jackson D. Shedd. 2025. Princeton University Press. 528 pages, 48.00 CAD, Paper, 38.99 CAD, E-book.

**The Golden Toad: an Ecological Mystery and the Search for a Lost Species.** By Trevor Ritland and Kyle Ritland. 2025. Diversion Books. 368 pages, 37.50 CAD, Hardcover, 20.99 CAD, E-book.

**The Lives of Frogs: a Natural History.** The Lives of the Natural World Series. By Jim Labisko and Richard Griffiths. 2025. Princeton University Press. 288 pages and 150 colour illustrations, 48.00 CAD, Hardcover. Also available as an E-book.

**Slither: How Nature's Most Maligned Creatures Illuminate Our World.** By Stephen S. Hall. 2025. Grand Central Publishing. 416 pages, 39.00 CAD, Hardcover, 19.99 CAD, E-book.

**Status of Decline and Conservation of Amphibians of the Middle East: Amphibian Biology, Volume 11, Part 8, Status of Conservation and Decline of Amphibians: Eastern Hemisphere.** Edited by Harold Heatwole, Indraneil Das, and Susan King. 2025. Springer. 301 pages, 142 colour illustrations, and 15 black and white illustrations, 145.95 CAD, Hardcover, 127.63 CAD, E-book.

**Techniques for Photographing Reptiles and Amphibians in the Field: How to Tell Better Stories.** By L. Lee Grismer. 2024. Edition Chimaira. 127 pages and 119 colour photos, 29.80 EUR, Paper.

#### ORNITHOLOGY

**Bird Talk: Hilariously Accurate Ways to Identify Birds by the Sounds They Make.** By Becca Rowland. 2025. Storey. 256 pages, 22.99 CAD, Paper, 15.99 CAD, E-book.

**Birds, Sex and Beauty: the Extraordinary Implications of Charles Darwin's Strangest Idea.** By Matt Ridley. 2025. HarperCollins. 352 pages, 37.00 CAD, Hardcover, 14.99 CAD, E-book.

**Birds of the Tropical Andes.** By Owen Deutch and Michael J. Parr. Foreword by Alvaro Jaramillo. 2025. Princeton University Press. 264 pages and 200+ colour illustrations, 48.00 CAD, Hardcover. Also available as an E-book.

**Birdwatching Guide: Turn Yourself into a Birdwatching Expert.** DK North American Bird Guides. By DK. 2025. DK. 160 pages, 26.99 CAD, Hardcover, 11.99 CAD, E-book.

**Birdwatching in New York City and on Long Island. Second Edition.** By Deborah Rivel and Kellye Rosenheim. 2025. Brandeis University Press. Distributed by University of Chicago Press. 320 pages, 57 colour plates, 42 maps, and 22 tables, 45.50 CAD, Paper.

**The Cuckoo's Lea: the Forgotten History of Birds and Place.** By Michael J. Warren. 2025. Bloomsbury Wildlife. 304 pages, 37.00 CAD, Hardcover, 20.99 CAD, E-book.

**The Feather Detective: Mystery, Mayhem, and the Magnificent Life of Roxie Laybourne.** By Chris Sweeney. 2025. Avid Reader Press/Simon & Schuster. 320 pages, 39.99 CAD, Hardcover, 20.99 CAD, E-book.

**FLACO: the Owl Who Escaped Captivity and Won the Hearts of the World.** Edited by Jonathan Hollingsworth. Foreword by Carl Safina. 2025. Blurring Books. 244 pages and colour photos and illustrations, 77.99 CAD, Hardcover, 51.99 CAD, Paper.

**The Great Auk: Its Extraordinary Life, Hideous Death and Mysterious Afterlife.** By Tim Birkhead. 2025. Bloomsbury USA. 288 pages, 37.00 CAD, Hardcover, 20.99 CAD, E-book.

†**Mission Penguin: a Photographic Quest from the Galápagos to Antarctica.** By Ursula Clare Franklin. 2025. Bloomsbury Wildlife. 240 pages and colour photos, 47.00 CAD, Hardcover, 26.99 CAD, E-book.

**No Island Too Far: Searching for Seabirds on Remote Specks of Land.** By Michael Brooke. 2025. Pelagic Publishing. 344 pages and 16 colour plates, 50.00 CAD, Paper.

**Nova Scotia Birds: a Field Guide. Third Edition.** By Jeffrey C. Domm. 2024. Formac Publishing Company Limited. 224 pages, 27.95 CAD, Paper.

**The Starling: a Biography.** By Stephen Moss. 2025. Random House UK. 208 pages, 31.99 CAD, Hardcover.

**Sunbirds of the World: Sunbirds, Flowerpeckers, Spiderhunters and Sugarbirds. Second Edition.** Helm Identification Guides. By Clive F. Mann and Robert A. Cheke. Illustrations by Richard Allen. 2025. Helm. 608 pages and colour plates and photos, 120.00 CAD, Hardcover.

**Turning to Birds: the Power and Beauty of Noticing.** By Lili Taylor. 2025. Crown. 208 pages, 39.99 CAD, Hardcover, 16.99 CAD, E-book.

#### ZOOLOGY

**Atlas of Marine Invertebrate Larvae. Second Edition.** Edited by Craig M. Young, Michael J. Boyle, and Mary A. Sewell. 2025. Academic Press. 691 pages, 259.50 CAD, Paper.

**East Coast Whales, Dolphins and Sharks: a Visual Guide to Sea Life in Nova Scotia, New Brunswick and Prince Edward Island. Edition, Revised and Updated.** Formac Pocketguides. By Jeffrey C. Domm. 2025. Formac Publishing Company Limited. 96 pages, 19.95 CAD, Paper.

**Fishes of the Strait of Georgia: Over 240 Life Histories.** By Dick Beamish and Jeff Marliave. 2025. Harbour Publishing. 512 pages, 99.95 CAD, Hardcover.

**Living with Lynx: Sharing Landscapes with Big Cats, Wolves and Bears.** By Jonny Hanson. 2025. Pelagic Publishing. 280 pages, 37.00 CAD, Hardcover, 31.99 CAD, E-book.

**Lone Wolf: Walking the Line Between Civilization and Wildness.** By Adam Weymouth. 2025. Knopf Canada. 288 pages, 36.00 CAD, Hardcover, 16.99 CAD, E-book.

**Portrait of an Oyster: a Natural History of an Epicurean Delight.** By Andreas Ammer. Translated by Renée von Paschen. Illustrations by Falk Nordmann. 2025. Greystone Books. 184 pages and colour illustrations, 29.95 CAD, Hardcover.

**Reefs of Time: What Fossils Reveal about Coral Survival.** By Lisa S. Gardiner. 2025. Princeton University Press. 280 pages and 23 black and white illustrations, 41.00 CAD, Hardcover. Also available as an E-book.

**Sea Otter Conservation II: Nearshore Ecosystem Restoration. Second Edition.** Edited by Shawn Larson, James Bodkin, and Erin Foster. 2025. Academic Press. 404 pages, 222.50 CAD, Hardcover. Also available as an E-book.

**A Year with the Seals: Unlocking the Secrets of the Sea's Most Charismatic and Controversial Creatures.** By Alix Morris. 2025. Algonquin Books. 320 pages, 40.00 CAD, Hardcover, 12.99 CAD, E-book.

#### OTHER

**After the North Pole: a Story of Survival, Mythmaking, and Melting Ice.** By Erling Kagge. Translated by Kari Dickson. 2025. HarperCollins. 368 pages, 39.50 CAD, Hardcover, 17.99 CAD, E-book.

**Alexander von Humboldt: Writings in English, Part I: 1789–1859.** Edited by Oliver Lubrich and Thomas Nehrlich. 2025. The American Philosophical Society Press. Distributed by University of Pennsylvania Press. 1500 pages, 97.99 CAD, Hardcover.

**Alexander von Humboldt: Writings in English, Part II: 1825–1859.** Edited by Oliver Lubrich and Thomas Nehrlich. 2025. The American Philosophical Society Press. Distributed by University of Pennsylvania Press. 700 pages, 58.99 CAD, Hardcover.

**The Beast in the Clouds: the Roosevelt Brothers' Deadly Quest to Find the Mythical Giant Panda.** By Nathalia Holt. 2025. Atria/One Signal Publishers.

288 pages, 39.00 CAD, Hardcover, 20.99 CAD, E-book.

**A Cold Colonialism: Modern Exploration and the Canadian North.** By Tina Adcock. 2025. UBC Press. 376 pages and 33 photos, 110.00 CAD, Hardcover.

**The Elephant in the Room: How to Stop Making Ourselves and Other Animals Sick.** By Liz Kalaugher. 2025. University of Chicago Press. 288 pages and 20 colour plates, 39.00 CAD, Hardcover. Also available as an E-book.

**Ends of the Earth: Journeys to the Polar Regions in Search of Life, the Cosmos, and Our Future.** By Neil Shubin. 2025. Dutton. 288 pages, 42.00 CAD, Hardcover, 18.99 CAD, E-book.

**The Everyday Naturalist: How to Identify Animals, Plants, and Fungi Wherever You Go.** By Rebecca Lexa. Illustrations by Ricardo Macía Lalinde. 2025. Ten Speed Press. 272 pages, 25.99 CAD, Paper, 14.99 CAD, E-book.

**Flora of Lichenicolous Fungi, Volume 2: Hyphomycetes.** By Paul Diederich, Damien Ertz, and Uwe Braun. 2025. Musée National d'Histoire Naturelle, Luxembourg. 544 pages, colour photos, colour and black and white illustrations, and colour maps, 57.50 EUR, Hardcover. Also available for free online at <https://ps.mnhn.lu/pub/FloraLichenicolousFungi2.pdf>.

**In the Footsteps of the Traveller: the Astronomy of Northern Dene.** Contemporary Studies of the North Series. By Chris M. Cannon. Foreword by Chief Fred Sangris. 2025. University of Manitoba Press. 34.95 CAD, Paper. Also available as an E-book.

**Forest Euphoria: the Abounding Queerness of Nature.** By Patricia Ononiwu Kaishian. 2025. Spiegel & Grau. 280 pages, 37.99 CAD, Hardcover.

†**Fossils: an Essential Guide.** By Paul D. Taylor. 2025. University of Chicago Press. 224 pages and 230 colour plates, 33.95 CAD, Hardcover. Also available as an E-book.

**Infinite Paradise: Witnessing the Wild, a Memoir.** By Dianne Eberth Beeaff. 2025. She Writes Press. 256 pages, 24.99 CAD, Paper, 11.99 CAD, E-book.

**Lichens du Québec Nordique.** Par Catherine Boudreault, Kim Damboise, et Serge Payette. 2024.

Presses de l'Université Laval. 430 pages, 54.95 CAD, livre de poche, 44.95 CAD, livre électronique.

**Mushroom Day: a Story of 24 Hours and 24 Fungal Lives.** By Alison Pouliot. Illustrations by Stuart Patience. 2025. University of Chicago Press. 176 pages and 24 halftones, 23.50 CAD, Hardcover.

**Near the Forest, By the Lake: Discovering Nature Close to Home.** By Angela E. Douglas. 2025. Comstock Publishing. 208 pages, 29.95 CAD, Paper. Also available as an E-book.

**Nightshining: a Memoir in Four Floods.** By Jennifer Kabat. 2025. Milkweed Editions. 360 pages, 20.00 USD, Paper.

**Senescence: a Year in the Canadian Rockies.** By Amal Alhomsy. 2024. Rocky Mountain Books (RMB). 176 pages, 20.00 CAD, Paper, 9.99 CAD, E-book.

**Summers in Squid Tickle: a Newfoundland Odyssey.** By Robert Finch. 2025. W.W. Norton. 304 pages, 39.99 CAD, Hardcover, 30.99 CAD, E-book.

**Understanding Visuals in the Life Sciences.** Understanding Life Series. By Han Yu. 2025. Cambridge University Press. 232 pages, 22.95 CAD, Paper.

**The Urban Naturalist: How to Make the City Your Scientific Playground.** By Menno Schilthuis. Illustrations by Jono Nussbaum. 2025. MIT Press. 312 pages and 19 black and white illustrations, 43.95 CAD, Hardcover, 35.99 CAD, E-book.

**Vancouver Island: the Art of the Landscape.** By Kelly Hutchison. Photography by Dave Hutchison. 2025. Two Trees Art. 224 pages, 49.95 CAD, Hardcover.

**Water Borne: a 1,200-Mile Paddleboarding Pilgrimage.** By Dan Rubinstein. 2025. ECW Press. 400 pages, 28.95 CAD, Paper, 16.99 CAD, E-book.

**Wedding of the Foxes: Essays.** By Katherine Larson. 2025. Milkweed Editions. 208 pages, 30.95 CAD, Paper.

**Wild and Wonderful: an Ethnography of English Naturalists.** By Vanessa Manceron. Translated by Michael Taylor. Preface by Stephen Hugh-Jones. 2025. HAU Books. Distributed by University of Chicago Press. 250 pages and 15 halftones, 45.50 CAD, Paper.

# The Canadian Field-Naturalist

## News and Comment

Compiled by Amanda E. Martin

### Upcoming Meetings and Workshops

#### Northeast Natural History Conference

The Northeast Natural History Conference to be held 4–6 April 2025 at the Sheraton Springfield Monarch Place Hotel, Springfield, Michigan. Registration

is currently open. More information is available at [https://eaglehill.us/NENHC\\_2025/NENHC2025.shtml](https://eaglehill.us/NENHC_2025/NENHC2025.shtml).

#### Entomological Society of America, North Central Branch Meeting

The annual meeting of the North Central Branch of the Entomological Society of America to be held 12–16 April 2025 at the Embassy Suites by Hilton Lincoln,

Lincoln, Nebraska. Registration is currently open. More information is available at <https://www.entsoc.org/membership/branches/northcentral/meeting>.

#### IALE-North America Annual Conference

The annual conference of the North American Regional Chapter of the International Association for Landscape Ecology (IALE–North America) to be held 13–17 April 2025 at the Sheraton Raleigh Hotel, Raleigh, North Carolina. The theme of the conference

is: ‘Landscapes of Change: Dynamic Interactions between Nature and People’. Registration is currently open. More information is available at <https://www.ialena.org/annual-meeting.html>.

#### Northeast Fish & Wildlife Conference

The 80th annual Northeast Fish & Wildlife Conference to be held 21–24 April 2025 at the Omni Mount Washington Hotel, Bretton Wood, New Hampshire.

Registration is currently open. More information is available at <https://www.neafwa.org/conference.html>.

#### Watersheds Canada National Conference

The inaugural Watersheds Canada National Conference to be held 1–2 May 2025 at the Pinestone Resort Golf and Conference Centre, Haliburton, Ontario. Registration is currently open. More information is

available at [https://watersheds.ca/conference/?gad\\_source=1&gclid=EAlaIqObChMI5O3M7Y7XigMVzB-tBh1LmjGmEAYASAAEgKUWvD\\_BwE](https://watersheds.ca/conference/?gad_source=1&gclid=EAlaIqObChMI5O3M7Y7XigMVzB-tBh1LmjGmEAYASAAEgKUWvD_BwE).

#### International Conference on Ecology and Transportation

The 14th biennial International Conference on Ecology and Transportation to be held 11–15 May 2025 as a hybrid event, with online content and an in-person

meeting at the Sheraton Denver Downtown Hotel, Denver, Colorado. Registration is currently open. More information is available at <https://icoet.net/>.

#### Canadian Society of Zoologists/Société canadienne de zoologie 2025

The 64th annual meeting of the Canadian Society of Zoologists/Société canadienne de zoologie to be held 12–15 May 2025 at Wilfred Laurier University,

Waterloo, Ontario. Registration is currently open. More information is available at <https://sites.google.com/view/csz-scz2025?usp=sharing>.

#### 2025 Ontario Biodiversity Summit

The 2025 Ontario Biodiversity Summit to be held 21–22 May 2025 at Trent University, Peterborough-Nogojiwanong, Ontario. The theme of the summit is:

‘Our Turning Point for Nature’. Registration is currently open. More information is available at <https://ontariobiodiversitycouncil.ca/summit/>.

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