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Review article

Hungry grouse in a warming world: emerging risks from plant chemical defenses and climate change

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Conservation and management of habitat is central to the conservation of grouse. Identifying thresholds of biotic and abiotic risks that may reduce habitat quality is therefore a component of habitat management of grouse. We propose that dietary phytochemicals, specifically plant secondary metabolites (PSMs), represent an ecological risk to grouse, which are not often considered in the management of grouse. Most species of grouse consume PSMs, which have negative consequences at some concentration. Moreover, several studies provide evidence that the risks posed by PSMs will likely increase under projected climate change scenarios. We discuss potential risks of PSMs for grouse and propose theoretical models, which can be used to test current and future physiological, behavioural and ecological risks of PSMs. We propose that dose-response thresholds can be used to predict and monitor the synergistic risks of PSMs and climate change for grouse. We further suggest that identifying dose-response thresholds to PSMs is needed in the management of vertebrate herbivores in general.

Key words: climate, diet, grouse, habitat risk, herbivore, plant secondary metabolite

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Habitat loss and degradation of habitat are considered the most important risks to grouse populations globally (Storch 2007). Habitats and associated plant communities have undergone significant changes because of invasion of non-native species, wildfires, development and management practices that reduce the availability of plants (Beck et al. 2012, Keeley & Brennan 2012, Kutt & Kemp 2012). Degraded habitats therefore reduce the availability of food for grouse. Climate change is also predicted to reduce both the availability and palatability of many plants consumed by grouse (Bidart-Bouzat & Imeh-Nathaniel 2008, Revermann et al. 2012). Grouse populations are therefore expected to continue experiencing not only losses in the quantity of food but also increases in chemical defenses (i.e. secondary metabolites) in the remaining available food.

Our objective is to demonstrate that grouse management should include efforts to mitigate the risks of plant secondary metabolites (PSMs). Before management actions can be defined, we must better understand how herbivores respond to the risks of PSMs. Therefore, we propose that the identification and management of the synergistic risks of PSMs and climate change are important in the development of current and future

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management plans for grouse. Our proposal is based on two connected and supported arguments: 1) PSMs create dose-dependent risks for grouse and 2) climate change will increase the risks of PSMs for grouse.

Methods

To provide a scientific basis for our arguments, we performed a literature search using the ISI Web of Knowledge database using the keyword search parameters of climate OR diet AND dose OR plant secondary metabolite OR grouse OR habitat selection OR herbivore from the time frame 1945-2013. From this search, we selected the most relevant articles which presented data showing the physiological, behavioural or ecological consequences of PSMs or climate change on vertebrate herbivores in general and grouse specifically.

Dose-dependent risks of PSMs

Although necessary to sustain life, plants pose significant dietary challenges to herbivores because of their high fibre content, relatively low nutritional value and potentially toxic PSMs (Forbey et al. 2013). Nutrients and PSMs often interact to determine the relative quality of plants as food for herbivores, and herbivores are unlikely to encounter plants that do not contain PSMs. Although PSMs consumed can be both therapeutic and toxic (Forbey et al. 2009), strong evidence suggests that PSMs are generally avoided by herbivores because they have deleterious (i.e. toxic) consequences (Forbey et al. 2013). PSMs can mechanistically inhibit important enzymatic reactions and interrupt cellular energy production in dose-dependent ways (Forbey et al. 2011). For example, monoterpenes (volatile oils) and phenolics are common constituents of plants which can influence digestibility (Degabriel et al. 2009), compromise water balance (Dearing et al. 2001) and impact acid-base homeostasis (Guglielmo et al. 1996) in vertebrate herbivores.

Regulation of dose-dependent risks of PSMs

Herbivores have several physiological and behavioural adaptations to regulate the plasma concentrations of PSMs and therefore the dose-dependent consequences of ingested PSMs. Physiological counter defenses (Sorensen & Dearing 2006, Sorensen et al. 2006) and behavioural intake regulation (Torregrossa & Dearing 2009) can synergistically act to lower systemic exposure to PSMs.

Several physiological mechanisms act in concert to regulate plasma concentrations of PSMs ingested by herbivores. Limited absorption of ingested PSMs may reduce the maximum plasma concentration of PSMs and is evidenced by the excretion of ingested PSMs unchanged in the faeces of vertebrate herbivores (Sorensen & Dearing 2006). Higher expression and activity of metabolizing enzymes can increase the rate of detoxification of ingested PSMs and allow herbivores to achieve a faster return to a plasma concentration of PSMs below a physiological (toxic) threshold (Sorensen et al. 2006). Compared to mammalian herbivores, the mechanisms that regulate absorption, distribution, metabolism and excretion of ingested PSMs have not been adequately explored in grouse. Moreover, the functional constraints of flight (Dudley & Vermeij 1992) may limit the size and complexity of the digestive tract and liver in grouse which are required to process plants with a high diversity and concentration of PSMs. However, grouse specializing on woody plants that have chemical defenses have larger intestinal tracts than birds that do not (Moss 1983, Sedinger 1997). Similar to mammals, grouse excrete ingested PSMs unchanged in their faeces (Frye 2012, Thacker et al. 2012) and use a variety of detoxification pathways to excrete ingested PSMs (Guglielmo et al. 1996, Liukkonen-Anttila et al. 2003).

Despite evidence that physiological mechanisms can regulate plasma concentration of ingested PSMs, it remains difficult to directly measure the capacity of these mechanisms in any species (McLean et al. 2008). Therefore, researchers typically use behavioural regulation of feeding bouts as an indirect measure of regulation of PSM concentrations in plasma. Behavioural regulation of PSM ingestion is generally defined as a herbivore's ability to modify feeding bout duration (i.e. meal size), feeding bout number (number of meals) and/or inter-bout intervals (time between each meal; Wiggins et al. 2006a, Torregrossa & Dearing 2009; Fig. 1). Smaller feeding bouts reduce the increase in plasma concentrations of PSMs and longer inter-bout intervals provide time for plasma concentrations to decrease prior to the next feeding bout (McLean et al. 2008). Recent empirical evidence in mammalian herbivores demonstrates that in the absence of behavioural and physiological regulation of PSMs, higher concentrations of PSMs will result in higher concentrations of PSMs in plasma (Mclean et al. 2008; see Fig. 1).

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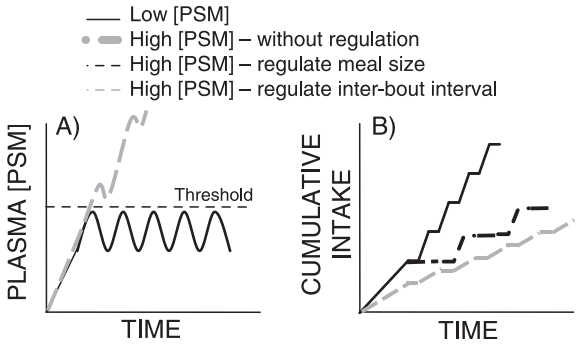


Figure 1. Predicted physiological and behavioural risks of plant secondary metabolites (PSMs) for herbivores, where: A) herbivores regulate plasma PSM concentrations ([PSM]) at or below a physiological threshold (black dashed line) under lower dietary [PSM] (solid black line). We predict that higher [PSM] and lack of physiological or behavioural regulation will result in physiological risks for herbivores, observed as an increase in plasma [PSM] (dashed thick grey line) above a physiological threshold limit; and B) we predict that behavioural intake regulation (excluding physiological adaptations) in response to higher [PSM] (dashed lines) will result in reduced cumulative intake compared to lower [PSM] (solid black line). Figure adapted from (Foley et al. 1999, Wiggins et al. 2006a, Torregrossa & Dearing 2009).

Regulating plasma concentrations of PSMs can be risky

Although physiological and behavioural mechanisms used by herbivores can regulate plasma concentrations of PSMs, these mechanisms can be costly. For example, mechanisms such as efflux transporters which limit the absorption of ingested PSMs are energetically expensive as they are dependent on adenosine triphosphate (ATP; Sorensen & Dearing 2006). In addition, metabolic costs of transporters and metabolizing enzymes have been demonstrated in herbivores, including grouse (Guglielmo et al. 1996, Sorensen et al. 2005). The physiological mechanisms used to limit systemic concentrations of PSMs can also increase water and energy demands (Dearing et al. 2001, Sorensen et al. 2005). While behavioural regulation of intake may be used to minimize the physiological costs of processing PSMs, it can simultaneously result in an additional cost of reduced intake or increased time allocated to feeding (Wiggins et al. 2006a, Torregrossa & Dearing 2009; see Fig. 1).

Selection of diets with the lowest concentrations of PSMs is an additional behavioural strategy that can reduce plasma concentrations of PSMs. This strategy requires that herbivores can detect and select for PSMs. Grouse may use visual cues to detect PSMs which reflect or absorb different wavelengths of light. For example, the ability to detect near-ultraviolet (UV) light has been proposed to explain how black grouse *Tetrao tetrix* detect and select UV-reflecting berries (Siitari & Viitala 2002). In contrast to vision, it has been suggested that birds have lower evolutionary diversity and functionality of olfactory (Zelenitsky et al. 2011) and taste receptors (Davis et al. 2010) compared with mammals. However, mounting evidence demonstrates that birds consuming foods which are patchily distributed, emit volatiles or contain bitter compounds, have evolved a capacity to taste and smell (Davis et al. 2010, Steiger et al. 2010, Amo et al. 2013). For example, the trigeminal nerve is responsible for the detection and reduced intake of coniferyl benzoate (a dominant PSM in quaking aspen *Populus termuloides*) by European starlings *Sturnus vulgaris* and may explain regulated intake of that PSM by ruffed grouse *Bonasa umbellus* (Jakubas & Mason 1991). These studies suggest that grouse may be able to respond to PSMs detected through visual, olfactory or bitter receptors at various spatial scales. In support of their ability to detect PSMs, the plants, patches and habitats selected by free-ranging grouse had lower PSMs than those that were available but not selected by grouse (Remington & Braun 1985, Frye et al. 2013). Experiments have also shown that grouse exposed to higher levels of PSMs in food reduce their intake of food (Jakubas et al. 1993). However, potential trade-offs of habitat, patch or plant selection may include increased movement between patches (Wiggins et al. 2006b), and therefore increased locomotor costs or greater risks of detection of grouse by predators. The restriction of habitats and trade-offs associated with limitations of food quantity or quality can compromise the persistence and growth of grouse populations (Martin 1987). However, the risks of PSMs are not currently monitored for, or considered, when managing grouse.

Synergistic risks of PSMs and climate change

We suggest that consideration of PSM risks under an adaptive management framework for grouse management will be particularly important in the future, especially when considering the predicted effects of climate change. Climate change is predicted to result in the shift of currently available habitat for grouse (Revermann et al. 2012, Zurell et al. 2012), and predicted higher temperatures may limit grouse reproduction (Selas et al. 2011). We propose that climate change will create an additional stressor for grouse by exacerbating the risk of PSMs for grouse. First, concentrations of many classes of PSMs con-

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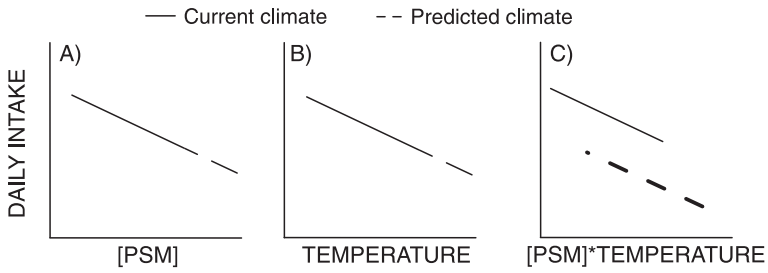


Figure 2. Predicted daily intake of herbivores, where: A) herbivores decrease intake as concentration of plant secondary metabolites ([PSM]) increases at current climate levels (solid black line) and decrease intake even further at higher [PSM] which are predicted under climate change (dashed black line); B) herbivores decrease intake of PSMs at higher temperatures and decrease intake even further under higher temperatures which are predicted under climate change (dashed black line); and C) herbivores decrease intake of PSMs under predicted climate change (dashed black line) compared with current climate conditions (solid black line) when [PSM] and temperature are considered simultaneously.

sumed by grouse, including terpenes, phenolics, tannins, flavonoids and glycosides (e.g. Guglielmo et al. 1996, Iason et al. 2011, Frye et al. 2013), can increase in plants under elevated UV light, temperature and drought (Bidart-Bouzat & Imeh-Nathaniel 2008, Robinson et al. 2012). For example, elevated CO_2 and temperature can result in increased monoterpene concentrations (Raisanen et al. 2008), and elevated UV radiation can result in increased phenolic concentrations (Lavola et al. 2003) in Scots pine *Pinus sylvestris*, which are consumed by black grouse. Second, tolerance to PSMs is expected to decrease due to dose-dependent water stress (Dearing et al. 2001), and climate change is predicted to result in increased temperature-dependent toxicity (Fig. 2; Dearing 2012). For example, the white-throated woodrat *Neotoma albigula* experienced elevated body temperature and resting metabolic rate when consuming PSMs at increased temperature, which increased the thermoregulatory costs of its diet (Mclister et al. 2004). Thus, limited availability of forage with concentrations of PSMs below toxic thresholds to grouse, and reduced availability of habitats with optimal temperatures, may work synergistically to compromise intake and reduce habitat quality for grouse in the future (see Fig. 2).

Predicting and managing grouse responses to PSMs

Challenges

While researchers have identified several causal foraging consequences of PSMs in captive herbivores, it is not always possible to predict dose-response thresholds of wild herbivores to PSMs (see Forbey et al. 2013). Certainly, captive feeding trials using PSM treatments can help assess the concentrations and environmental conditions which elicit feeding responses by herbivores. However, feeding responses observed in studies using single PSMs in artificial diets often miss the synergistic, compensatory and antagonistic interactions among PSMs and nutrients that exist when animals eat plants in nature (Forbey et al. 2013).

Estimating thresholds to PSMs

Dose-response thresholds from wild grouse can simultaneously integrate dose-dependent behavioural (i.e. intake regulation and habitat selection), physiological (i.e. mechanisms of tolerance to PSMs) and ecological (i.e. increasing PSM concentration and toxicity under climate change) responses by grouse into a single measure that depicts relative risks of PSMs. Dose-response thresholds can reveal the non-linear relationship between the extent of selection (positive or negative) for a particular habitat feature and the mean concentration (i.e. dose) of PSM in a foraging patch or habitat (Fig. 3). These thresholds can be compared among populations or species consuming diets with the same PSMs to determine relative risks for grouse which may vary in their physiological capacity to process a PSM or are exposed to different temperatures. For example, we modeled threshold concentrations of different PSMs in different species and populations of sagebrush *Artemisia* spp. to assess the magnitude of plant selection by different populations of greater sage-grouse *Centrocercus urophasianus* (Frye 2012). We found that a low concentration of the PSM 1,8-cineole in some species of sagebrush was associated with a lack of plant selection by sage-grouse, but when the mean concentration of 1,8-cineole in other species of sagebrush exceeded 25 AUC/100 μg/g dry

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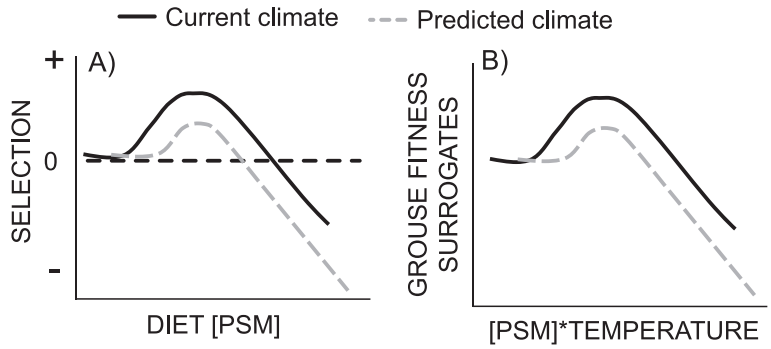


Figure 3. Predicted dose-dependent thresholds for A) relationship between selection for (+) and against (-) plant secondary metabolites (PSMs) by grouse as a function of the mean concentration ([PSM]) of foraging patches or habitats. Positive values on the y-axis indicate a higher [PSM] in plants browsed by grouse than those not browsed by grouse, and indicates a potential therapeutic use of a PSM, whereas negative values indicate a higher [PSM] in non-browsed plants, and indicates avoidance of a PSM. The dashed black line represents a value of 0 on the y-axis, at which point [PSM] is not a factor influencing grouse selection; and B) relationship between grouse fitness response and PSM risks where [PSM]*Temperature represents an increasing risk associated with [PSM] by temperature interaction under predicted climate change scenarios. Surrogates for grouse fitness may for instance include body condition, movement, clutch size, hatch success, survival and population growth. In both, a hypothetical change in herbivore threshold level for an individual PSM is shown for a grouse under predicted climate change (grey dashed line) and indicates that the potential for therapeutic benefit and tolerance by grouse for a given [PSM] is lower than what they experience under current climate conditions (solid lines).

weight, sage-grouse selected against 1,8-cineole (Frye 2012). As mean concentrations of individual PSMs vary among species and populations within species, estimating dose-response thresholds for PSMs in grouse requires the knowledge of both the composition (i.e. presence) and concentration of PSMs in each plant species.

Like most selection models, identifying thresholds of PSMs which correlate selection with plants, patches or habitats does not demonstrate causal responses to PSMs. Indeed, some PSMs may be used as cues by herbivores for the presence of other more toxic PSMs that are not as readily detected (Lawler et al. 2000). However, comparing dose-response thresholds among PSMs, grouse populations or species and environmental conditions can be used to generate new hypotheses which can be validated in controlled experiments and further verified in the field. For example, selection for a particular PSM concentration could suggest a fitness benefit, rather than a detriment, derived from that PSM under certain climatic or physiological conditions (Forbey et al. 2009; see Fig. 3). Captive herbivores may select PSMs to reduce thermoregulatory costs (Dearing et al. 2008) and the effects of parasites (Villalba et al. 2010). It is therefore plausible that habitats with PSM concentrations below a therapeutic threshold may also negatively impact grouse populations. Comparing thresholds to PSMs among species or populations of herbivores could reveal the relative benefits and risks of PSMs. We emphasize that threshold curves obtained from field observations should be replicated under controlled conditions where specific PSMs can be individually manipulated to determine the causal relationships between PSMs and grouse responses.

Identification of fitness risks of PSMs

To evaluate fitness risks of PSMs to grouse populations for purposes of management, scientists need to identify how the distribution of varying concentrations of PSMs and environmental temperatures synergistically influence grouse fitness parameters. We acknowledge that observations of diet selection provide the primary evidence of the fitness risks of PSMs to grouse (e.g. Frye et al. 2013). Additional controlled feeding trials (e.g. Jakubas et al. 1993) are needed to strengthen the link between PSMs and fitness risks in herbivores. We propose that estimating dose-response thresholds to PSMs can predict how the concentration and distribution of PSMs in and among foraging patches will impact fitness of grouse under climate change scenarios (see Fig. 3).

As fitness risks are difficult to measure in long-lived species, it is more informative to use other measured responses and fitness surrogates that may directly or indirectly influenced by PSMs and climate interactions. Intake (e.g. Jakubas et al. 1993, Wiggins et al. 2006a) and body condition indices (e.g. Guglielmo et al. 1996, Shipley et al. 2012) provide useful fitness surrogates in systems for which captive studies are feasible. As browsing by grouse is often easily distinguished from browsing by other species

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(Frye 2012), it is possible to use browsing intensity to estimate the threshold of PSMs that are correlated with grouse feeding intensity. Habitat-selection studies provide informative ecological surrogates for fitness risks in both captive (e.g. Wiggins et al. 2006b) and free-ranging herbivores across multiple spatial scales (e.g. Frye et al. 2013). Many direct fitness parameters and surrogates such as body condition, movement, clutch size, hatch success, survival and population growth are already measured by wildlife managers during routine work, and the thresholds of these responses relative to PSMs and climate change are ripe for study.

Mapping PSMs at multiple scales

Mapping and monitoring PSM concentrations over time would enable researchers and wildlife managers alike to predict dose-dependent responses of herbivores to PSMs associated with climate change. The historical quantification of PSMs using chemical assays is relatively labour-intensive and costly, requires extensive collection of leaf tissue and is generally not feasible for land managers to conduct. However, recent technological advances in handheld and remote sensing devices have improved the accessibility of techniques to map the distribution and concentration of PSMs within and across habitats. For example, visible to short-wave infrared (VSWIR) and near infrared (NIR) spectrometry can be used to quantify the distribution and concentration of nutrients and PSMs that are reflected in different wavelengths of light (Kokaly et al. 2009). Hyperspectral remote sensing data (HyMap) have been used to quantify profiles of PSMs (Youngentob et al. 2012). Additionally, the electronic nose (Delgado-Rodriguez et al. 2012) and Fourier Transform Infrared Systems (FT-IR; Geron & Arnts 2010) offer new opportunities to monitor volatile PSMs remotely. Recent advances in sensors for nitrogen, phenolics and terpenes on manned and unmanned aerial vehicles make it possible to map the distribution and concentration of PSMs and other phytochemicals across landscapes.

Grouse management implications

Emerging technologies provide new and powerful tools for the rapid assessment and monitoring of PSMs and climate change across landscapes. Simultaneous monitoring of fitness of herbivores relative to PSM and climate gradients will allow for more effective conservation and management of grouse habitats. The distribution of PSMs can be integrated with climate data to create maps of the synergistic risks of PSMs and atmospheric temperatures for grouse. To date, PSM and temperature gradients across landscapes have not been linked to maps of habitat use by grouse or other managed herbivores. Such maps, when coupled with known dose-response thresholds, could allow managers to identify areas which have the lowest risks of PSMs for conservation, restoration and reintroduction efforts. We propose that identifying and comparing thresholds to PSMs for different populations and species of grouse under different climates can identify populations that are the most vulnerable to effects of PSMs. The identification of PSM thresholds offers a new management strategy for herbivore populations, and offers additional and testable explanations for changes in herbivore population distributions when other habitat parameters fail to do so.

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