

Biology 108 Case Study #2 – Pika adaptations

Please see the assignment description included in this folder.

From Rankin et al. (2017):

American pikas (*Ochotona princeps*; Order Lagomorpha) are non-hibernating alpine mammals primarily restricted to high-altitude distributions. They exhibit poor heat tolerance (MacArthur and Wang 1973; Smith 1974; Stafl and O'Connor 2015) and limited capacity for dispersal (Henry et al. 2012; Castillo et al. 2014; Robson et al. 2016). Present-day populations occupy western North American mountain ranges—environments characterized by low mean annual temperature, short growing seasons, and hypoxia. American pikas appear to have a number of physiological adaptations to this niche, including an unusually high resting metabolic rate, low thermal conductance (MacArthur and Wang 1973; Otto et al. 2015) and elevated hemoglobin-oxygen (*Hb-O₂*) affinities (Tufts et al. 2015). In addition, they show positive correlations between altitude and oxidative metabolic enzyme activities (for both heart and diaphragm tissues) and total lactate dehydrogenase (*LDH*) activity (Sheafor 2003). They also have unusual feeding patterns, including high selectivity when foraging, and notable caching behavior (Conner 1983; Huntly et al. 1986; Dearing 1997). Given the physiological and behavioral evidence for adaptation of pika phenotypes toward greater specialization for a niche characterized by cold and hypoxia, these animals are an excellent system to use for detecting genetic changes associated with adaptation to these conditions.

... As most pika species inhabit either high altitudes or high-latitude regions and live in extreme climates, pikas reveal evidence for adaptation to cold or hypoxic conditions through an increase in non-shivering thermogenesis (Wang et al. 1999, 2006; Yang et al. 2008, 2011; Bai et al. 2015), regulation of neuroendocrine function (Du and You 1992), pulmonary circulation (Ge et al. 1998), heart function (Qi et al. 2008), regulation of gene expression (Chen et al. 2007; Li et al. 2009, 2013; Pichon et al. 2013; Xie et al. 2014), and genetic adaptation (Ge et al. 2013; Luo et al. 2013). ...

Pikas have been shown to exhibit physiological characteristics that may reflect underlying genetic adaptations for survival in hypoxic environments. For example, various lines of evidence suggest that insulin-like growth factor 1 (*IGF-1*) has a role in the hypoxia response of hepatocytes in pikas. ... In addition to secreted proteins like *IGFs*, key enzymes involved in energy metabolism pathways seem to be critical components of the response to hypoxia in pikas. For instance, metabolic enzyme activity of 3-hydroxyacyl CoA dehydrogenase was shown to have a positive relationship with altitude in cardiac tissue for 3 species of pika (*O. princeps*, *O. collaris*, and *O. hyperborea*), and activity in the cardiac and diaphragm tissue of the high-elevation American pika was significantly greater than that of its lowland sister species, the collared pika (Sheafor 2003). Several genes encode proteins with 3-hydroxyacyl CoA dehydrogenase activity, including *EHHADH*, and measures of 3-hydroxyacyl CoA dehydrogenase activity are often used to indicate relative fatty acid oxidation capacity (Wakil et al. 1954). ... Our molecular evolutionary analyses support the hypotheses of adaptive molecular evolution of *IGF-1* and *EHHADH* in pikas. That is, our examination of interspecific and intraspecific genetic variation of both the *IGF-1* and *EHHADH* loci suggests a pattern consistent with positive selection that could not be explained by neutral evolution. ...

An in-text citation from this source would look like: Pikas demonstrate adaptation to low oxygen environments (hypoxia) that allow survival of the animals at altitudes where oxygen is limited (Rankin et al. 2017), and the citation would look like:

Rankin, A.M., K.E. Galbreath, and K.C. Teeter. 2017. Signatures of adaptive molecular evolution in American pikas (*Ochotona princeps*). *Journal of Mammalogy* **98**: 168-174. doi: 10.1093/jmammal/gyx059

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From Varner and Dearing (2014):

Anthropogenic climate change is occurring at an unprecedented rate and is already dramatically affecting the abundance and diversity of species worldwide (Parmesan 2006). For mammals, rapid and pronounced responses have been documented in community structure (Rowe et al. 2011), phenology (Ozgul et al. 2010), population dynamics (Kausrud et al. 2008), and species distributions, including range retractions (Moritz et al. 2008), population declines, and localized extinctions (Cahill et al. 2013). Across many taxa, habitat specialists are suffering particular declines (e.g., Warren et al. 2001; Jiguet et al. 2007; Rowe et al. 2011), presumably because they are less flexible than generalists in adapting to atypical climates or to the changing availability or quality of food resources. Indeed, altered food availability is the most common mechanism of climate-mediated extinctions or population declines (Cahill et al. 2013). Alpine and arctic specialists may be particularly vulnerable to climate change because, in addition to having restricted ranges, they are often also sensitive to warm temperatures (Parmesan 2006). ...

Despite an apparent reliance on cold climates (Hafner 1993) and a documented sensitivity to aspects of climate (Beever et al. 2011), pikas have existed near sea level in the Columbia River Gorge (CRG) in Oregon and Washington for more than a century (Horsfall 1925; Simpson 2009). This population persists well outside of the previously assumed climatic niche for pikas, in terms of both temperature and precipitation patterns (Simpson 2009). Although the existence of pikas in the CRG was deemed “worthy of further study” 15 years ago (Verts and Carraway 1998 p. 128), only 1 study to date has examined their persistence in this unusual habitat (Simpson 2009). This study documented that the CRG is well outside of the climate niche predicted by previous research (e.g., Hafner 1993), but it did not elucidate how pikas persist in this seemingly unsuitable climate.

A unique feature of pika habitat in the CRG is its high degree of moss cover (Simpson 2001). Moss is typically nutritionally deficient and is therefore not extensively consumed by herbivores (Richardson 1981; Prins 1982). However, in this habitat, moss could potentially be an abundant resource that requires little energy to harvest. Given the unusual distribution and abundance of food resources for pikas in this environment, we hypothesized that utilizing an atypical food resource (i.e., moss) may allow, at least in part, pika persistence in this climate, which is unusual relative to the geographic range of this species. Furthermore, if pikas could consume moss, we hypothesized that they would be released from constructing large winter food caches during the warmest times of year. ...

We investigated behavioral and dietary plasticity of an alpine habitat specialist, *O. princeps*, in an atypical temperate rain-forest climate. Pikas are dietary generalists (Dearing 1996a): they typically consume a variety of graminoids and forbs present in alpine meadows (Huntly et al. 1986; Dearing 1996a), and they are unable to specialize on a diet high in tannins (Dearing 1996b). Here, we demonstrate that some pikas are capable of incorporating large amounts of bryophytes into their diet in the low-elevation habitat of the CRG.

To our knowledge, this study represents the highest degree of voluntary moss consumption reported for a mammalian herbivore in the wild. Few herbivores consume mosses because mosses are high in fiber, low in nitrogen, and low in digestible energy (Richardson 1981; Prins 1982). Some mammals are known to incorporate moss into their winter diets, particularly in winter in the Arctic, when little other forage is available, but few to the degree that we observe in CRG pikas. ...

An in-text citation from this source would look like: A lower elevation population of pika found at warmer temperatures relies on a diet of moss despite the low nutritional value moss provides (Varner and Dearing 2014), and the citation would look like:

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Varner, J., and M.D. Dearing. 2014. Dietary plasticity in pikas as a strategy for atypical resource landscapes. *Journal of Mammalogy* **95**: 72-81 doi: 10.1644/13-MAMM-A-099.1

From Kohl et al. (2016):

Associations between complex communities of gut microbes and animal hosts can have profound influences on ecology and evolution (McFall-Ngai et al., 2013). For instance, microbial communities can affect host nutrition, immune function, and even behaviour (Ezenwa, Gerardo, Inouye, Medina, & Xavier, 2012; Kohl & Carey, 2016; McFall-Ngai et al., 2013). ... Within a host species, populations may exhibit differential microbial communities as a result of a numerous factors. ... In an evolutionary sense, host genetics may contribute to microbial community structure in such a way that more closely related species would harbour more similar gut microbial communities (Brucker & Bordenstein, 2012a, 2012b). This congruence between host evolutionary history and similarities in microbial communities has been termed “phylosymbiosis” (Brucker & Bordenstein, 2012a, 2012b). While phylosymbiosis has been demonstrated across host species under laboratory-controlled settings (Brooks, Kohl, Brucker, van Opstal, & Bordenstein, 2016), its prevalence among animals under natural conditions is unclear and has not been investigated across populations of the same species.

One of the strongest determinants of gut microbial community structure is diet. In mice, dietary effects overwhelm genetic effects in sculpting microbial diversity (Carmody et al., 2015). Across mammalian feeding groups, herbivores, omnivores and carnivores harbour distinct microbial communities with specialized functions for their given diets (Ley et al., 2008; Muegge et al., 2011). Associations with gut microbes are particularly important for mammalian herbivores, thereby allowing them to consume high-fibre plant material often laden with toxic compounds (Kohl, Weiss, Cox, Dale, & Dearing, 2014; Mackie, 2002). Understanding the specific microbial taxa involved in permitting herbivores to consume novel food sources has been well studied in agricultural ruminants, but far less so in other free-living species. ...

In terms of diet, pikas are herbivorous and feed largely on a variety of grasses and forbs (Dearing, 1997). Pikas collect plants from alpine meadows and store them in haypiles within barren talus fields. Through these actions, pikas alter the plant community structure of alpine meadows (Huntly, 1987) and nutrient concentrations in talus fields (Aho, Huntly, Moen, & Oksanen, 1998). In some locations, pikas exhibit remarkable dietary flexibility. For example, the diet of populations of pikas in the Columbia River Gorge of Oregon, USA is composed of roughly 60% moss (Varner & Dearing, 2014). Feeding on moss presents extreme nutritive challenges, as it contains roughly double the fibre and significantly less nitrogen than typical food sources (Varner & Dearing, 2014). Remarkably, pikas in the Columbia River Gorge exhibit the highest moss intakes documented for any wild mammalian species (Varner & Dearing, 2014). Thus, populations of pikas in the Columbia River Gorge may harbour distinct microbial communities that help them to cope with these nutritive challenges. ...

Pikas from Oregon, especially those from sites where animals are known to feed on moss, exhibit the highest relative abundance of *Melainabacteria* for any mammal studied to date. This microbial phylum is present in the guts of herbivorous Asian pika species (Li, Li, Beasley et al., 2016), although at a lower abundance (<1% of the community). We hypothesize that these bacteria may be instrumental in allowing Oregon pikas to feed on high amounts of moss. It would be interesting to inventory the microbial communities of other herbivores that incorporate substantial amounts of moss into their diets, such as Svalbard reindeer (Bjrkvoll, Pedersen, Hytteborn, Jónsdóttir, & Langvatn, 2009) or brown lemmings (Batzli & Pitelka, 1983). ...

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An in-text citation from this source would look like: The gut bacteria sampled in pika eating high quantities of moss has a different community structure than from pika eating a traditional diet of grasses and forbs (Kohl et al. 2018), and the citation would look like:

Kohl, K.D., J. Varner, J.L. Wilkening, and M.D. Dearing. 2018. Gut microbial communities of American pikas (*Ochotona princeps*): Evidence for phylosymbiosis and adaptations to novel diets. *Journal of Animal Ecology* **87**: 323-330. doi: 10.1111/1365-2656.12692