Too hot to trot? Evaluating the effects of wildfire on patterns of occupancy and abundance for a climate-sensitive habitat specialist

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Abstract. Wildfires are increasing in frequency and severity as a result of climate change in many ecosystems; however, effects of altered disturbance regimes on wildlife remain poorly quantified. Here, we leverage an unexpected opportunity to investigate how fire affects the occupancy and abundance of a climate-sensitive habitat specialist, the American pika (*Ochotona princeps*). We determine the effects of a fire on microclimates within talus and explore habitat factors promoting persistence and abundance in fire-affected habitat. During the fire, temperatures in talus interstices remained below 19°C, suggesting that animals could have survived *in situ*. Within 2 years, pikas were widely distributed throughout burned areas and did not appear to be physiologically stressed at severely burned sites. Furthermore, pika densities were better predicted by topographic variables known to affect this species than by metrics of fire severity. This widespread distribution may reflect quick vegetation recovery and the fact that the fire did not alter the talus microclimates in the following years. Together, these results highlight the value of talus as a thermal refuge for small animals during and after fire. They also underscore the importance of further study in individual species' responses to typical and altered disturbance regimes.

Additional keywords: *Ochotona*, pika, talus, thermal refuge, wildlife.

Introduction

Climate change has already profoundly affected species distributions in terrestrial ecosystems (Parmesan 2006), but evidence suggests that indirect effects of climate change, such as changes in interspecific interactions (Mason *et al.* 2014), food availability (Cahill *et al.* 2012) or invasion of exotic species (Mooney and Hobbs 2000) may be more frequent drivers of distribution shifts than the direct effects of climate change (e.g. altered temperature and precipitation). One aspect of climate change that is particularly under-studied with regard to effects on species distributions is altered fire regimes. Globally, wildfires have increased in both frequency and severity in recent decades (Williams *et al.* 2001; Westerling *et al.* 2006; Flannigan *et al.* 2009). These trends are likely due to more severe fire weather (i.e. warmer, drier summers) and earlier snowmelt, and they appear to be particularly significant in mountainous ecoregions (Dale *et al.* 2001; Dennison *et al.* 2014; Stavros *et al.* 2014).

Severe fires profoundly alter habitat for wildlife through changes in resource availability (e.g. via soil nutrients or plant communities) and local microclimates (e.g. through changes in albedo and loss of forest canopy cover; Agee 1996). However, relatively little evidence exists regarding the potential synergistic effects of altered fire regimes and climate change on species distributions (Driscoll *et al.* 2010). Indeed, it is difficult to directly study how fire affects animal distributions in the context of climate change due to logistical and ethical constraints and because these effects are complex (Roberts *et al.* 2008; Engstrom 2010). Furthermore, large, severe fires predicted under climate change may also increase landscape heterogeneity, complicating analyses of habitat suitability (Cansler and McKenzie 2014).

It is difficult to make generalisations about wildlife responses to fire because these responses depend on both the degree of specialisation of the species in diet or habitat preferences and on the characteristics of the fire (i.e. intensity, size or season in which the fire occurs; Smucker *et al.* 2005; Wiebe 2014). Trade-offs between habitat requirements and the functional traits or diet requirements of a species may further complicate responses to fire. For example, cavity-nesting birds often benefit from the habitat structure created by high-severity fire, but the invertebrates upon which these species depend for food are more widely available after low-severity fire or in unburned areas (Nappi *et al.* 2010; Azeria *et al.* 2011). A species may also respond differently to fires in different seasons as a result of its reproductive phenology or other short-term vulnerabilities (Engstrom 2010).

Despite these difficulties, a few generalisations have emerged from the literature. For example, evidence suggests that species that prefer open habitat are likely to have positive responses to fire (i.e. higher abundance in burned areas compared with unburned reference areas; Fontaine and Kennedy 2012). Some species that rely on short-term sources of food caused by fire (e.g. early colonising herbaceous species or conifer seeds; Engstrom 2010) are also likely to exhibit positive responses, including cavity-nesting birds that depend on dead or dying trees (Smucker *et al.* 2005; Wiebe 2014). Similarly, some bats may benefit from open habitat and abundant flying insects (Perry 2011). In contrast, species that prefer mesic, closed-canopy conditions tend to exhibit negative responses to fire (i.e. higher abundance in unburned reference areas compared with burned areas; Fontaine and Kennedy 2012). For example, fire may be driving declines in small mammal populations of Australian savanna habitat because ground cover removal increases predation risk (Oakwood 2000; Radford 2012).

High-severity fires also appear to favour species with generalist habitat preferences in both Argentina (Albanesi *et al.* 2014) and North America (Fontaine and Kennedy 2012). Similarly, negative responses correlate with high-elevation distributions and poor dispersal abilities (Panzer 2002). As a result, altered disturbance regimes may be particularly deleterious for high-elevation habitat specialists, which necessarily have strict requirements and may already be more susceptible to climate change than lowland generalist species (Rowe *et al.* 2011).

Here, we leverage an unexpected opportunity to investigate the effect of a severe wildfire on a climate-sensitive, mammalian habitat specialist, namely the American pika (*Ochotona princeps* Richardson). Pikas are ideal for investigating responses to climate change and disturbance because they are typically restricted to high-elevation talus (i.e. rock slides and boulder fields) and lava flows in mountain ranges of western North America (although several populations persist near sea level, particularly along the Pacific coast; e.g. Henry *et al.* 2012*a*; Varner and Dearing 2014*a*). This distribution is thought to be limited by susceptibility to heat stress (due to a narrow margin between resting body temperature and lethal body temperature; MacArthur and Wang 1974; Smith 1974*b*) and a limited ability to disperse between patches of talus (Smith 1974*a*; Smith and Ivins 1983; Henry *et al.* 2012*b*), especially in warm, dry contexts (Castillo *et al.* 2014).

The factors that limit pika distribution may also render them susceptible to climate change (Smith *et al.* 2004). Indeed, localised extinctions linked to climate have already been documented in many parts of the species' range (Beever *et al.* 2011; Erb *et al.* 2011; Stewart and Wright 2012; Stewart *et al.* 2015), although the effects of climate on pika distribution appear to be complex and locality specific (Millar and Westfall 2010; Jeffress *et al.* 2013). Finally, the foraging strategy of pikas may affect their vulnerability. Because they do not hibernate, pikas spend the short alpine growing season collecting and storing vegetation in food caches called haypiles, which sustain them over the winter (Dearing 1997). Warmer summer temperatures due to climate change may limit foraging, resulting in low-quality food caches for winter (Ray *et al.* 2009). Furthermore, because snow provides pikas with essential insulation against winter temperature minima, reduced snowpack may expose the animals to more extreme winter temperatures (Smith 1978; Beever *et al.* 2010) and affect vegetation availability or quality (Wilkening *et al.* 2011).

Despite widespread recent interest in climate-mediated pika extirpations, very little is known about how this species responds to disturbances like wildfire or whether altered disturbance regimes will heighten the species' susceptibility to climate change. Much of our knowledge about habitat recolonisation comes from meta-population studies where pikas were experimentally removed but resource availability was not manipulated (e.g. Tapper 1973). In contrast, pika recolonisation of Mt St Helens in the years following its 1980 eruption has also been documented (MacMahon *et al.* 1989; Crisafulli *et al.* 2005); however, this extreme event provides little information about responses to more common and less severe disturbances. A better understanding of how this species will respond to disturbance is particularly timely because the current distribution of pikas in western North America overlaps strikingly with areas that are predicted to experience more frequent and severe wildfires as a result of climate change (see fig. 4 in Westerling *et al.* 2006).

We had a unique opportunity to investigate the effect of a wildfire on microclimate refugia and the response of this species to disturbance when a severe forest fire burned many of the instrumented study sites (i.e. talus patches) where we had recently conducted occupancy surveys for *O. princeps* in the Mt Hood National Forest of western North America. In the present study, we addressed three aims. First, we determined how fire affected biologically relevant microclimates during and after the disturbance. We hypothesised that severely burned sites would experience more thermally stressful temperatures than unburned sites. Second, we explored habitat factors that permit populations to rebound in disturbed habitat. Specifically, we examined trends in pika abundance at 24 study sites over 3 years following the fire. We also used a non-invasive measure of physiological stress to assess the health of individual animals. We used abundance and physiological stress as more sensitive predictors of habitat suitability than occupancy because they provide a more detailed and mechanistic understanding of how this species is affected by the disturbance (Millspaugh and Washburn 2004; Beever *et al.* 2013). Finally, to assess how fire affects pika population sizes in this region, we used an information theoretic framework to evaluate competing hypotheses
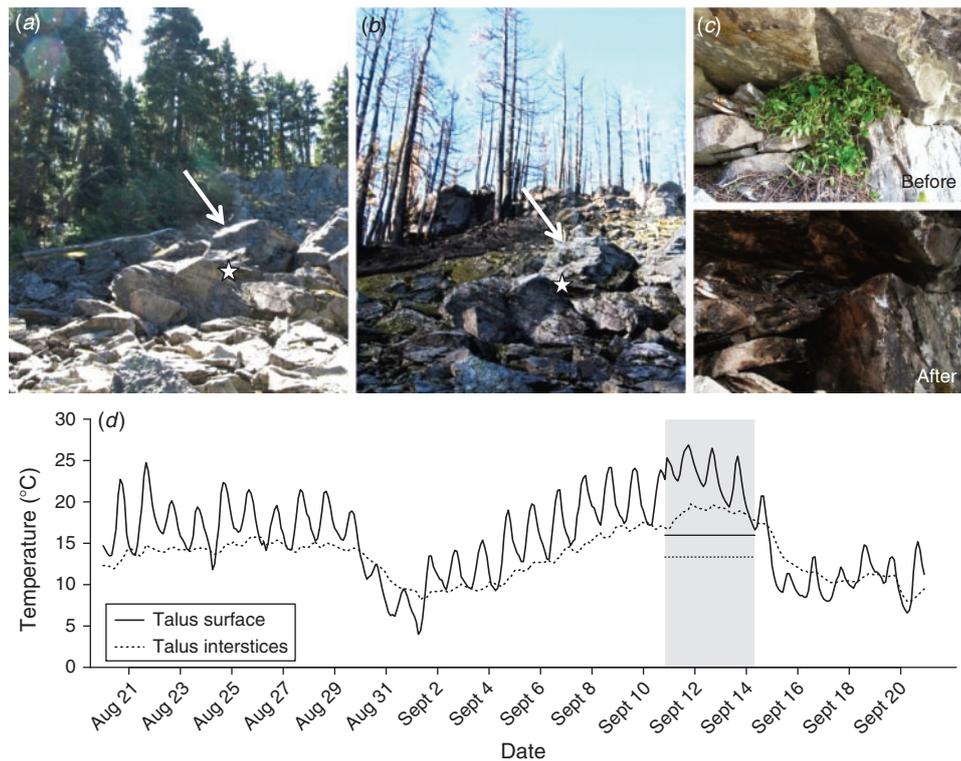
Fig. 1. Fire impacts at a severely burned site. Photographs taken in July (*a*) 2011 and (*b*) 2012. Arrows mark temperature datalogger location. Stars mark a pika haypile shown in (*c*) that burned in the fire. (*d*) Temperatures before, during and after the fire, recorded by the dataloggers in (*a*) and (*b*). Solid lines represent surface temperatures and dotted lines represent temperatures approximately 1 m down into the talus interstices. The grey shaded area indicates fire duration at this site, determined from infrared heat source images. Within this shaded area, horizontal lines represent average temperatures before the fire at the talus surface (solid) and talus interstices (dashed).

regarding whether pika densities are mediated more strongly by topographic factors known to affect this species or by metrics of fire severity and resource availability.

Methods

Study area and the Dollar Lake fire

In August 2011, before the fire, we collected data on pika behaviour and habitat on the north face of Mt Hood (OR, USA). Our aim was to compare talus microclimates and thermoregulatory behaviour with nearby low-elevation habitat in the Columbia River Gorge; thus, vegetation data collected before the fire are limited. In mid-August 2011, we searched for pikas at nine patches of talus (hereafter 'sites'), each separated from other sites by at least 25 m. Sites ranged in elevation from 900 m in a mixed-conifer forest dominated by western red cedar, Douglas fir and western hemlock to nearly 1700 m in a subalpine forest dominated by several species of huckleberry, Sitka mountain ash and subalpine fir. At each of three sites, two temperature dataloggers (HOBO UA-001-08 Pendant; Onset Computer Corporation, Bourne, MA, USA) were deployed to measure pika-relevant microclimates. One datalogger was placed near the surface, protected from direct solar radiation by multiple rocks. A second datalogger was threaded into the talus

interstices approximately 1 m below the surface logger. Each datalogger recorded temperatures every 2 h. Finally, at one site, we trapped and tagged four adult pikas, collected fresh faecal samples and observed the behaviour of the pikas.

One week after completing fieldwork in 2011, a lighting strike ignited the Dollar Lake Fire. From 26 August to 16 September 2011, this fire burned approximately 2430 ha across the north face of Mt Hood and was typical for the fire regime of the western Cascade region. In this area, wildfires are infrequent (approximately every 300–400 years), high severity and stand replacing; however, as these fires reach the subalpine zone, they become highly patchy in nature (due to the variable nature of interfaces between the forest and rocks, meadows and patches of persistent snow; Agee 1996). Within this mosaic of burned habitat, the fire reached four of the nine sites where we had previously surveyed for pikas, including two of three sites where we had placed temperature loggers (Fig. 1*a–c*). Therefore, these sensors measured temperatures at the talus surface and interstitial space every 2 h before, during and after the fire.

We learned of the fire in June 2012, approximately 9 months after the disturbance. In early August 2012, we surveyed 18 sites for pika abundance, including the nine sites that we visited before the fire (Table 1). Although we could not determine whether the nine new sites were occupied before the fire, all sites

Table 1.   Pika occupancy and abundance, before and in the 3 years following the Dollar Lake Fire

NA, not applicable

	2011 pre-fire	2012 summer	2013 spring	2013 autumn	2014 spring	2014 autumn
Years since fire	0	1	2	2	3	3
No. sites sampled	9	18	24	24	23	24
Unburned	9	5	8	8	7	8
Moderate burn	NA	6	8	8	8	8
Severe burn	NA	7	8	8	8	8
Occupancy[A]	89%	83%	83%	96%	83%	96%
Unburned	89%	100%	100%	100%	85.7%	87.5%
Moderate burn	NA	100%	100%	100%	100%	100%
Severe burn	NA	57.1%	50%	87.5%	62.5%	100%
Abundance[B]	3.2 ± 1.2	3.5 ± 0.6	2.7 ± 0.4	3.9 ± 0.6	2.2 ± 0.3	4.0 ± 0.5
Unburned	3.2 ± 1.2	3.8 ± 1.2	3.0 ± 0.5	4.1 ± 1.1	2.3 ± 0.7	3.9 ± 0.9
Moderate burn	NA	4.7 ± 0.8	3.1 ± 0.6	5.8 ± 0.9	2.8 ± 0.3	6.1 ± 0.6
Severe burn	NA	1.3 ± 0.3	1.0 ± 0.0	1.4 ± 0.3	1.5 ± 0.5	2.1 ± 0.4

[A]All unoccupied sites had evidence of past occupancy (e.g. old haypiles or scat).
[B]Mean $\pm$ s.e. abundance of pikas at occupied sites.

had evidence of pikas (i.e. characteristic faecal pellets, haypiles or both), suggesting recent occupancy. However, at this time we could not distinguish between sites where pikas survived the fire *in situ* versus sites that were recolonised during the summer of 2012. To monitor this discontinuous recovery process, we sampled each site twice in each of 2013 and 2014. We also added six additional sites in 2013 for a total of 24 sites (Table 1). At each site, our 'spring' sampling period took place at an ecologically equivalent time for the species: as soon as possible after snowmelt, which varied between late May at low elevations to mid-July at high elevations. In contrast, our 'autumn' sampling period took place at all sites on equivalent Julian dates: 19–27 August 2013 and 17–27 August 2014.

Classification of burn severity

Fire severity was assessed in 2012 at 10 locations along the perimeter of the talus at each site using a rubric that assesses severity in four ecosystem components: substrate (soil and litter), herbaceous plants (non-woody plants such as graminoids and forbs), shrubs (woody plants without a central trunk) and trees (woody plants with a central trunk; Keane 2007). We then averaged these four metrics to capture overall severity. We also used a laser rangefinder to estimate the percentage of the linear patch perimeter that was burned (i.e. where we found evidence of burned vegetation within 1 m of the talus boundary). Finally, we recorded the presence and extent of white ashes along the burned perimeter, which indicate high fire temperatures ($>500°C$; Keeley 2009). We used this information to classify sites into three categories of burn severity: severely burned, moderately burned and unburned (see Fig. S1 available as Supplementary Material to this paper). Importantly, average patch size did not differ between these burn severity categories (ANOVA: $F_{1,22} = 0.6$, $P = 0.46$), indicating that the fire did not differentially burn smaller talus patches.

Effects of fire on microclimates

During the fire, temperatures at the talus surface and in talus interstices were recorded by dataloggers placed at three sites in 2011. None of these sensors malfunctioned during the fire.

The dates at which the fire reached each site were determined from fire progression maps and infrared heat maps available online (InciWeb Incident Management System 2011), which indicated zones of intense and scattered heat throughout the fire. To determine temperatures that pikas may have experienced during the fire, we inspected temperature data during the period in which our instrumented sites were zones of intense heat.

After the fire, we hypothesised that pika-relevant microclimates would be most thermally stressful at severely burned sites, either through loss of canopy cover (and therefore shade) or through alterations in surface reflectivity (i.e. darker rocks and soil that would absorb more heat). Alternatively, the fire could have preferentially burned the sites that were naturally the hottest and driest, which may also result in warmer temperatures at the most severely burned sites. To test our hypotheses, we deployed a temperature datalogger (HOBO UA-008; Onset Computer Corporation) in the top 20 cm of the talus at each site in the sampling season in which that site was first surveyed. The sensor was shielded from direct sunlight by multiple rocks (following Varner and Dearing 2014b) and was always placed within 5 m of the lower talus margin, which typically experiences cold air pooling (Millar and Westfall 2010) and therefore often has higher pika densities (Tapper 1973). These sensors were programmed to record temperatures every 2 h. For the purpose of temperature analyses, we combined unburned and moderately burned sites because moderately burned sites did not experience significant changes in either canopy cover or surface reflectivity. Furthermore, moderate-intensity fires typically do not have significant effects on post-fire soil microclimates (Agee 1996).

Habitat suitability for pikas and other talus-dwelling animals may be affected by both heat stress and cold stress, and these stresses can each act acutely or chronically (Beever *et al.* 2010, 2011). Thus, at each site, we calculated several previously validated metrics of thermal stress for pikas. First, we assessed chronic cold stress by estimating snowpack duration and average winter minimum temperatures at each site. Reduced snowpack (extent and duration) can result in lower winter minimum temperatures (Smith 1978; Beever *et al.* 2011). Snowpack

duration was calculated as the number of days in which diel surface temperature fluctuations were <2°C (Lundquist and Lott 2008). We also quantified acute cold stress by counting the number of days during winter in which minimum temperatures were less than −5°C (Beever *et al.* 2010).

Snowpack persisted at the highest elevation sites until mid-July. To avoid confounding the effects of persistent snowpack on summer temperatures, we indexed chronic summer heat stress as the average August temperature, which is biologically relevant for pikas because it is: (1) the only month that was snow free at all sites; (2) the hottest month of the year; and (3) the time at which pikas are most active constructing their winter food caches (Smith 1974*b*; Dearing 1997). We indexed acute heat stress by the number of days each year that surface temperatures exceeded 28°C. Finally, we quantified the August diel temperature range (i.e. daily maximum–daily minimum), which is an indicator of both acute and chronic heat stress. This variable has only recently been considered in analyses related to pikas and climate change (Wilkening *et al.* 2015); however, both climate change (Braganza *et al.* 2004) and wildfire (Agee 1996) are known to affect diel temperature range, and other species appear to be responding to this increased temperature variability (Walther *et al.* 2002).

Because the fire burned most severely at intermediate elevations, severely burned sites are non-randomly associated with elevation. To control for the inevitable effects of elevation and interannual variation on microclimate temperatures, each of our response variables was modelled as a function of elevation, year and burn status (i.e. severely burned vs moderately burned and unburned) using multiple linear regression. We then used the *step* function in R (v.3.0.2 for Mac OSX) to eliminate non-significant main effects and interactions (R Core Team 2014).

Trends in pika occupancy and abundance

In each sampling season (Table 1), we comprehensively searched each site for pika sign along line transects. Transects followed elevational contours and were spaced 15 m apart. To enumerate individuals, we recorded locations of unequivocal evidence of pikas (e.g. sightings, vocalisations or active haypiles). Multiple pieces of evidence separated by <20 m were considered to be the same individual unless two animals were calling or visible at the same time. Surveys were conducted in the morning (0600–1000 hours) when temperatures are cool and pikas are most active. At sites where no fresh pika sign was found, we exhaustively resurveyed with greater sampling density (i.e. spacing transects 5–7 m apart) to confirm lack of occupancy (following Beever *et al.* 2011; Erb *et al.* 2011). The amount of talus habitat with rock diameters suitable for pikas (0.2–1.0 m; Tyser 1980) was quantified with a laser rangefinder in the field and pika density was defined as the number of individuals detected per 20-m diameter home range of appropriate habitat. Although we did not explicitly conduct detectability surveys, detectability for this species is reliably high (>0.9) when sampling occurs at appropriate times of day and season (Beever *et al.* 2008, 2011, 2013; Rodhouse *et al.* 2010; Erb *et al.* 2011; Jeffress *et al.* 2013).

To estimate forage availability for pikas, we quantified aboveground edible biomass and species richness of herbaceous plant material in five 1-m^2 quadrats per site, which were marked with rebar for repeated sampling. For forbs, shrubs and trees, we counted the number of stems or branches of each plant that would be accessible to pikas (i.e. within 15 cm of the ground). For graminoids, mosses and cushion plants, we estimated the percentage cover of that species within the quadrat. The average biomass of each species was determined from samples ($n = 4$–10) collected in the same way that the abundance of that species was counted (i.e. by the stem for herbaceous plants, branch for shrubs and trees or area of cover for graminoids, mosses and cushion plants). Samples were also collected in the same way that a pika would consume the vegetation, as determined by previous behavioural observations (e.g. only leaves were collected from shrubs and trees; Varner and Dearing 2014*a*). To allow repeated sampling of quadrats and avoid influencing vegetation recovery at burned sites, we harvested plant samples from outside of quadrats, primarily at unburned sites. In any given season of sampling, we did not observe any qualitative differences in the average stature of several herbaceous plant species in burned areas versus those outside of the burn.

We analysed trends in pika abundance, density and vegetation characteristics (biomass and species richness) with repeated-measures ANOVA. In each analysis, we used burn severity and sampling season as main effects and year as a repeated measure on each site. This analysis only included sites that were sampled in all five seasons ($n = 17$ sites).

Stress hormone analysis

To assess the health of individual pikas, we collected fresh faecal pellets at 11 occupied sites during the autumn sampling of 2013 ($n = 19$ samples, from five severely burned sites and six unburned or moderately burned sites). Each sample ($n = 19$) was collected from a separate home range; thus, samples likely came from distinct individuals. Samples were kept on ice in the field and were transferred to a −80°C freezer within 2 weeks of collection.

Faecal glucocorticoid metabolite (GCM) levels have been previously validated as a biologically relevant measure of chronic physiological stress in pikas (Wilkening *et al.* 2013; Wilkening 2014) and environmental samples collected within the same ecoregion in the same sampling season can be used reliably for comparisons (Wilkening *et al.* 2015). In our analysis, we followed previously validated protocols (Wilkening *et al.* 2013) to measure GCM in fresh faeces collected in August 2013 and in four faecal samples collected from trapped individuals in August 2011 before the fire. We used a commercially available corticosterone enzyme immunoassay kit (no. K014-H1; Arbor Assay Design, Ann Arbor, MI, USA) according to the manufacturer's instructions. Final concentrations of faecal GCM were expressed as ng GCM per g faeces.

One-way ANOVA was used to test for differences in GCM concentration between severely burned sites, unburned or moderately burned sites and samples collected before the fire. Prior to analysis, data were checked for outliers and a Fligner–Killeen test was conducted to check for homogeneity of variances.

Modelling pika density

At each site, we also collected biophysical and topographic information known to affect habitat suitability for pikas.

Table 2. Predictor variables used in modelling analysis

	Predictor variable	Description (units)
Vegetation availability	veg	Average biomass of vegetation in quadrats (g m^{-2})
	veg_rich	Average plant species richness in quadrats (n)
	moss[A]	Talus area covered in moss (%)
Topographic predictors	insol	Estimated potential solar insolation, sine(slope angle) × cosine(aspect)
	crevice	Deepest crevice in talus (cm)
	elevation	Site elevation (m above sea level)
Fire severity predictors	burncategory	Categorical classification of burn severity (levels = 'severe' or 'unburned or moderately burned')
	fireseverity	Average fire severity (quantified by rubric scores at the level of substrate, herbaceous cover, shrub cover and tree canopy)
	perim_burned	Linear talus patch perimeter burned (%)

[A]Talus moss cover may also reflect microclimates (Varner and Dearing 2014*b*).

We estimated potential solar exposure at each site using a previously described insolation index (Jeffress *et al.* 2013). The aspect and slope angle of each site were measured using a compass and clinometer, and potential solar insolation was calculated as sine(slope) × cosine(aspect). This index ranges from −1 to 1, where 1 indicates steeper north-facing slopes with little solar exposure and −1 indicates steep south-facing slopes with high exposure (Jeffress *et al.* 2013). Talus depth is notoriously difficult to estimate (Rodhouse *et al.* 2010), but observers visually estimated the deepest crevice encountered at each site (i.e. the vertical distance between the lowest rock at the bottom of the crevice and the highest rock at the crevice opening). We also visually estimated percentage moss cover at each site because mosses are a food resource for pikas in this region (Varner and Dearing 2014*a*) and may also mediate microclimates (Varner and Dearing 2014*b*).

To evaluate the relative contributions of these traditional metrics of habitat suitability compared with the effect of the fire on pika density, we used an information theoretic framework to evaluate a suite of models including combinations of uncorrelated ($r < 0.6$) predictor variables (Table S1). Predictor variables were determined *a priori* and included metrics of vegetation availability, fire severity and topographic variables known to affect pikas (Table 2). All continuous predictors were centred and scaled by their standard deviation, which improves computation and simplifies the interpretation of model intercepts (Gelman and Hill 2007). We modelled pika density with linear regression in R (R Core Team 2014) using a *glm*. For each model, we calculated Akaike's Information Criterion corrected for small sample size (AIC$_c$; Burnham and Anderson 2002). We considered models with ΔAIC$_c$ <2 to have substantial support (Burnham and Anderson 2002).

Results

Effects of fire on microclimates

Serendipitously, of the three sites that we outfitted with data-loggers before the fire in 2011, one site was unburned, one was moderately burned and one was severely burned. Elevated temperatures were observed during the fire at the severely burned site only. The timing of the elevated talus temperatures (Fig. 1*d*) corresponded perfectly with infrared heat maps indicating that this site was a part of an intense heat zone from 11 to

13 September 2011, with the area cooling to isolated heat sources by 14 September 2011 (InciWeb Incident Management System 2011). During the fire, daily maxima at the talus surface were similar to temperatures observed before the fire; however, daily minima were elevated by 10–15°C during the fire relative to the daily minima before the fire. Similarly, sub-talus temperatures ranged from 18–19°C during the fire, compared with 7–14°C immediately before and after (Fig. 1*d*).

Following the fire, severely burned sites experienced fewer days of snowpack ($F_{4,36} = 69.0$, elevation $P = 0.003$, burn status $P = 0.001$, year $P < 0.001$, elevation × year $P = 0.003$; Fig. 2*a*). However, even when accounting for elevation, we found no evidence that reduced snowpack translated into increased cold stress in the talus at severely burned sites. Burn status was not significant in explaining variation in winter minimum temperatures ($F_{2,38} = 29.5$, elevation $P < 0.001$, burn status $P = 0.24$, year $P < 0.001$; Fig. 2*b*) or the number of days where temperatures were less than −5°C ($F_{4,36} = 27.8$, elevation $P = 0.002$, burn status $P = 0.24$, year $P < 0.001$, elevation × year $P = 0.002$; Fig. 2*c*).

Similarly, we found little evidence that severely burned sites experienced increased heat stress during the summer. Contrary to our predictions, there was no effect of elevation, year or burn status on August diel temperature range ($F_{7,38} = 0.5$, elevation $P = 0.36$, burn status $P = 0.32$, year $P = 0.66$; Fig. 2*d*). Burn status was a significant predictor of average August temperature; however, the presence of an interaction term with elevation makes this result difficult to interpret ($F_{4,41} = 15.9$, elevation $P < 0.001$, burn status $P = 0.03$, year $P < 0.001$, elevation × burn status $P = 0.04$; Fig. 2*e*). Finally, burn status was not a significant predictor of the number of days where surface temperatures exceeded 28°C ($F_{1,43} = 9.1$, elevation $P = 0.004$, burn status $P = 0.81$, year $P = 0.95$; Fig. 2*d*).

Trends in pika occupancy and abundance

We never resighted any of the four tagged animals after the fire, either at the severely burned site where they were initially tagged (Fig. 1) or at any nearby talus patches. However, pikas were widely distributed after the burn, with overall occupancy rates >83% (Table 1). In fact, overall occupancy rates did not significantly decrease from before the fire (89%) to approximately 10 months after the fire (83%; $\chi^2 = 0$, d.f. = 1, $P = 1.0$; Table 1).
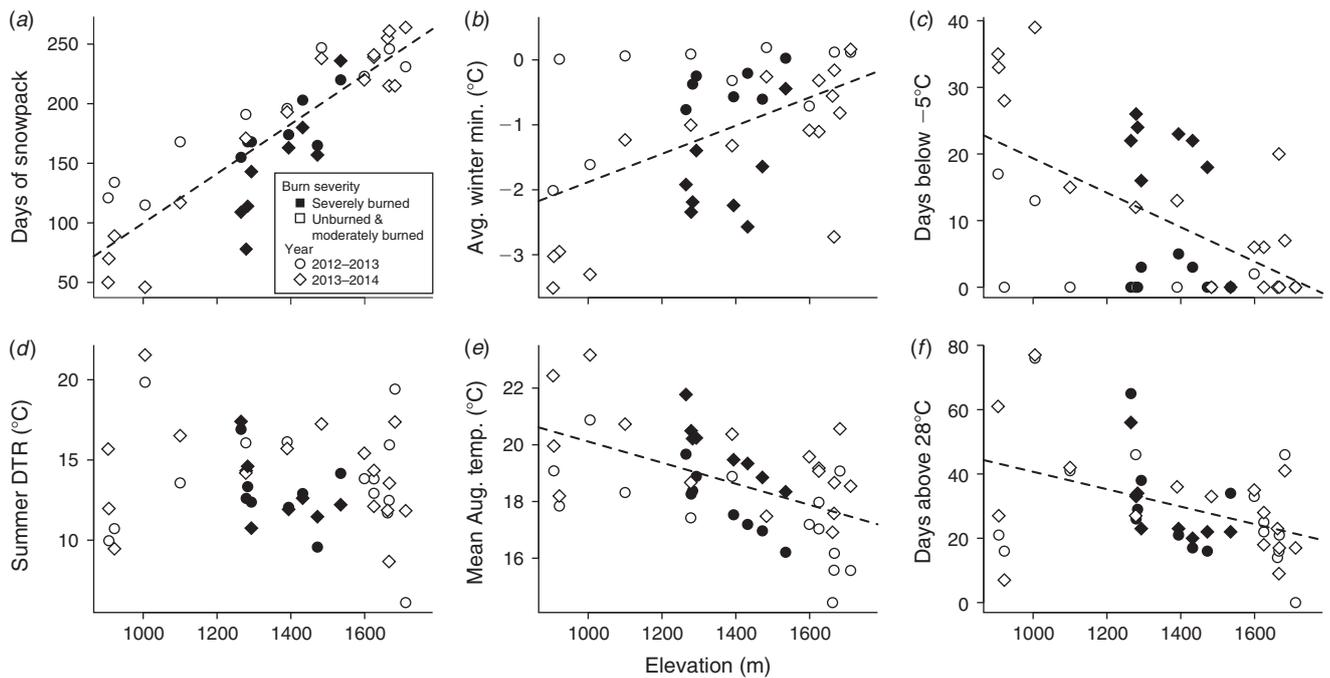
Fig. 2. Metrics of pika thermal stress determined by talus surface sensors following the fire. Thermal stress for pikas was estimated by six metrics (see Methods for details) in 2 years following the fire. Dashed lines indicate significant regressions against elevation using all data points. Chronic cold stress was estimated as (*a*) the number of days of snowpack and (*b*) average daily winter minimum temperature. (*c*) Acute cold stress was estimated as the number of days during which surface temperatures reached −5°C or lower. (*d*) Summer diel temperature range (DTR) is a metric of both chronic and acute heat stress and represents the average difference between each day's maximum and daily minimum temperatures. (*e*) Chronic heat stress was estimated as the mean surface temperature during August. (*f*) Acute heat stress was estimated as the number of days during which surface temperatures exceeded 28°C.

Furthermore, every moderately burned site was occupied in all seasons following the fire, and occupancy rates for severely burned sites recovered from 57.1% (summer 2012) to 87.5% (autumn 2013) in less than 14 months (Table 1). In autumn 2013, only one severely burned site was left unoccupied, and this site had been previously occupied in 2012. Thus, within 2 years of the fire, all sites were occupied by pikas in at least one season of sampling. By autumn 2014, all severely burned sites were occupied, and the only unoccupied site was a small, unburned site at high elevation.

In 2013 and 2014, both pika occupancy and average abundance increased from spring to autumn (Table 1); however, there was no significant effect of sampling period on pika abundance or density (i.e. number of individuals detected per 20-m diameter home range of suitable habitat; time $F_{1,14} = 2.9$, $P = 0.11$; Fig. 3*a*). Across all sampling periods, pika density was lowest at severely burned sites (burn status $F_{2,14} = 9.8$, $P = 0.002$; Fig. 3*a*). Vegetation availability was also lowest at severely burned sites in all sampling periods (burn status $F_{2,14} = 7.0$, $P = 0.008$; time $F_{1,14} = 2.6$, $P = 0.13$; Fig. 3*b*). Severely burned sites had fewer plant species in all sampling periods (burn status $F_{2,14} = 15.2$, $P < 0.001$; Fig. 3*c*): vegetation was typically limited to a few early colonisers (beargrass, *Xerophyllum tenax*; fireweed, *Chamerion angustifolium*; pearly everlasting, *Anaphalis margaritacea*; and white avalanche lily, *Erythronium montanum*). However, species richness increased significantly at these sites over the study (time $F_{1,14} = 32.1$, $P < 0.001$; Fig. 3*c*).

We hypothesised that vegetation availability would predict pika abundance. Indeed, a vegetation threshold of approximately 55 g m^{-2} dry weight vegetation appeared necessary to support a population of pikas with two or more individuals, which represents the minimum size of a reproducing population (Fig. 4; Fig. S2). Above this threshold, there were very few unoccupied sites and vegetation biomass appears to have little impact on pika abundance. In contrast, below this threshold, few sites have two individuals and no sites have more than two individuals (Fig. 4).

Stress hormone analysis

We found no difference in stress hormone concentrations between samples collected before the fire in 2011, at severely burned sites in 2013 and those collected at unburned or moderately burned sites in 2013 (mean (± s.e.) 11.55 ± 1.84, 10.99 ± 0.82 and 12.49 ± 1.49 ng g^{-1} respectively; $F_{2,20} = 0.412$, $P = 0.67$). These values are well within those reported previously across the range of the species (Wilkening *et al.* 2013, 2015; Wilkening 2014).

Modelling pika density

Pika density was best predicted by a single model that included terms for vegetation species richness and percentage moss cover on the talus (Table 3). The next-best models also included terms for vegetation species richness, but these models did not receive substantial support (Table 3). Burn severity predictors did not appear in any of the top models.
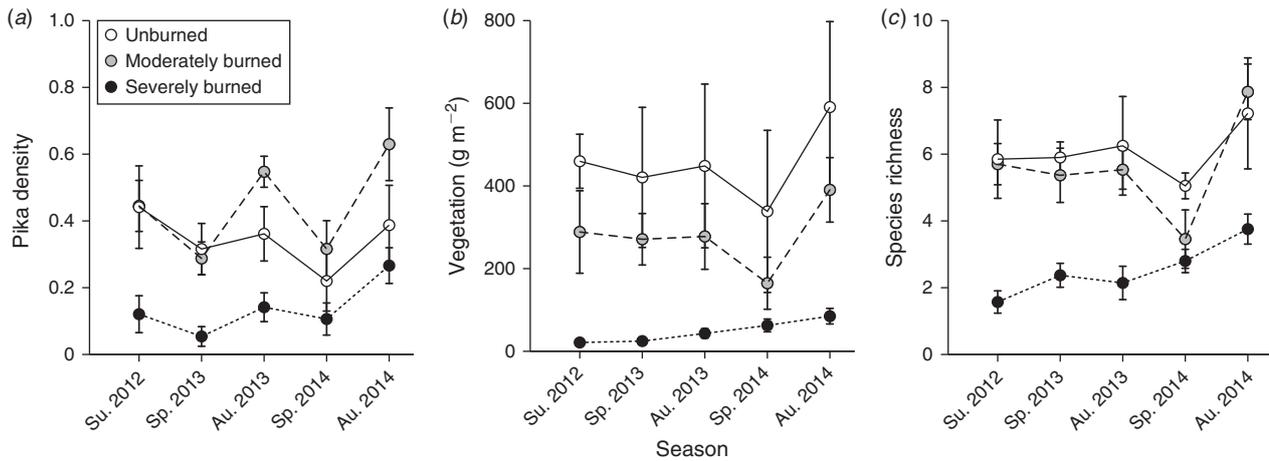
Fig. 3. Trends in pika density and vegetation across sampling periods. Trends in (*a*) pika density (i.e. pikas detected per 20-m diameter home range of talus), (*b*) vegetation biomass per m^2 and (*c*) plant diversity as measured by species richness per m^2. Only sites that were sampled in all five seasons (*n* = 17) are shown. Sampling dates are given in the Methods. Su.: summer; Sp.: spring; Au.: autumn.
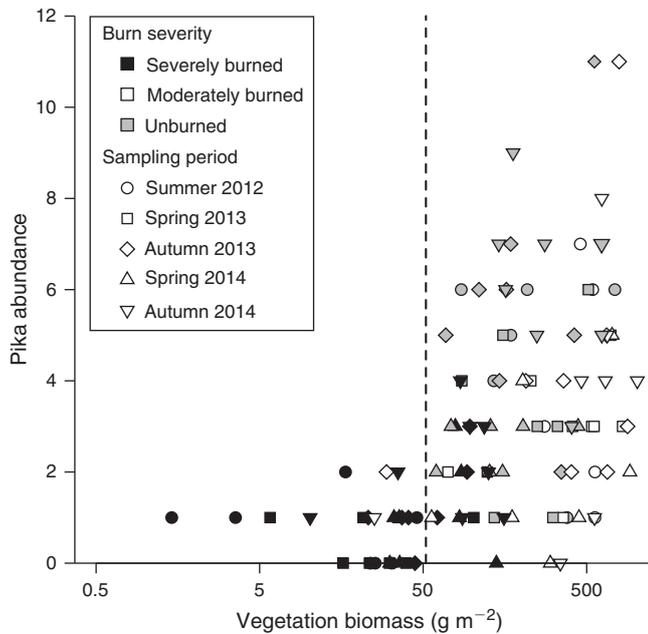

Fig. 4. Vegetation threshold for pika abundance. Shading indicates burn status, shape indicates sampling period. The horizontal axis represents the average vegetation biomass (across five quadrats) at each site in each sampling period. The threshold appears to be approximately 55 g m^{-2} dry weight vegetation.

Table 3. Linear regression results from analysis of pika density at 17 study sites, including the top six models, plus the null model

Only the first model had substantial support. Variables are defined in Table 2. AIC$_c$, Akaike's Information Criterion corrected for small sample size

Model	AIC$_c$	ΔAIC$_c$	K	Model weight
veg_rich + moss	22.1	0	4	0.9823
veg_rich	30.8	8.7	3	0.0129
veg + veg_rich	32.9	10.8	4	0.0045
insol + crevice + moss	40.5	18.4	5	<0.001
burncategory + insol	40.6	18.5	4	<0.001
burncategory	41.3	19.2	3	<0.001
null	60	37.9	2	<0.001

Discussion

Although wildfires are predicted to increase in frequency and severity in many environments as a result of contemporary climate change (e.g. Westerling *et al.* 2006; Dennison *et al.* 2014), relatively little is known about how wildlife will respond to altered fire regimes (Driscoll *et al.* 2010). A better understanding of short- and long-term consequences of fire on habitat quality is needed on a species-by-species basis. In the present study, we investigated the effects of wildfire disturbance on

habitat quality for a sensitive, montane habitat specialist, namely the American pika. Consistent with their high-elevation distribution and specialisation to talus habitat, pikas exhibited an overall negative response to a severe burn (Fig. 3*a*). However, pikas exhibited high occupancy rates in all seasons of sampling, and the severe burn did not leave a lasting effect on pika-relevant microclimates. Together with the results of our modelling analyses, these results suggest that pikas may be relatively resilient to altered disturbance regimes in the future, at least in the Pacific Northwest ecoregion.

To our knowledge, these are also the first data to document the thermal effects of fire in talus, both during the fire and for 3 years following the fire. During the fire, temperatures in the talus were very different from typical patterns in soil, which have been well documented (Agee 1973; Swezy and Agee 1991). Although temperatures in the burrows of small mammals may exceed 50°C for many hours (Lawrence 1966), talus interstitial temperatures approximately 5 m from the burned perimeter remained between 18 and 19°C during the fire (Fig. 1*d*) and even temperatures at the talus surface at this location rarely reached 27°C. Measurements in the talus were

always well below our best estimate of a threshold for acute heat stress in pikas (2 h at 25.5°C; MacArthur and Wang 1974; Smith 1974*b*), suggesting that pikas and other animals may be able to survive fires *in situ* by retreating into the talus. Pikas could have been subject to oxygen depletion and smoke inhalation during this time. However, in this regard, talus microhabitats are likely similar to burrows, which appear to be relatively safe shelters from toxic gases (O'Brien *et al.* 2006).

In the longer term, soil surface temperatures tend to be warmer during the day and cooler at night due to loss of the insulating forest canopy after a severe burn (Fowler and Helvey 1978; Fontaine *et al.* 2010). Furthermore, charred surfaces absorb more sunlight and re-radiate more heat at night (Agee 1996). Because canopy cover and surface reflectivity are slow to recover after a severe fire, these microclimate effects can last for years (Viereck 1973; Fowler and Helvey 1978; Engstrom 2010). Even microclimates measured 1.5 m into burrows can be altered for years by severe fire (Fellers *et al.* 2004). In contrast, we found little evidence that the fire affected talus microclimates at severely burned sites in the 3 years following fire (Fig. 2). Burn severity was only a significant predictor in two of our six metrics of thermal stress: average August temperature and duration of snowpack. However, the presence of an interaction term between burn severity and elevation makes the average August temperature result difficult to interpret: it may be a statistical artefact of the non-random distribution of burn severity with regard to elevation and not biologically significant. Furthermore, reduced snowpack duration at severely burned sites did not result in colder winter temperatures, at either acute or chronic time scales.

The fact that we did not observe substantial differences in microclimates between severely burned sites and unburned or moderately burned sites, despite marked changes in canopy cover and surface reflectivity, suggests that microclimates in these talus slopes are likely driven by sub-talus features rather than surface heat-transfer processes, such as incident radiation or convection. The relatively cool temperatures that we measured in the talus during the fire further reinforce the low thermal diffusivity of talus in this region, which buffers subsurface microclimates from surface processes. Together, these results highlight the capacity of talus to buffer against ambient temperatures and reinforce its conservation value as both a natural fire break (Baker 2009) and a thermal refuge for animals (e.g. Henry *et al.* 2012*a*; Shi *et al.* 2014; Varner and Dearing 2014*b*).

Several lines of evidence suggest that pikas may have survived the fire *in situ* and that these sites provide suitable habitat for pikas after fire. Because we did not re-sight any tagged animals after the fire, we cannot say for certain that animals survived the fire *in situ*. In addition, severely burned sites consistently had lower pika density compared with other sites (Fig. 3*a*). However, within 2 years of the fire, all 24 of our study sites were occupied by pikas in at least one season of sampling (Table 1). Furthermore, increased density in autumn (relative to spring, in both 2013 and 2014) suggests that juveniles are being recruited into the population at these sites (Fig. 3). Finally, stress hormone levels from pikas in severely disturbed habitat did not differ from pikas in other habitats, which further highlights the suitability of severely burned habitats. Stable talus microclimates may be an important

driver of the widespread distribution of pikas within severely disturbed habitat.

In many ways, wildfire disturbance can be viewed as a natural experiment in resource manipulation that permits critical habitat thresholds for persistence to be determined. Here, we found that pika abundance appeared closely related to a threshold in vegetation biomass (55 g m^{-2}; Fig. 4). Below the threshold, few sites supported more than a single individual. Above the threshold, pika abundance was highly variable, suggesting that abundance depends on other factors when enough vegetation is present. These data provide a first quantitative estimate of resources necessary for a minimum reproducing population of pikas. Such thresholds could potentially be used both to inform predictions of species distributions under continued environmental changes and as evidence-based targets for conservation and management applications (Mawdsley *et al.* 2009; Touihri *et al.* 2014).

Although burned sites had less vegetation overall, the new plants at these sites may be more nutritious as a result of the burn. The fact that moderately burned sites had the highest pika densities of all sites in the autumn of both 2013 and 2014 (Fig. 3*a*) suggests that an intermediate level of disturbance may benefit pikas, perhaps through plant nutrition or diversity. Indeed, several studies have demonstrated increased nutritional quality after a burn (i.e. higher nitrogen content, fewer plant secondary compounds and greater digestibility; Leigh *et al.* 1991; Jakubas *et al.* 1994; Moe and Wegge 1997). However, reduced snowpack at severely burned sites (Fig. 2*a*) may also affect soil moisture and the pace of vegetation recovery.

Vegetation species richness was the most significant predictor of pika density (Table 3). As generalist herbivores, pikas feed on a diverse range of plant species (Huntly *et al.* 1986; Dearing 1996), which may explain the importance of diversity. The only significant model to predict pika density also included moss cover (Table 3). In our study region, pikas consume moss (Varner and Dearing 2014*a*); thus, the appearance of moss cover in our top model may indicate that pikas are supplementing their diets with moss. Alternatively, moss may also affect talus microclimates (Varner and Dearing 2014*b*) or may indicate microclimatic conditions (e.g. high humidity, cool temperatures) that are favourable for pikas. No other topographic predictors or metrics of burn severity were present in any of the top models, suggesting that the effects of the fire on habitat quality (as indexed by animal density) were most saliently mediated through food quality and diversity. Similarly, in arid Australia, mammalian communities and distributions were better predicted by food resources and geographic location (Letnic *et al.* 2004) or the timing and spatial distribution of rainfall events (Letnic and Dickman 2005) rather than habitat structure or burn severity, suggesting that post-fire succession did not directly influence mammalian species assemblages *per se*.

Even within a species, it may be difficult to generalise responses to fire because of existing variation in habitat quality. To this end, more research will be necessary to determine the response of pikas to fire in ecoregions where their distribution has already been affected by climate change (Beever *et al.* 2011; Jeffress *et al.* 2013). For example, in Yellowstone National Park in north-western Wyoming, a site burned during that park's

famous 1988 fires now has the highest pika density of any patch surveyed in the park (among 66 talus patches; E. Beever, unpubl. data). Similarly, in the western Great Basin, fire appears to have stimulated vegetation growth, favouring higher pika haypile densities at a recently burned site compared with nearby unburned areas (Millar *et al.* 2013). In contrast, only a single pika was detected on two mountains in semi-arid north-eastern California within the perimeter of fires from 1990, 2001 or 2012 (among 10 talus patches that collectively span hundreds of home ranges; E. Beever and T. Rickman, unpubl. data).

Several ecological factors could have influenced these differential responses to fire. In warmer and drier regions, post-fire food availability may be critical, particularly if native vegetation is replaced by unpalatable exotic species (D'Antonio and Vitousek 1992). Furthermore, warmer ecoregions may lack habitat features that functionally decouple talus microclimates from ambient conditions (e.g. sub-talus ice or water features, forest canopy or vegetation cover; Varner and Dearing 2014*b*), which are present in our study area. As a result, these ecoregions may experience longer-term post-fire alterations in microclimates that could affect the status and distribution of pika populations. This climatic harshness (i.e. high ambient temperatures and low annual precipitation) may also reduce the dispersal capabilities of pikas and thus their ability to recolonise burned areas (Henry *et al.* 2012*b*; Castillo *et al.* 2014). Finally, like temperature and precipitation (Henry and Russello 2013), fire regimes may act as a selective force driving pika evolution such that some populations of pikas are better adapted to recolonising disturbed habitat than others. Together, these factors may result in lags in recolonisation of burned patches in certain ecoregions, leading to protracted periods of reduced occupancy after a fire in parts of the species' range.

Increases in frequency and intensity of wildfires pose a complicated challenge for land managers. Our results highlight the importance of maintaining thermal refugia for sensitive species during wildfires and make an important first contribution towards understanding how pikas, climate-sensitive habitat specialists, may cope with changing disturbance regimes. Our results also reinforce the need for investigations to comprehensively portray the taxonomic, topographic, climatic and ecological contexts that mediate responses to wildfires. Such data will allow later meta-analyses to synthesise patterns that advance from species-by-species bases to a more holistic understanding (Driscoll *et al.* 2010).

Acknowledgements

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