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Impact of wildfire size on snowshoe hare relative abundance in southern British Columbia, Canada

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Abstract

Background: Large wildfires result in more heterogeneous fire scars than do smaller fires because of differences in landscape context and high variability in burn intensity and severity. Previous research on mammal response to wildfire has often considered all fires as comparable disturbances regardless of size. Here, we explicitly examine whether fire size affects relative abundances of a keystone herbivore, snowshoe hare (*Lepus americanus* Erxleben, 1777), in regenerating stands of the same age. We surveyed vegetation and fecal pellets of snowshoe hares in nine 13-year-old wildfires, specifically, three fires in three size categories—small (80 to 200 ha), medium (1000 to 5000 ha), and large (>10 000 ha)—and in mature forests in southern British Columbia, Canada.

Results: Snowshoe hare density was low (0.4 hares ha^{-1}), but hares were present at 57% of mature sites. Hares were absent from all areas where small fires had burned and were found in only one medium area post fire (0.2 hares ha^{-1}). Hares were found within the fire scars of all three large burned areas, and with much higher numbers (3.8 hares ha^{-1}) than in the medium fire area or mature forest. Snowshoe hare abundance was highly correlated with the number of sapling trees, especially lodgepole pine (*Pinus contorta* Douglas ex Loudon). Sapling densities were highly variable, but dense stands of saplings were found only in burn scars from large wildfires.

Conclusions: Fire size is an important predictor of snowshoe hare relative abundance in areas that are regenerating post fire; fires of different sizes are not comparable disturbances. Specifically, the post-fire heterogeneity after large fires enabled both the highest hare numbers as well as patches with no hares. These results suggest that forest and wildlife managers should protect areas with dense regeneration post fire, as these sites are necessary for hares after large wildfires.

Keywords: forest regeneration, heterogeneity, relative abundance, snowshoe hare, wildlife

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Resumen

Antecedentes: Los grandes incendios producen cicatrices de fuego más heterogéneas que pequeños incendios, debido fundamentalmente a diferencias en el contexto del paisaje y la gran variabilidad en la intensidad y severidad de las quemas. Investigaciones previas sobre la respuesta de los mamíferos a incendios han considerado frecuentemente a todos los fuegos como disturbios comparables sin tener en cuenta el tamaño de cada uno. En este trabajo examinamos explícitamente si el tamaño de los incendios afecta la abundancia relativa de un herbívoro clave, la liebre americana (*Lepus americanus* Erxleben, 1777), en la regeneración de rodales de la misma edad. Relevamos la vegetación y las heces de liebre americana en nueve incendios de 13 años de antigüedad; específicamente en tres incendios de tres categorías en tamaño—pequeños (80 a 200 ha), medianos (1000 a 5000 ha), y grandes (>10 000 ha)—y en bosques maduros, en el sur de la Columbia Británica, Canadá.

Resultados: La densidad de liebre americana fue baja (0,4 liebres ha^{-1}), aunque estuvieron presentes en el 57% de los bosques maduros. Las liebres estuvieron ausentes en todos los lugares donde hubo pequeños incendios, y fueron encontradas solo en un área mediana post incendio (0,2 liebres ha^{-1}). Muchas más liebres (3.8 liebres ha^{-1}) fueron encontradas dentro de las cicatrices de fuego de las tres áreas grandes quemadas que en las áreas medianas o en el bosque maduro. La abundancia de liebres fue altamente correlacionada con el número de plántulas de árboles, especialmente de pino contorta (*Pinus contorta* Douglas ex Loudon). Las densidades de plántulas fueron altamente variables, pero los rodales que contenían mayor densidad de estas plántulas fueron solo encontrados en las cicatrices de incendios producidas por grandes incendios.

Conclusiones: El tamaño de los incendios es un predictor importante de la abundancia relativa de la liebre americana en áreas que están regenerando luego de incendios; los incendios de diferente tamaño no son disturbios comparables. Específicamente, la heterogeneidad post fuego luego de grandes incendios permitió que haya tanto mayor densidad de liebres como también parches sin liebres. Estos resultados sugieren que los agentes forestales y los manejadores de fauna silvestre deben proteger áreas con regeneración densa post fuego, ya que esos sitios son necesarios para las liebres luego de grandes incendios.

Background

Wildfires are growing in size, severity, and frequency as a result of climate change and fire suppression (Westerling et al. 2006; Keane et al. 2008; Miller et al. 2009; Harvey 2016). Fire is the leading disturbance in North American conifer forests (Keane et al. 2008) and is a natural part of the regrowth cycle (Turner et al. 1994). Fire regimes range from small, frequent, low-severity fires in southern conifer forests (Keane et al. 2008) to severe, large, infrequent fires in northern boreal forests (Turner et al. 1998; Kennedy and Fontaine 2009). However, large fires are increasingly common, with wildfires in many regions burning larger and more frequently than during historic fire regimes (Keane et al. 2008).

The size and severity of any given wildfire are important to understanding the effect that fire will have on vegetation and regrowth patterns (Perera and Buse 2014), with larger disturbances creating more heterogeneous landscapes (Turner et al. 1997; Turner et al. 1998; Kashian et al. 2004). The size and shape (*e.g.*, edge to area ratio) of a fire determines the spatial structure of post-fire habitat (Schoennagel et al. 2008; Perera and Buse 2014; Harvey et al. 2016). Large fires burn over more spatially diverse landscapes than smaller fires, which can lead to more diversity in post-fire vegetation (Turner et al. 1994, 1997). Large fires also burn hotter

than smaller fires, with more severely burned areas typically concentrated in the center of the burn and lower tree mortality at the edges (Turner et al. 1994, 1997; Haeussler and Bergeron 2004; Harper et al. 2004). The distance from edge to center of a burn affects the regrowth patterns following large and small fires. Regeneration after a large fire is less reliant on seed dispersal from the surrounding unburned forest because of the sheer distance between the edge and center (Turner et al. 1997; Harvey et al. 2016), whereas regeneration after smaller burns is greatly affected by available seed-banks of forest edges because seed dispersal is less distance-limited and there are more living trees remaining (Perera and Buse 2014).

The value of post-fire vegetation for wildlife habitat depends on how burn severity and size influence vegetation regrowth. For example, after the 1988 fires in Yellowstone National Park, Wyoming, USA, lodgepole pine (*Pinus contorta*) grew more densely in large patches that experienced moderate or severe fires (Turner et al. 1997; Anderson et al. 2004; Kashian et al. 2004). Small fires are less patchy than large fires, largely because they cannot encompass the same variety of severities (Bessie and Johnson 1995; Cui and Perera 2008; Perera and Buse 2014). Given that animals move across landscapes and use habitat on multiple spatial scales (Boyce et al. 2003),

it is likely that animals respond differently to wildfires of different sizes because of associated patterns in quantity and quality of available habitat. Reviews of small mammal response to wildfire have shown that responses to post-fire vegetation vary greatly across taxa, with some species (deer mice; *Peromyscus maniculatus* Wagner, 1845) experiencing population increases, while others (*e.g.,* voles) experience declines (Fisher and Wilkinson 2005; Fontaine and Kennedy 2012; Griffiths and Brook 2014).

Previous work on how small mammals respond to post-fire landscapes have tended to focus on one or a few fires (Zwolak 2009; Griffiths and Brook 2014; Hutchen et al. 2017). Very few studies of small-mammal response to fire have compared multiple fires in a single study (Hutchen et al. 2017), and those that did tended to focus on multiple prescribed burns of the same size (Kennedy and Fontaine 2009; Fontaine and Kennedy 2012). We are not aware of studies that have examined how wildfire size affects post-fire population responses of wildlife.

Here, we focus on the relative abundance of snowshoe hares (*Lepus americanus* Erxleben, 1777) in relation to fire size. Snowshoe hares are an abundant keystone prey species found across Canada and the northern United States in a range of fire-disturbed ecosystems (Hodges 2000a, 2000b; Krebs et al. 2001a). Hares display immediate population declines post fire (Hodges et al. 2009), but recolonization by individual animals has been noted as early as one year post fire (Keith and Surrendi 1971), and, within several decades, hare abundances are highest in areas with dense regenerating forest (Hodges et al. 2009, Hodson et al. 2011, Allard-Duchene et al. 2014, Cheng et al. 2015). Snowshoe hares favor early seral, regenerating stands, but also use closed-canopy mature stands (Paragi et al. 1997; Hodges et al. 2009; Hodson et al. 2011), especially where canopy gaps provide a high density of shrubs and saplings for foraging and cover (Hodges 2000a, 2000b; Hodson et al. 2010a, 2010b; Holbrook et al. 2017). In the context of large wildfires, there still remain large knowledge gaps as to how the high heterogeneity of post-fire vegetation affects the distribution of preferred snowshoe hare habitat. Previous work has not examined impacts of fire size on hares (Hutchen et al. 2017).

Given these known habitat preferences of snowshoe hares, it is possible to predict how snowshoe hare populations will respond to wildfire size. Here, we test whether these predictions are upheld: (1) snowshoe hare abundances will be higher in large burns than small burns, because large burns support patches of dense sapling regrowth; and (2) snowshoe hare abundances will be more variable among sampling plots in large burns relative to small burns, due to high landscape heterogeneity in large burn scars.

Methods

Study sites

We used Geographic Information System data layers obtained from iMapBC (http://maps.gov.bc.ca/ess/sv/imapbc/) to locate all wildfires that burned in 2003 or 2004 in the southern interior ecoprovince of British Columbia, Canada. This ecoprovince contains the Thompson-Okanagan ecozone as well as proximate montane forested regions (Scudder and Smith 2011). Dominant canopy species in the Thompson-Okanagan are ponderosa pine (*Pinus ponderosa* Douglas ex P. Lawson) and lodgepole pine at low elevations, transitioning into Douglas-fir (*Pseudotsuga menziesii* [Mirb.] Franco), redcedar (*Thuja plicata* Donn ex D. Don), and western hemlock (*Tsuga heterophylla* [Raf.] Sarg.) at higher elevation, with subalpine fir (*Abies lasiocarpa* [Hook.] Nutt) at high elevations.

We sampled hare abundances in 2016, some 12 to13 years post fire, which corresponds to the establishment stage of forest succession, at which snowshoe hare abundance is thought to be highest post fire (Fisher and Wilkinson 2005). We classified fires as: (1) small, 80 to 200 ha; (2) medium, 1000 to 5000 ha; and (3) large, 10 000 to 26 000 ha. There were no wildfires in the 200 to 1000 ha range that fit our years of burn criteria in the Okanagan, and we wanted clear separation in size among the three categories. Our threshold of 80 ha for small fires was chosen with respect to snowshoe hare ecology, as this area is big enough to support multiple hare home ranges (which average 5 to 10 ha; Hodges 2000a). Previous researchers have classified large wildfires as over 400 ha (Westerling et al. 2006) or over 10 000 ha (Daniel et al. 2007; Keane et al. 2008). We chose to define large fires as >10 000 ha, and identified medium fires as the intermediate order of magnitude between small and large fires. Smaller fires are far more common than medium or large fires, but large fires are responsible for the majority of the area burned in any year (Cumming 2001; Cui and Perera 2008; Baker 2009).

We sampled three fires from each size class (Table 1; for maps, see Hutchen 2017). To limit confounding factors such as forest type, elevation, and other habitat features, we chose fires that were as similar to each other in physical context as possible, while still being accessible from a road or trail (*e.g.,* within a 4-hour hike). Only two accessible fires burned more than 10 000 ha of forest in the 2003 fire year (Okanagan Mountain Park Fire at >25 000 ha, and McClure Fire at >27 000 ha). However, the McClure Fire jumped the North Thompson River, essentially creating two independent wildfires. The river does not freeze over in winter and BC Highway 5 is also adjacent to the river; these barriers would be extremely difficult for a hare to cross. We therefore treat the two sides of the McClure Fire as independent

Table 1 Site descriptions in the Thompson-Okanagan region of British Columbia, Canada, from June to August 2016, based on data from iMapBC and the British Columbia Land Classification system with the Vegetation Resources Inventory data set (https://www.for.gov.bc.ca/hfd/library/documents/bib107006_2002.pdf). Leading species are the dominant species

Site name	Fire number	Size class	Size (ha)	Ignition date	Ignition source	Elevation range (m)	Leading species[1]
Okanagan Mountain Park	K50628	Large	25 635	16 Aug 2003	Lightning	360 to 1600[3]	Lodgepole pine (var. *latifolia*), Douglas-fir, ponderosa pine
McClure West	K20272	Large	17 954[2]	30 Jul 2003	Person	380 to 1400	Interior Douglas-fir (var. *glauca*), lodgepole pine (var. *latifolia*), aspen (*Populus tremuloides* Michx.), spruce hybrid
McClure East	K20272	Large	9 183[2]	30 Jul 2003	Person	380 to 1300	Interior Douglas-fir (var. *glauca*), lodgepole pine (var. *latifolia*), paper birch (*Betula papyrifera* Marshall)
Vaseux Lake	K50661	Medium	4 313	22 Aug 2003	Person	340 to 1420	Ponderosa pine, interior Douglas-fir (var. *glauca*), western larch
Falkland (Cedar Hills)	K40300	Medium	1 223.1	1 Aug 2003	Person	500 to 1160	Interior Douglas-fir, ponderosa pine, lodgepole pine (var. *latifolia*)
Vermellion Creek	K20436	Medium	1 223.1	7 Aug 2003	Lightning	660 to 1600[4]	Interior Douglas-fir (var. *glauca*), spruce hybrid, Engelmann spruce (*Picea engelmannii* Parry ex Engelm.)
Queest Mountain	K30551	Small	169.8	20 Aug 2003	Lightning	1420 to 1900	Subalpine fir, spruce hybrid
Chase	K30400	Small	109.5	28 Aug 2002	Person	400 to 900	Douglas-fir (var. *glauca*), ponderosa pine
Owlhead	K30236	Small	84.3	24 Jul 2003	Person	360 to 780	Interior Douglas-fir (var. *glauca*), aspen

[1]Based on Stand Age classes. Names represent the exact description on the Land Classification system (*e.g.*, "spruce hybrid" and "spruce" were different names, and since the considered polygons were named "spruce hybrid," that is the name used here)
[2]Total fire size was 27 137 ha. Division was done by measuring the perimeter of the fire using the North Thompson River as a barrier in iMapBC
[3]We did not go to the highest point on Okanagan Mountain
[4]Only the lower portion of the burn was accessible. Total elevation was 1820 to 2000 m

fires from the perspective of a snowshoe hare (hereafter McClure East and McClure West; Table 1).

Snowshoe hare surveys

To estimate relative abundance of snowshoe hares, we used fecal pellet surveys (Krebs et al. 1987; Krebs et al. 2001b), which are feasible across large spatial scales and can provide accurate information on low versus high hare densities when compared to live-trapping methods (Mills et al. 2005; Hodges and Mills 2008). We conducted field work between May and August 2016 using uncleared pellet surveys (pellets were not removed). Prior to sampling, we used ArcGIS software (ESRI, Redlands, California, USA) to create a series of 20 ha plots in each burn; sites were randomly selected but with the constraint that they had to be reasonably accessible (within a 4-hour hike from the nearest road). The number of field sites per fire area varied from one to seven because small fires could not accommodate the same number of sites as large fires (Table 2). We also placed eight 20 ha plots in mature forest (control; Table 2). Each 20 ha sample plot was populated with 80 random points for the uncleared pellet transects (Krebs et al. 1987; Krebs et al. 2001b; Mills et al. 2005; Hodges and Mills 2008). A rectangular transect (0.155 m², 5.08 cm × 305 cm) was laid due north at each survey point. Pellets were counted only if they were intact and at least one half were within the transect

area. To calculate the mean density of hare pellets in each burn, we first averaged within each 20 ha stand independently, then averaged across all sample stands in each fire. We then translated the average number of pellets in each 20 ha stand into hares ha⁻¹ by using the formula developed in Krebs et al. (2001b). We do not provide estimates of variance in hare density because pellet variance increases with the mean count and the log:log equation relating pellets to hares results in biologically implausible upper estimates of snowshoe hare density.

Vegetation surveys

Within each forest stand, we sampled vegetation at 15 randomly selected points. At each location, we used a densitometer to measure canopy cover and a 2 m coverboard (profile board; tool for estimating percentage cover) read from 10 m due south of the pellet plot to measure understory cover (Hodges et al. 2009). Shrub cover was recorded as the percent cover per species along a 10 m × 0.5 m belt transect. Total shrub cover could be greater than 100% because cover from individual species could overlap. The number of downed logs (coarse woody debris, >5 cm diameter) was recorded in the transect. Within a 1 m radius circle at the north end of the pellet plot, we recorded the species, height class, and diameter at breast height (DBH) of all sapling trees

Table 2 Snowshoe hare pellets compared between burn sites in the Thompson-Okanagan region of British Columbia, Canada, from June to August 2016

Fire name	Mean pellets per transect per fire ($n \pm$ SD)	Sites with pellets (%)	Mean pellets per transect when pellets present ($n \pm$ SD)	Site name	Average pellets per transect ($n \pm$ SD)
Large fires					
Okanagan Mountain Park	7.1 ± 8.4	66.7	10.7 ± 8.1	1. Crawford	4.3 ± 8.1
				2. Forest Service Road	21.0 ± 15.3
				3. Myra Valentine	4.1 ± 4.8
				4. FSR- Logs	13.3 ± 18.4
				5. Kupier	0.0 ± 0
				6. Okanagan Lookout	0.0 ± 0
McClure East	18.6 ± 23.6	66.7	28.0 ± 24.4	1. Cow Pond	10.7 ± 14.8
				2. Highway	0.0 ± 0
				3. Badger Lake	45.2 ± 31.9
McClure West	9.3 ± 12.9	60.0	15.5 ± 13.8	1. Km 10	0.0 ± 0
				2. Fishtrap	0.0 ± 0
				3. Gorman Scotte	29.0 ± 26.3
				4. Wolsey Road	1.3 ± 3.0
				5. Snake Lake	16.2 ± 23.0
Medium fires					
Falkland	0.9 ± 1.3	50.0	1.9 ± 0	1. Cow Kill	1.8 ± 0
				2. Rest Stop	0.0 ± 0
Vaseux	0 ± 0	0.0	0 ± 0	1. Fence	0.0 ± 0
				2. Logging Road	0.0 ± 0
				3. Dutton Creek	0.0 ± 0
Vermellin	0 ± 0	0.0	0 ± 0	1. Middle	0.0 ± 0
				2. South	0.0 ± 0
Small fires					
Chase	0 ± 0	0.0	0 ± 0	1. Middle	0.0 ± 0
				2. Edge	0.0 ± 0
Owlhead	0 ± 0	0.0	0 ± 0	1. Owlhead	0.0 ± 0
Queest	0 ± 0	0.0	0 ± 0	1. Low	0.0 ± 0
				2. High	0.0 ± 0
Mature forest					
Unburned	0.8 ± 1.0	57.1	1.4 ± 0.9	1. Falkland	0.6 ± 1.2
				2. Gillard–Okanagan	0.0 ± 0
				3. Angel Springs–Okanagan	2.7 ± 5.3
				4. McClure	1.5 ± 2.7
				5. Owlhead	0.0 ± 0
				6. Vaseux	0.0 ± 0
				7. Vermellin	0.9 ± 1.6

(DBH < 7.5 cm). We used variable distance sampling with a relascope and a metric basal area factor of four (Husch et al. 2003; Hodges et al. 2009) to identify canopy trees and snags, which were then measured with a DBH tape.

Statistical analyses

We used one-way analysis of variance (ANOVA) to test whether the relative abundance of snowshoe hares differed among large, medium, or small fires, and mature forest. Linear regressions were used to relate hare pellet abundance to the vegetation variables as univariate tests of how well each variable predicted hare abundance.

To determine what set of variables (*e.g.*, individual habitat features and fire size) best explained snowshoe hare abundance within post-fire stands, we used Akaike's Information Criterion corrected for small sample sizes (AICc; Burnham and Anderson 2004). We tested a set of *a priori* models developed prior to field surveys based on previously identified relationships between hare abundance and post-fire vegetation (Table 3, Hodges et al. 2014, Cheng et al. 2015). All vegetation variables were considered individually or with additive impact in the models and without interaction variables. We took this approach to determine if any one vegetation measure is a more effective predictor of hare abundances than others, or if sampling more habitat attributes would lead to more robust predictions of hare densities in post-fire forest stands. We included mature forest in all models to sample a fuller spectrum of forest attributes. All statistics were done in R 3.3.2 (R Core Team 2016) using R Studio 1.0.136 (RStudio Team 2016) with the

package `AICcmodavg` (Mazerolle 2016) used to evaluate candidate AIC models.

Results

Snowshoe hares were found at 14 of 33 sampled forest stands (42%). Hare pellet abundance varied with fire size and between burned areas and mature forests (Fig. 1; $F_{3,27}$ = 3.21, P = 0.038); large burned areas had the highest pellet counts (10.4 ± 13.1 pellets transect^{-1}, $\overline{X}$ ± 1 standard deviation), followed by mature forest sites (0.8 ± 1.0 pellets transect^{-1}), whereas hare pellets were scarce in medium burned areas (0.3 ± 0.7 pellets transect^{-1}), and absent in small burned areas (0 ± 0 pellets transect^{-1}). These pellet numbers translate to estimated snowshoe hare densities of 3.8, 0.2, 0, and 0.4 hares ha^{-1} in large-, medium-, and small-fire areas and mature forests, respectively (Fig. 1). Snowshoe hare pellets were found at more than half of the sites in all three large-fire areas, although there was high variability in hare pellet density across stands (Okanagan Mountain Park: 4 of 6 sites, McClure East: 2 of 3 sites and McClure West: 3 of 5 sites; Table 2).

Within large fires, there was high variability in the hare pellet densities. The average number of hare pellets found in large fires was 10.4 ± 13.6 pellets transect^{-1} (3.8 hares ha^{-1}). McClure East had the highest mean number of hare pellets with 18.6 ± 23.6 pellets transect^{-1} (6.3 hares ha^{-1}). McClure West had 9.3 ± 12.9 pellets transect^{-1} (3.4 hares ha^{-1}) and Okanagan Mountain Park had the lowest number of hare pellets with 7.1 ± 8.4 pellets transect^{-1} (2.7 hares ha^{-1}). When only study sites

Table 3 Ranked AIC models relating vegetation to snowshoe hare pellet abundance in all sites (burned and mature) in the Thompson-Okanagan region of British Columbia, Canada, from June to August 2016. K = number of model parameters. AICc = second order AIC scores for small sample sizes, ΔAICc = the relative difference between the best model (which has a ΔAIC of zero) and each other model in the set. Akaike weights (AICcWt) and the cumulative weight (Cum.Wt) give the probability that the model is the best from the set

Model variables	K	AICc	ΔAICc	Model likelihood	AICcWt	Cum.Wt
Saplings	3	167.68	0.00	1.00	0.53	0.53
Saplings + Shrub cover	4	169.99	2.31	0.31	0.17	0.70
Saplings + Canopy trees	4	170.25	2.58	0.28	0.15	0.85
Saplings + Fire class[1]	4	170.26	2.58	0.27	0.15	0.99
Saplings + Snags + Fire class	6	176.71	9.04	0.011	0.01	1.00
Canopy cover	3	202.48	34.80	0.00	0.00	1.00
Fire class	3	202.98	35.30	0.00	0.00	1.00
Canopy trees	3	204.67	37.00	0.00	0.00	1.00
Canopy cover + Understory cover	4	205.15	37.47	0.00	0.00	1.00
Snags + Understory cover	4	206.13	38.45	0.00	0.00	1.00
Canopy cover + Understory cover + Shrub cover	5	206.45	38.77	0.00	0.00	1.00
Canopy cover + Understory cover + Fire class	5	206.72	39.04	0.00	0.00	1.00
Canopy trees + Understory cover	4	206.96	39.28	0.00	0.00	1.00

[1]Fire class is divided into four categories: small, medium, large, and mature
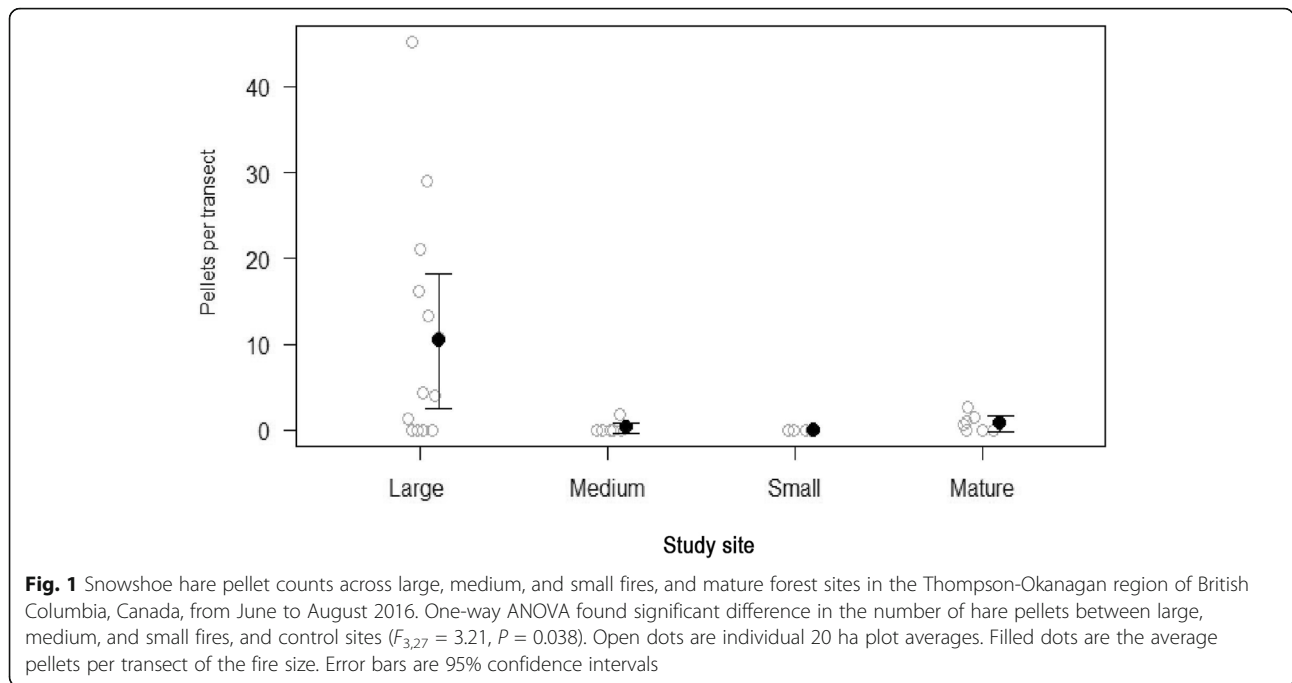
Fig. 1 Snowshoe hare pellet counts across large, medium, and small fires, and mature forest sites in the Thompson-Okanagan region of British Columbia, Canada, from June to August 2016. One-way ANOVA found significant difference in the number of hare pellets between large, medium, and small fires, and control sites ($F_{3,27} = 3.21$, $P = 0.038$). Open dots are individual 20 ha plot averages. Filled dots are the average pellets per transect of the fire size. Error bars are 95% confidence intervals

that had hares were considered, the numbers of pellets were 28.0 ± 24.4 pellets transect^{-1} (9.1 hares ha^{-1}), 15.5 ± 13.8 pellets transect^{-1} (5.4 hares ha^{-1}), and 10.7 ± 8.1 pellets transect^{-1} (3.9 hares ha^{-1}) for McClure East, McClure West, and Okanagan Mountain Park, respectively. When only sites that had hare pellets were considered, the mean was 16.1 ± 14.0 pellets transect^{-1} (5.6 hares ha^{-1}; Table 2).

Hare pellets were found at only one of the medium fire sites (Table 2). The Falkland Fire averaged 0.9 ± 1.3 pellets transect^{-1} (0.4 hares ha^{-1}). The average pellets at medium-fire sites that had hares was 1.9 ± 0 pellets transect^{-1} (0.8 hares ha^{-1}). When all medium-fire sites were combined, there was an average of 0.3 ± 0.7 pellets transect^{-1} (0.3 hares ha^{-1}). No hare pellets were found in small-fire sites (Table 2). Mature forest sites had hare pellets in 57% of sites (4 of 7 sites). Pellet density ranged from 0 to 2.7 pellets transect^{-1}, with an average of 0.8 ± 1.0 pellets transect^{-1} (0.4 hares ha^{-1}). In the sites that had hares, the average was slightly higher at 1.4 ± 0.9 pellets transect^{-1} (0.6 hares ha^{-1}).

The number of living canopy trees and canopy cover were strongly positively correlated with fire size (Table 4; $R^2 = 0.66$, $P < 0.01$, $F_{2,29} = 18.90$, and $R^2 = 0.78$, $P < 0.01$, $F_{2,29} = 35.04$, respectively). Sapling number, understory cover, shrub cover, coarse woody debris, and snags were not significantly correlated to fire size (Table 4, saplings shown in Fig. 2). Large wildfires had the highest variability in the number of sapling trees present (Fig. 2; small: 7.2 ± 10.6, medium: 18.9 ± 27.5, large: 50.1 ± 51.5).

Pellet and vegetation regressions

The density of sapling trees was significantly and positively correlated to number of hare pellets across all sites, including mature forest and burned sites ($F_{1,31} = 99.75$, $P < 0.01$; Fig. 3). Lodgepole pine was the most common species (48.9% of saplings); density of lodgepole pine saplings was also significantly correlated to numbers of hare pellets ($F_{1,31} = 90.24$, $P \leq 0.001$; Fig. 4), but no other species was a significant predictor of pellet numbers (Douglas-fir was the second-most common, at 14.1% of seedlings). No other vegetation variable was correlated to the number of hare pellets (Table 5).

The AIC models showed that only the number of sapling trees was substantially supported in predicting pellet densities in burned and mature forests (Table 3). The next three strong models all had saplings as a variable, then included shrub cover, fire size class (large, medium, small, or mature forest), or the number of canopy trees

Table 4 ANOVA results for all vegetation variables in relation to fire size in the Thompson-Okanagan region of British Columbia, Canada, from June to August 2016

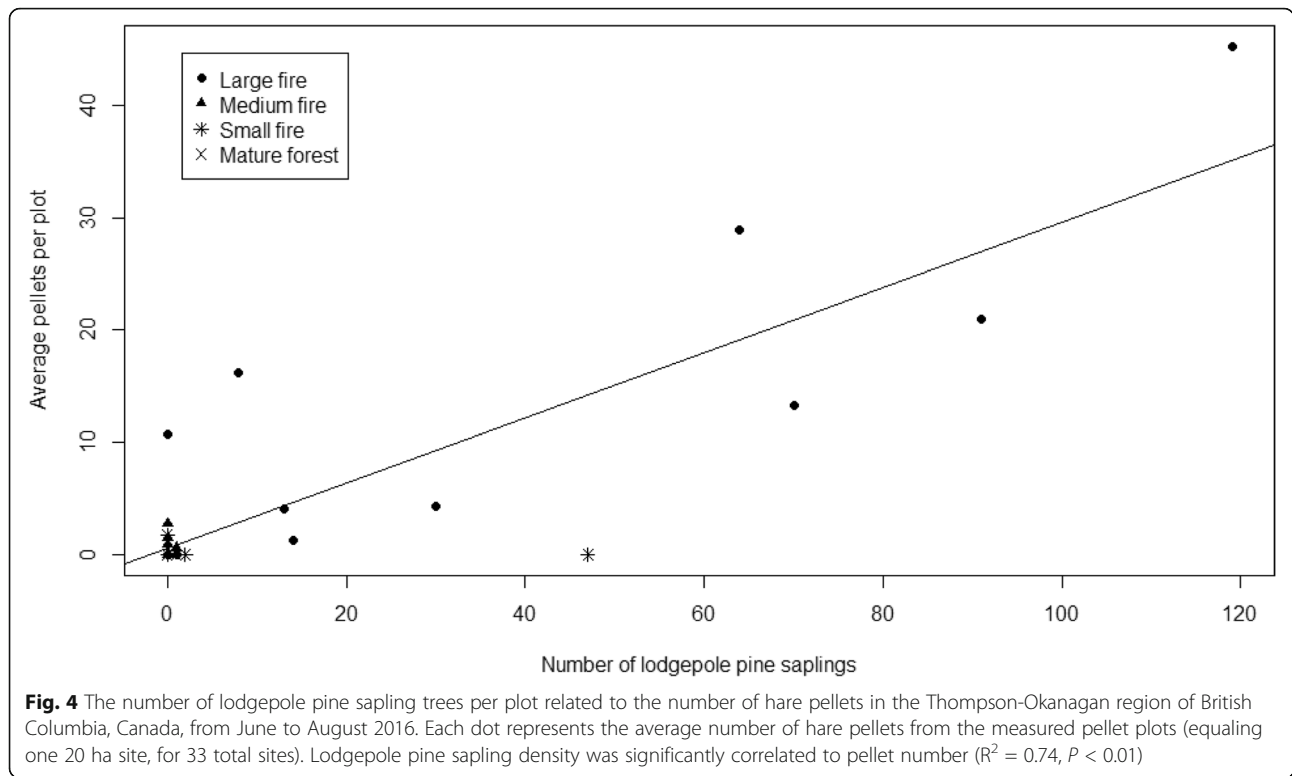| Variable	$F_{2,29}$	R^2	P
Living canopy trees	18.90	0.66	<0.01
Snag trees	1.50	0.13	0.23
Canopy cover	35.04	0.78	<0.01
Understory cover	1.60	0.14	0.21
Saplings	2.57	0.18	0.10
Shrub cover	1.94	0.17	0.15
Coarse woody debris	2.97	0.23	0.05
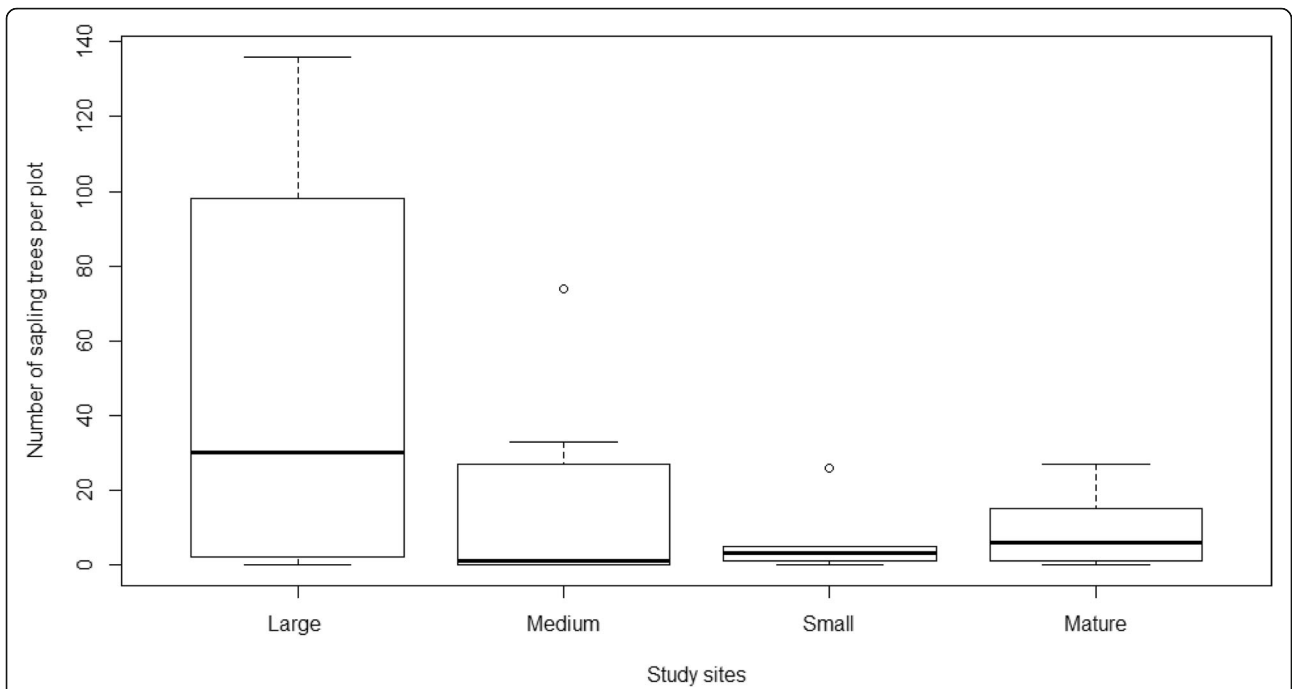
Fig. 2 Sapling density across large, medium, and small fires, and mature forest sites in the Thompson-Okanagan region of British Columbia, Canada, from June to August 2016. Sapling density was not significantly correlated to fire size due to high variability in large fires ($R^2 = 0.18$, $P = 0.10$). Middle line represents the median, the rectangle extends the first and third quartile range, and whiskers extend to the minimum and maximum value. Open circles are outliers that are outside of the quartile range
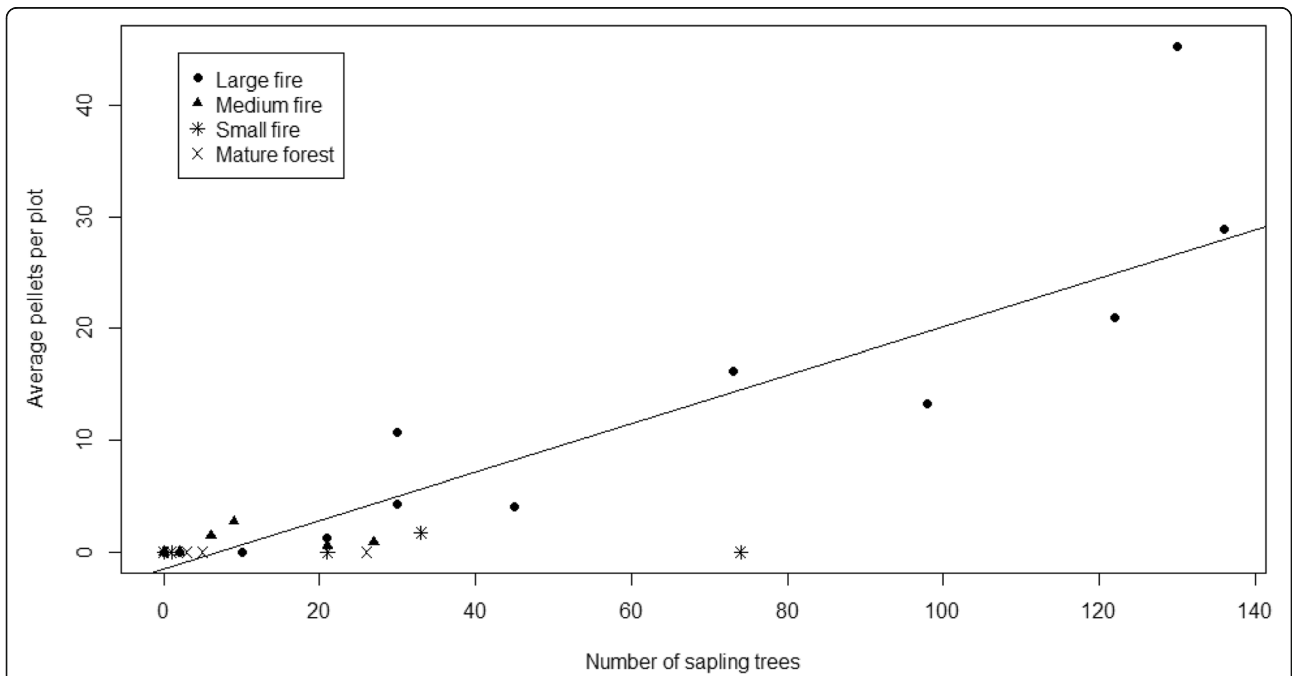
Fig. 3 The number of sapling trees per plot related to the number of hare pellets in those plots in the Thompson-Okanagan region of British Columbia, Canada, from June to August 2016. Each dot represents the average number of hare pellets from the measured pellet plots (equaling one 20 ha site, for 33 total sites). Pellet number was strongly correlated with the density of sapling trees in burns and mature forest ($R^2 = 0.76$, $P < 0.01$)

Fig. 4 The number of lodgepole pine sapling trees per plot related to the number of hare pellets in the Thompson-Okanagan region of British Columbia, Canada, from June to August 2016. Each dot represents the average number of hare pellets from the measured pellet plots (equaling one 20 ha site, for 33 total sites). Lodgepole pine sapling density was significantly correlated to pellet number ($R^2 = 0.74$, $P < 0.01$)

(Table 5; ΔAIC = 2.58). The model that contained sapling trees only was 3.12 times more likely than the next highest model based on AICc weights.

Discussion

The relative abundance of snowshoe hares is highly variable after wildfire. Wildfire size had large impacts on hare abundances, with large fires having the highest abundances of hares, but also showing substantial within-burn variability in hare abundances. Our first prediction was

Table 5 ANOVA results for all vegetation variables considered in analysis of snowshoe hare pellet correlations in the Thompson-Okanagan region of British Columbia, Canada, from June to August 2016

Variable	$F_{1,31}$	R^2	P
Living canopy trees	0.84	0.03	0.37
Snag trees	0.49	0.02	0.48
Total canopy trees	1.49	0.05	0.23
Canopy cover	0.42	0.01	0.52
Understory cover	1.39	0.04	0.25
Shrub cover	0.20	0.006	0.66
Saplings	99.75	0.76	<0.01
Lodgepole pine saplings	90.24	0.74	<0.01
Coarse woody debris	0.28	0.02	0.49
Total tree basal area	3.41	0.1	0.07

therefore supported, because hares were indeed more abundant in large burns than small or medium burns, and there was a strong trend toward saplings being more abundant after large fires. The stands that had the highest abundances of hares were also those that had the highest density of lodgepole pine saplings, echoing results from Montana (Cheng et al. 2015) and Wyoming (Hodges et al. 2009), USA. Our second prediction was also supported: snowshoe hare abundance was much more varied in large burns. In large burns, snowshoe hares were either absent or they were present in high numbers. In small burns, medium burns, and mature forest, hares were either absent or at low density. In regions where hares have clear population cycles, peak hare densities are often 4 to 6 hares ha^{-1} (Hodges 2000a), with the highest densities typically somewhat lower in the southern parts of the geographic range (Hodges 2000b). The average hare densities that we observed in large fires (3.8 hares ha^{-1}) are toward the high end of hare densities, but with large variability within the fire scar (from 0 to 9.1 hares ha^{-1} on individual stands that we sampled).

The large-fire sites in this study were heterogeneous in their vegetative structure. This high variability is likely the reason that we did not find significant differences in overall vegetation among the different sizes of fires, as the large variation in large fires overlapped the measurements from medium and small fires. Habitat heterogeneity is expected in large fires (Turner et al. 1994, 1997;

Turner et al. 1998; Turner and Dale 1998) and may contribute to higher populations of animals. For example, related hare species (*Lepus timidus* Linnaeus, 1758) have highest abundances in heterogeneous habitats when compared with more uniform habitats (Rehnus et al. 2016). Snowshoe hares use a variety of habitats for breeding and foraging (Hodges 2000a, 2000b; Hodson et al. 2011), so heterogeneity within the landscape may enable overall higher densities than what occur in regions that are more uniform. In the case of wildfires, this physical context matters. The physical placement of sapling patches, distance from fire edge, and pre-fire forest structure may all impact where available forage and cover are for hares; additional work on these aspects of fire-wildlife ecology would be valuable.

Snowshoe hares were absent or at very low density in the small- and medium-burned areas that we sampled. These results likely reflected the sparser post-fire regeneration on these sites. Alternatively, it is possible that, because hares had higher access to unburned stands adjacent to these small- and medium-burned areas, they simply could have avoided the burned areas. In contrast, in large-burned areas, hares cannot easily move between the interior of the burned area and mature forest on the edge, and thus hares may remain within the patches of dense regeneration within the burn. Finally, our small- and medium-fire sites may have been slightly drier and hotter than the large-burned areas, and subtle site variation of this sort also affects sapling regeneration. It would be valuable to examine hares in more burned areas to see if our findings in relation to fire size are robust across a wider region and more site conditions.

Of the habitat characteristics examined in this study, only the density of sapling trees was correlated with the hare pellet index as a univariate predictor. AIC models also found that shrub cover, fire size, and the number of canopy trees had moderate explanatory power when considered with sapling trees. These results support previous studies that found that regenerating lodgepole pine stands offer particularly good habitat for snowshoe hares (Hodges 2000b; Mowat and Slough 2003; Cheng et al. 2015). In our system, about half of the sapling regrowth consisted of lodgepole pine. In forests where more species regrow soon after fire, or where lodgepole pine is scarce, sapling density is likely to remain a strong predictor of hare density given that young trees provide both food and cover for hares, especially in large burns where hares no longer have easy access to mature forest cover. Lodgepole pine is a favorite food of snowshoe hares due to its nutritional value (Hodges 2000a, 2000b; Ellsworth et al. 2013; Ellsworth et al. 2016), and we found that foraging snowshoe hares in the large Okanagan Mountain Park fire preferentially selected dense thickets of saplings in winter and foraged primarily on lodgepole pine (Hutchen and Hodges 2019).

The relationship between snowshoe hare density and dense lodgepole pine stands is also found in forestry studies examining post-harvest stands (Berg et al. 2012; Ivan et al. 2014). Animals respond to vegetation and habitat, not the disturbance per se that enabled regeneration to proceed (Monamy and Fox 2000; Boyce et al. 2003; Lindenmayer et al. 2008), so it is unsurprising that the associations between vegetation and hares are similar in post-fire and post-harvest habitats. Large fires, however, typically leave far more heterogeneous conditions than do clear-cuts, and operate at different spatial scales. Specifically, within a large burned area, there often are numerous small remnant patches of unburned or lightly burned trees that enable hare movement across landscapes to find larger areas of dense regeneration (or fire skips), whereas harvested stands or smaller burned stands typically lack such residual structure. Further, lodgepole pine is a serotinous conifer, with cones that open most readily following severe crown fires (Turner et al. 1997; Nyland 1998; Turner and Dale 1998; Anderson et al. 2004), although some trees also have non-serotinous cones. Large fires enable hot temperatures that maximize germination from serotinous lodgepole pine cones (Despain et al. 1996), whereas small fires burn cooler and may have poorer post-fire regeneration. In large fires, the density of serotinous trees pre fire affects lodgepole density post fire (Tinker et al. 1994), again leading to high heterogeneity of tree regrowth in large burn scars compared to small fires or to harvested areas.

Our work demonstrates clear patterns in hare abundance in post-fire landscapes that varied with fire size. These patterns could develop via multiple non-exclusive mechanisms. For example, hares could select stands because of browse availability, which is higher when saplings are dense. Hares could also select stands for thermal or protective cover—both of which are also higher when saplings are dense. In our case, all sites had abundant forage (*e.g.*, lodgepole pine saplings, rose bushes [*Rosa* L. spp.]), regardless of whether hares were also found, but the large burns did have patches with particularly dense regeneration. Small and medium fires had lower sapling densities. Cover density and perceived safety from predation can also affect hare presence. Hares can trade off food and safety from predation at small spatial scales (*e.g.*, foraging paths, or between adjacent forest stands (Hik 1995, Hodges 1999, Griffin and Mills 2009), but Canada lynx (*Lynx canadensis* Kerr, 1792), using large post-fire landscapes, cue in on forest stands that retain or regrow the densest cover and are thus likely to have the highest densities of hares (Vanbianchi et al. 2017a, 2017b). Thus, at the landscape scale, hares may not be able to trade off food and safety; they use dense regenerating patches within burn scars even though predators also seek out these stands.

Conclusions

More heterogeneous landscapes support overall higher abundances of snowshoe hares after fire. Large wildfires induce high post-fire heterogeneity, and our results suggest that forest and wildlife managers should protect post-fire forest patches that either have legacy forests (*e.g.*, unburned or lightly burned fire skips) or dense post-fire regeneration. These areas will support the highest hare numbers in landscapes affected by large fires, and are known to attract mesopredators such as Canada lynx (Lewis et al. 2011, Vanbianchi et al. 2017a, 2017b).

This study focused solely on snowshoe hares and did not attempt to measure the presence or abundances of other small mammals or predators. Future research into other prey species in response to fire size would be insightful, especially in the context of trying to manage mesopredators or raptors that prey on small mammals in these altered landscapes. Few studies have addressed the impact of fire size on wildlife responses (Hutchen et al. 2017), but the results of this paper contribute to the growing body of literature suggesting that mammal responses to wildfire disturbances are spatially nuanced.

Authors' contributions
JH and KEH jointly designed the study and co-wrote the manuscript. JH collected the data and did the analyses. KEH assisted with interpretation. Both authors read and approved the final manuscript.

Availability of data and materials
Please contact author for data requests.

Ethics approval and consent to participate
Not applicable.

Consent for publication
Not applicable.

Competing interests
The authors declare that they have no competing interests.

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