

RESEARCH ARTICLE

Spatial patterns and rarity of the white-phased 'Spirit bear' allele reveal gaps in habitat protection

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Abstract

1. Preserving genetic and phenotypic diversity can help safeguard not only biodiversity but also cultural and economic values.

2. Here, we present data that emerged from Indigenous-led research at the intersection of evolution and ecology to support conservation planning of a culturally salient, economically valuable, and rare phenotypic variant. We addressed three conservation objectives for the white-phased 'Spirit bear' polymorphism, a rare and endemic white-coated phenotype of black bear (*Ursus americanus*) in Kitasoo/Xai'xais and Gitga'at Territories and beyond in coastal British Columbia, Canada. First, we used non-invasively collected hair samples ($n = 385$ bears over $\sim 18,000$ km²) to assess the spatial variation in the frequency of the allele that controls the white-coloured morph (*mc1r*). Second, we compared our observed allele frequencies at *mc1r* with those expected under Hardy-Weinberg equilibrium. Finally, we examined how well current protected areas in the region aligned with spatial hotspots of Spirit bear alleles.

3. We found that landscape-level allele frequency was lower than previously reported. For example our systematic sampling estimated a frequency of 0.25 (95% CI [0.13, 0.41]) on Gribbell Island compared with the previously reported estimate of 0.56. Also, in contrast with previous reports, we failed to detect a statistically significant departure from Hardy-Weinberg equilibrium at *mc1r*, which calls into question the previously posited role of homozygote gene flow, heterozygote disadvantage, and positive assortative mating in the maintenance of this polymorphism. Finally, we found a discrepancy between the placement of protected areas and the 90th percentile hotspots

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(upper 10% of all estimated values) of Spirit bear alleles, with ~50% of hotspots falling outside of protected areas.

4. These results provide new insight into hypotheses related to the maintenance of this rare polymorphism, and directly relevant information to support evidence-based opportunities for Indigenous Nations of the area to attend to gaps in conservation planning.

KEYWORDS

Great Bear Rainforest, Kermode, phenotypic diversity, protected areas, Spirit bear, *Ursus*

1 | INTRODUCTION

Although protected areas and conservation strategies are often designed to protect populations, species, and community diversity, preserving genetic and phenotypic diversity is increasingly considered. Additionally, whereas most conservation genetics programs aim to preserve diversity by ensuring gene flow, considering the opposite – safeguarding spatially restricted phenotypic and genotypic variants – is also important (Funk, McKay, Hohenlohe, & Allendorf, 2012). Such variants, which may have distinctive morphology, life history traits, or habitat use, often signal local adaptation to ecological conditions (Crandall, Bininda-Emonds, Mace, & Wayne, 2000). Indeed, endemic and rare variants can represent a unique evolutionary lineage, and thereby warrant special protection (Moritz, 1994). Rare phenotypes can also have differing ecological relationships than the dominant form. For example colour morphs in monkeyflowers (*Mimulus lewisii* and *Mimulus cardinalis*) determine whether their primary pollinators are bumblebees (*Bombus* spp.) or hummingbirds (*Calypte* spp; Bradshaw & Schemske, 2003; Schemske & Bradshaw, 1999). Moreover, in the context of rapidly changing ecological conditions under climate change (Barnosky, 2008), habitat degradation (Newbold et al., 2016), and invasive species (Mack et al., 2000), phenotypic variants may signal higher genetic diversity and additional adaptive potential of populations (Forsman, Ahnesjö, Caesar, & Karlsson, 2008). Accordingly, there is increased urgency to plan for resilience by identifying and managing for the spatial distribution of rare and endemic variants.

Rare, endemic, or otherwise striking organisms can also hold cultural significance for people, thus further increasing interest in protection. Culturally salient organisms can be recognized in part by their unique naming and associated terminology, role in narratives, symbolism, and ceremonies, use in food or social practices, and persistence of use relative to cultural change (DeRoy, Darimont, & Service, 2019; Garibaldi & Turner, 2004). Although biocultural significance is often considered for species (Garibaldi & Turner, 2004), unique forms of variation within species may also confer saliency, and therefore contribute to conservation importance. For example the black panther, a rare dark-coated morph of the more common spotted-coated jaguar (*Panthera onca*), plays an integral role in the culture and mythology of Indigenous communities in the Americas (Saunders, 1998). More broadly, the need to safeguard organisms of cultural significance in relation to

Indigenous people's rights has been reaffirmed at international (United Nations General Assembly, 2007) and national (Indigenous Circle of Experts of Canada, 2018) governance forums. Important to both cultures and ecosystems, conservation is often more effective when targeted towards culturally valuable species or forms (DeRoy, Darimont, & Service, 2019; Gavin et al., 2015).

1.1 | Cultural, ecological, and evolutionary context of 'Spirit bears'

A portion of what is now recognized as British Columbia, Canada, hosts an endemic and rare form of a mammal about which little is known to Western ecologists, yet has been of cultural significance to local Indigenous Nations since time immemorial. There, the white-coated black bear (*Ursus americanus kermodei*), referred to as a 'Kermode' or 'Spirit bear', is one of the most conspicuous coat colour polymorphisms among all mammals (Caro, 2005). Previous genetic research identified a recessive mutation (a 'G allele') at the melanocortin 1 receptor (*mc1r*) gene underlying the white coat colour (Ritland, Newton, & Marshall, 2001). Heterozygotes and dominant homozygotes have black coats and are visually indistinguishable (Ritland et al., 2001). Population genetic models suggested the role of genetic drift in the establishment of the Spirit bear allele ('G allele'), and the potential for selection in its maintenance; additionally, previously reported heterozygote deficiency at *mc1r* implicated an unusually high level of positive assortative mating, even when combined with the effects of gene flow from black phase homozygotes, as well as potential heterozygote disadvantage (Hedrick & Ritland, 2011; Ritland et al., 2001). A separate line of inquiry, based on ecological and behavioural research, has suggested the polymorphism could be supported by a multi-niche mechanism, whereby the white morph is associated with a niche defined by increased consumption of salmon (*Oncorhynchus* spp.; Klinka & Reimchen, 2009; Reimchen & Klinka, 2017).

Earlier work described a limited distribution of Spirit bears with a distinct spatial pattern in allele frequency on which conservation planning was in part based. The Spirit bear phenotype primarily occurs on a handful of islands and nearby mainland over approximately a 6,500 km² range. Reported white-coat phenotypic frequencies were reported to be as high as 43% in the core range, approximately

70 km away from which its estimated frequency declined to near zero (Marshall & Ritland, 2002; Ritland et al., 2001). Existing population estimates, based on expert opinion or presumed black bear densities combined with available allele frequencies, vary from 100 to 500 white-phased individuals (Blood, 1997; McCrory, Bergdah, Paquet, & Cross, 2001; Sachs, 2010). Despite this limited information and uncertainty, Spirit bears were used as a flagship element to design a recently legislated protected area network, which includes the ~1,000 km² 'Kitasoo Spirit Bear Conservancy', and garnered worldwide attention to the area, commonly referred to as the 'Great Bear Rainforest' (Ministry of Forests, Lands, and Natural Resource Operations, 2016).

Addressing some of this uncertainty and with the intention of supporting Indigenous-led land-use planning, the Kitasoo/Xai'xais and Gitga'at First Nations in this area embarked on research to determine the spatial distribution of the allele underlying this rare white bear. These efforts emerged from relationships with, respect for, and reciprocity between people and wildlife of the region (Adams et al., 2014; Artelle et al., 2018). In the Tsimshian language group, Spirit bears are referred to as *Moksgm'ol*; relationships with and respect towards these unique bears are expressed through traditional stories, dance, and songs. Oral history belonging to the Kitasoo people tells of *Wee'get* (Raven, the Trickster) changing the coat colour of every 10th black bear on Princess Royal Island to white as a reminder of the harsh conditions endured during the ice age (Wisconsin glaciation: up to ~11,000 before present; Carter, 1966). In addition to cultural relationships, the Kitasoo/Xai'xais and Gitga'at Nations operate successful bear-based ecotourism businesses (Lemelin, Koster, & Youroukos, 2015). Against this cultural, ecological, and economic background, and reciprocating these benefits, the Kitasoo/Xai'xais and Gitga'at have invested in conservation-oriented research into these rare variants.

1.2 | Objectives

Here, we address three objectives of this community-engaged work at the intersection of ecology and evolution to support conservation planning of a culturally salient, endemic, and rare phenotypic variant. We (a) assess the spatial variation in the frequency of the allele ('G allele') that controls the colour polymorphism, (b) test our observed allele frequencies at mc1r to those expected under Hardy-Weinberg equilibrium, and (c) examine alignment of current protected areas in the Great Bear Rainforest with spatial hotspots of Spirit bear alleles.

2 | METHODS AND MATERIALS

2.1 | Study area

To survey for the Spirit bear allele at mc1r beyond its previously documented range (Blood, 1997; Ritland et al., 2001), we included in our study area additional portions of the territories of the Kitasoo/Xai'xais,

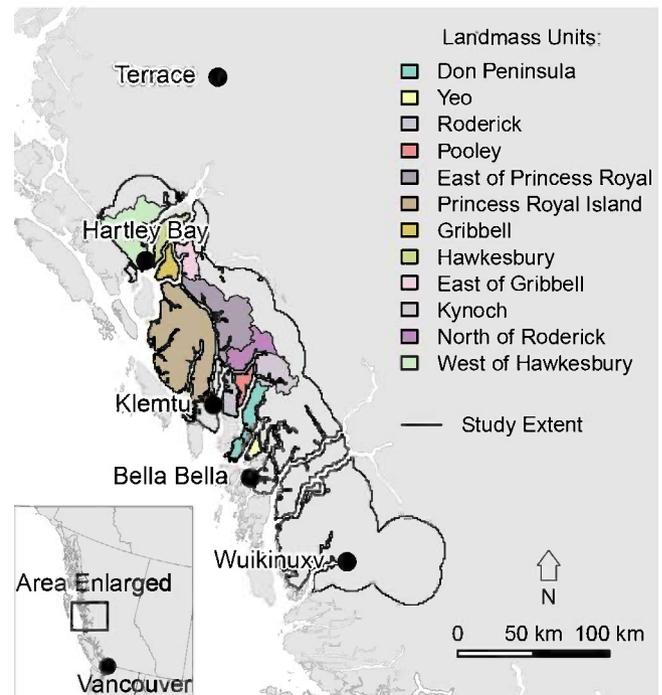


FIGURE 1 Study area (2012–2017) and corresponding communities in coastal British Columbia, Canada. Coloured polygons indicate each unique landmass for spatial scale A, and the solid line indicates the extent of spatial scale B (see Methods)

Gitga'at, Haizaqv (Heiltsuk), and Wuikinuxv First Nations on the central coast of British Columbia that were not previously sampled (Figure 1). This area consists of a large archipelago and nearby mainland valleys of temperate rainforest (Service et al., 2014). Whereas black bears are present across the entire landscape, grizzly bears (*Ursus arctos*) occur in mainland watersheds but are largely absent in most island watersheds (Service et al., 2014). The Spirit bear phenotype was previously reported to occur at the highest frequencies on Gribbell Island (~43%), followed by Princess Royal Island (~17%), with the frequency decaying to near zero on neighbouring islands and mainland watersheds (Marshall & Ritland, 2002; Figure 1; Table 2).

2.2 | Spatial scales

We used two different spatial scales of analysis. To allow for direct comparisons, we matched our primary study area to previous research on Spirit bears (~6,660 km²; Ritland et al., 2001; Marshall & Ritland, 2002; Hedrick & Ritland, 2011; Figure 1). We used this study area extent to bound our allele frequency estimates (see Section 2.5.1). Accordingly, consistent with Ritland et al.'s approach, we compared allele frequencies at the island scale for all detections on islands. For mainland detections, we used combinations of the ecologically informed management 'Landscape Units' (LUs) that best matched the spatial extent described by Ritland et al. (Ministry of Forests, Lands, and Natural Resource Operations, 2016). We refer to each island or mainland LU

as a 'landmass' throughout our analysis (Figure 1). The 'East of Gribbell' landmass was excluded from the analysis owing to its low sample size ($n = 2$ detected bears).

We used a second and larger spatial area and dataset for our analysis of how hotspots of G allele frequency (i.e. the top 10% of all estimated values across the landscape) might align with protected areas (~19,000 km²; Sections 2.5.2 and 2.5.3). This second spatial scale extends from the previously described extent of the G allele, particularly to the south to ensure we captured the full distribution of the G allele (Figure 1) in that direction.

2.3 | Field sampling

During May and June each year (2012–2017), we assembled non-invasive hair snagging sites ($n = 175$ average among years) baited with a non-reward fish-based liquid lure (Adams et al., 2017; Bryan, Darimont, Paquet, Wynne-Edwards, & Smits, 2013; Bryan, Darimont, Paquet, Wynne-Edwards, & Smits, 2014; Woods et al., 1999) to collect hair samples. Sites were approximately evenly spaced (~1 per 50 km²) and spanned ecological and elevational gradients (Figure 1). Hair samples were collected every 10–14 days over two or three sampling sessions each year. Our protocol was approved by the Stewardship Departments of the Kitasoo/Xai'xais, Gitga'at, Hałzaqv (Heiltsuk), and Wuikinuxv First Nations. Sampling in Parks occurred under BC Parks Use Permit 108648. Research was approved by the University of Victoria's Animal Care protocol 2016–020 and followed the Canadian Council for Animal Care's requirements concerning animal care and wildlife (Sikes & Gannon, 2011).

2.4 | Laboratory analysis

We determined individual identity and species using seven microsatellite loci, plus an amelogenin locus sex marker, at a commercial laboratory (Wildlife Genetics International Ltd., Nelson, BC, Canada). The laboratory also assigned mc1r genotypes (AA (black coat homozygote), AG (black coat heterozygote), and GG (white coat homozygote)) following a protocol they developed (see full details in Supporting Information), which drew from the general process previously described by Ritland et al. (2001). All hair samples of known individuals within the smaller study area were typed for their mc1r genotype. A random subsample of all detected individuals ($n = 120$ of 444) within the larger study area (collected as part of a larger unrelated ecological project in partnership with the aforementioned Nations; e.g., Adams et al., 2017; Bryan et al., 2013, 2014; Service et al., 2014, 2018) was scored for the mc1r genotype. This approach balanced the financial costs of genetic analyses with the benefits of a larger sample size to estimate allele frequencies for this portion of the study area for which we anticipated a very low frequency of the G allele. These assignments allowed us to estimate the spatial variation of the G allele frequency across the larger study area.

2.5 | Data analysis

We estimated the spatial pattern of Spirit bear allele frequency, compared patterns of Spirit bear allele frequencies with those expected under Hardy–Weinberg equilibrium, and assessed how well Spirit bear allele 'hotspots' (below) aligned with protected areas. All analyses were carried out in R (version 3.1.05; R Core Team, 2018).

2.5.1 | Testing whether the mc1r gene is in Hardy–Weinberg equilibrium

We tested whether our observed mc1r genotype frequencies conformed to expected Hardy–Weinberg proportions (Hardy, 1908) within each landmass. To match the approach previously applied to an independent dataset (Ritland et al., 2001), we used a Monte Carlo Exact Test derivation of a chi-squared Goodness of Fit test to compare expected versus observed genotypes. Additionally, we specifically tested for a deficit of heterozygotes as previously reported (Ritland et al., 2001) using a Monte Carlo Exact Test *U*-score statistic, where positive values indicate an excess of homozygotes, and negative values signal a surplus of heterozygotes. All calculations were conducted in the *HWxtest* package (Engels, 2009). We calculated a 95% confidence interval around all allele frequency estimates using a Jeffery's interval distribution in the R package *binom*, an approach suitable when values approach 0 or 1 (Brown, Cai, & Dasgupta, 2001). Finally, we tested for differences between our allele frequency estimates by landmass with those calculated during previous sampling efforts (Ritland et al., 2001) using Fisher's exact tests.

2.5.2 | Estimating spatial patterns of G allele frequency

We estimated the spatial pattern of G allele frequency at the larger landscape scale (18,861 km²) with a weighted-kriging approach that considers cost-based distance. This approach generates estimates of a response variable across a sampled landscape, while considering landscape connectivity (López-Quílez & Muñoz, 2009). Our input data points were the G allele frequency values (number of G alleles/total alleles) at each sampling site ($n = 175$), pooled across years. When individual bears ($n = 385$) were detected in multiple locations, we allowed their alleles to contribute to all sites of detection ($n = 988$ alleles included in analysis). We defined the boundaries of our spatial extent as 20 km away from outermost sampling sites and we excluded islands that did not have any sampling sites. Given that our multi-year (2009–2018) detection data suggest black bears in our study area rarely cross ocean channels (Darimont, unpublished data), we weighted the resistance of the ocean as 100 times greater than land, using the *gdistance* package (van Etten, 2017). Given that the number of alleles detected varied (range = 2–28) across sampling sites, we also weighted the contributions of each sampling site to the model by the number of total

TABLE 1 Observed (O) versus expected (E) mc1r genotypes of black bears (*Ursus americanus*) by landmass in coastal British Columbia, Canada (2012–2017). Monte Carlo Exact Chi-square *p*-values reflect results from tests for departures from genotype frequencies expected under Hardy–Weinberg equilibrium. *U*-score *p*-values reflect tests for an excess or deficiency of heterozygosity at mc1r

Landmass	GG (white)		AG (black)		AA (black)		Chi ² <i>p</i>	<i>U</i> -score <i>p</i>
	O	E	O	E	O	E		
Island								
Hawkesbury	0	0.00	0	0.00	24	24.00	–	–
Gribbell	1	1.13	7	6.75	10	10.12	1.00	0.74
Princess Royal	8	5.32	25	30.36	46	43.32	0.14	0.09
Roderick	0	0.01	1	0.98	21	21.01	1.00	1.00
Pooley	0	0.00	0	0.00	6	6.00	–	–
Yeo	0	0.00	0	0.00	5	5.00	–	–
Mainland								
West of Hawkesbury	0	0.03	2	1.94	34	34.03	1.00	0.99
East of Princess Royal	0	0.15	4	3.70	23	23.15	1.00	0.89
North of Roderick	0	0.02	1	0.96	11	11.02	1.00	1.00
Kynoch	0	0.00	0	0.00	15	15.00	–	–
Don Peninsula	0	0.01	1	0.98	21	21.01	1.00	1.00

alleles. We fit a Matern variogram model (Cressie, 1990) using maximum likelihood to account for spatial structure in G allele frequency values. The selected variogram model was used to fit a cost-based weighted kriging model using the *krig.conv* function in the *geoRcb* package (López-Quílez & Muñoz, 2009) to create the interpolated G allele frequency surface. We used the predicted surface to identify hotspots of G allele frequencies and assess their spatial alignment with protected areas (Section 2.5.3).

2.5.3 | Assessing alignment of protected areas with G allele hotspots

We assessed the alignment between our kriged G allele frequency surface and protected areas through two complementary approaches. First, we identified hotspots of allele frequency, defined as pixels with values in the 90th percentile (i.e. top 10% of the entire interpolated raster surface from Section 2.5.2) and assessed the percentage of the hotspot that corresponded with protected areas. To assess sensitivity of this arbitrary, but logical, cutoff value, we also report values for the 95th (top 5%) and 85th percentile (top 15%) hotspots. Secondly, we calculated the percentage of protected area in each landmass and tested if this value was predicted by G allele frequency through a linear regression model and a Pearson's correlation.

3 | RESULTS

Our estimates of Spirit bear allele frequencies varied by landmass and differed from previous reported values for the same area. Mean estimates for G allele frequencies ranged from 0.0 (e.g. Hawkesbury Island)

to 0.26 (Princess Royal Island), were mostly lower than previously reported estimates, and were significantly lower on Roderick (Odds ratio = 0.091; *p* = 0.018) and Gribbell (Odds ratio = .261; *p* = 0.007) Islands (Table 2). Also, in contrast with previous research, we did not detect a heterozygote deficiency. Rather, we failed to detect a statistically significant departure from Hardy–Weinberg equilibrium in any landmass (Table 1; Table 2).

We found that multiple regions of high G allele frequency occurred outside of protected areas. Specifically, approximately 50% of the 90th percentile hotspots corresponded with protected areas (Figure 2; Table 2). Similar results emerged for the 95th and 85th percentiles, at approximately 50% and approximately 45% protected area coverage, respectively. Across landmasses, protected area coverage was not related spatially to the G allele frequency (*R* = –0.012; *F* = 0.001; *p* = 0.971). The two landmasses with the highest G allele frequency differed strongly in protected area coverage, with Princess Royal Island (G frequency = 0.26) having high coverage (52% of area) and Gribbell Island (G frequency = 0.25) having very low protection (0.05%; Table 2).

4 | DISCUSSION

Our results suggest that landscape-level frequency of the G allele is lower than previously estimated, and that populations previously reported to demonstrate a heterozygote deficiency are in fact in Hardy–Weinberg equilibrium. Additionally, despite the role of Spirit bears as a flagship organism for conservation planning in the region, we found a discrepancy between the placement of protected areas and hotspots of G alleles, with approximately 50% of the '90th percentile hotspots' falling outside of protected areas.

TABLE 2 Estimated mean and 95% lower (LCL) and upper (UCL) confidence limits of G allele frequency ($q(G)$) in black bears (*Ursus americanus*) by landmass estimated in this study (2012–2017) and previous work by Ritland et al. (2001) in coastal British Columbia, Canada. 'PA coverage' denotes the percentage of each landmass in protected areas. Bolded q -values differed significantly between our sampling effort and previous estimates by Ritland et al. (2001) (Fisher's exact test: both $p < .05$)

Landmass	$q(G)$	$q(G)$ LCL	$q(G)$ UCL	n	$q(G)$ (2001)	n (2001)	PA coverage
Island							
Hawkesbury	0.00	0.00	0.36	24	0.02	25	0
Gribbell	0.25	0.13	0.41	18	0.56	23	0
Princess Royal	0.26	0.20	0.33	79	0.34	52	52
Roderick	0.02	0.00	0.10	22	0.21	12	1
Pooley	0.00	0.00	0.15	6	0.10	10	29
Yeo	0.00	0.00	0.17	5	0.05	10	0
Mainland							
West of Hawkesbury	0.03	0.01	0.09	36	0.08	6	26
East of Princess Royal	0.07	0.03	0.17	27	0.00	25	61
North of Roderick	0.04	0.00	0.18	12	0.13	12	59
Kynoch	0.00	0.00	0.06	15	–	–	100
Don Peninsula	0.02	0.00	0.10	22	0.04	24	21

Several limitations related to our restricted sampling in space and time exist. First, we were not able to sample allele frequencies from one nearby but non-adjacent mainland region with known Spirit bear phenotypes (near the town of Terrace, BC, Canada; Figure 1). However, the previously estimated G allele frequency for this area is low (.05; Ritland et al., 2001), and as such, we reason that we missed detecting very few G alleles. This inference would be particularly strong if the previous allele frequency estimates for this region (Ritland et al., 2001) were higher than those that would be predicted by a more systematic sampling protocol, a pattern we detected when comparing estimates from the two studies in our study area. Additionally, we know of several Spirit bear sightings across our broader study area (spatial scale used in Sections 2.5.2 and 2.5.3), where local Indigenous knowledge has documented their very rare occurrence (Jennifer Walkus, Wuikinuxv Nation, personal communication, 2019). Our sampling over 5 years, however, failed to detect a G allele in these regions. Rather, G allele detections were focused in the core of the primary study area and our G frequency estimates decayed to zero towards the boundaries of our southern sampling extent (Figure 2). Accordingly, we are confident that our sampling efforts were suitable to capture regions with high frequencies of G alleles (and phenotypes).

Our results suggest that Spirit bear alleles are considerably rarer than previously estimated in the literature (Table 2), likely a function of differences in sampling. Specifically, our estimates for Gribbell Island (mean = .25, 95% CI [.13, .41]) were significantly different than the previous mean estimate of .56 (Ritland et al., 2001). This discrepancy could in part be driven from the earlier work's spatially limited sampling, which occurred only at or near the mouths of salmon spawning streams in fall and targeted known areas of white phenotypes (Marshall & Ritland, 2002; Ritland et al., 2001). In addition to our lower estimates being driven by differences in sampling, landscape-level allele

frequency might have decreased in the approximately 20 years between sampling efforts. This decline could be driven by undetected but possible population declines under which rare alleles would be disproportionately lost due to non-random human- or naturally caused mortality biased to G allele-carrying individuals.

Our results show that Spirit bear populations are in Hardy-Weinberg equilibrium for $mc1r$, providing new insight into hypotheses related to the maintenance of this rare and endemic white variant. Specifically, the earlier reported patterns of a heterozygote deficiency for $mc1r$ (Ritland et al., 2001) but no departure from Hardy-Weinberg equilibrium for 10 microsatellite loci (Marshall & Ritland, 2002) implicated assortative mating, recent immigration of black-coated homozygotes, a heterozygote fitness disadvantage, or some combination of these processes. Recent classical population genetic modelling, however, has identified that positive assortative mating would need to be as high as 50% (50% white-white or black-black; and 50% random) to create the previously reported patterns of heterozygote deficiency (Hedrick & Ritland, 2011). Additionally, the proposed presence of a heterozygote fitness disadvantage would not maintain a balanced polymorphism (Futuyma, 1997). In contrast, evidence in this system supports this polymorphism being stable and therefore balanced, at least on Princess Royal Island, where Indigenous oral history (which identifies an enduring '1 in 10' frequency of the white phenotype; Carter, 1966), previous sampling efforts (Ritland et al., 2001), and our recent sampling all suggest similar phenotypic frequencies (Table 2). Finally, examinations of gene flow using F_{ST} confronted the role of gene swamping of white form-containing island populations by black-coated homozygotes from the mainland, showing that migration levels were not high enough to contribute substantially to the previously estimated pattern of a heterozygote deficiency (Harestad, 2007). Collectively, these findings and the lack of an observed heterozygote deficiency

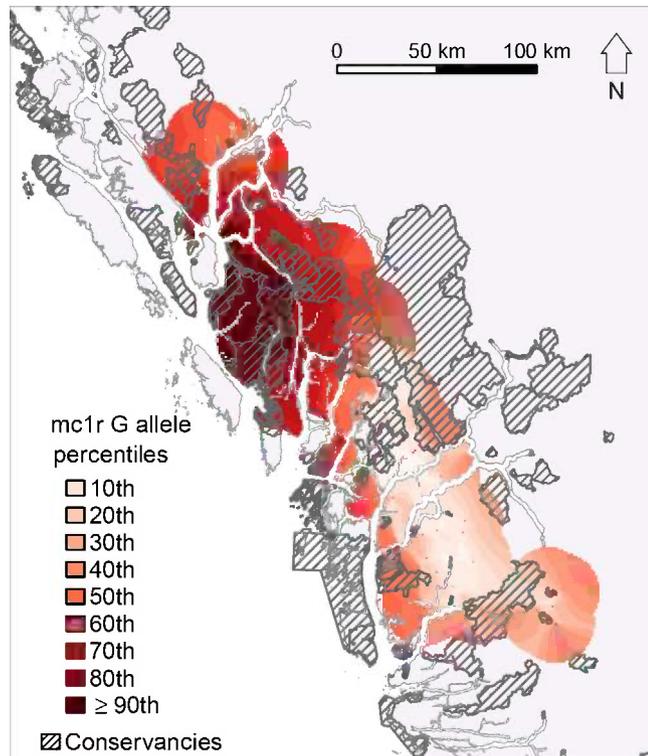


FIGURE 2 Comparison between protected areas ('Conservancies'), and percentiles (10th to ≥ 90 th) of G allele frequency of black bears (*Ursus americanus*) as estimated by cost-weighted kriging of allele ratio ($n = 988$ alleles) across 175 sampling sites in coastal British Columbia, Canada (2012–2017)

do not support the role of associative mating, heterozygous fitness disadvantage, and homozygote gene flow in the maintenance of this polymorphism. Given this new context, we predict that the geographic and subsequent genetic isolation of these island populations could play a significant role in maintaining this phenotype. Considerable evidence also exists that white phenotypes have an advantage in capturing salmon, a fitness-related food (Klinka & Reimchen, 2009; Reimchen & Klinka, 2017).

Our sampling program and analyses offered novel insight into the spatial patterns of the allele underlying this polymorphism and hypotheses related to its maintenance. We sampled a variety of elevational and ecological gradients via boat and helicopter (~ 1 sampling site per 50 km^2). This approach provided more representative coverage of available habitat, including areas far from shore in this nearly roadless environment, compared with the previous sampling design (Ritland et al., 2001). Sampling farther from the shore also provided additional insight into the maintenance of the phenotypic variant. Specifically, in the 'Mainland East of Princess Royal Island' (Figure 1), the one landmass where our G allele frequency estimate was higher than previous estimates (Table 2), we failed to detect G alleles at the shore (as per Ritland et al., 2001). We did, however, detect the allele among heterozygote individuals sampled up and into the headwaters of watersheds. Recent observational and isotopic research has identified the potential selective advantage of the white phenotype during

predation of salmon (Klinka & Reimchen 2009; Reimchen & Klinka 2017). Based on these data, Reimchen and Klinka (2017) proposed that targeted sampling during previous research near the mouths of salmon streams (where much of the spawning occurs) during the fall could have overestimated G allele frequency as the white morph might be more likely to be detected in those streams to capitalize on this foraging advantage. Spatial data here align with that hypothesis. The potential over-representation of the G allele frequency in previous estimates could be driven by non-random sampling of areas more likely to contain white individuals and heterozygotes.

4.1 | Conservation implications

We found a potential limitation in regional land-use plans to conserve Spirit bears as assessed by the spatial patterns in the mc1r G allele frequency. We identified multiple hotspots of the allele outside of protected areas, specifically on Gribbell and Princess Royal Islands, as well as watersheds on the Mainland East landmass of Princess Royal (Figure 2). Areas outside of formal protection are potentially subject to large-scale clear-cut logging and the creation of new road networks in watersheds never subjects to industrial activity. Disturbance from industrial activity could result in a myriad of adverse impacts. Broadly, emerging evidence suggests that initial industrial disturbances in otherwise intact landscapes exert disproportionately negative impacts on biodiversity (Betts et al., 2017; Watson et al., 2018). From an economic perspective, industrial disturbance-driven landscape change may compromise ecotourism potential of Spirit bear viewing, which relies in part on landscapes minimally disturbed by industry. Additionally, these disturbances could modify resources available to bears over the long term (e.g. berry and other plant-based foods, as well as salmon; Nielsen, Munro, Bainbridge, Stenhouse, & Boyce, 2004; Waples, Beechie, & Pess, 2009), and expose them to increased human-caused mortality (Boulanger & Stenhouse, 2014). If additional protection for Spirit bears is desired by Indigenous governments, Indigenous Protected and Conserved Areas (IPCAs; Zurba, Beazley, English, & Buchmann-Duck, 2019) – as well as negotiations among First Nations, provincial governments, and forestry operators – may provide appropriate mechanisms to protect these culturally salient and economically important animals and their ecosystems in a manner that benefits the bears and human communities of the area. These approaches are particularly timely for Spirit bear conservation against a backdrop of reduced Pacific salmon returns (Price, English, Rosenberger, MacDuffee, & Reynolds, 2017), and the recent movement of grizzly bears (*Ursus arctos*) onto islands inhabited by Spirit bears (Service et al., 2014), which has been demonstrated to reduce black bear salmon consumption by approximately 40% with likely negative implications for fitness (Service et al., 2018). We note, however, that 'hotspots' are likely dynamic, and prudent management of these rare alleles should include continued monitoring and adaptive management.

Although this research necessarily focused on the small spatial scale of this geographically restricted rare animal, several more broadly applicable lessons emerge. First, our work provides an example of

local Indigenous communities identifying and investing in scientific research into a unit of biodiversity of high local cultural, economic, and conservation value. Although the Spirit bear phenotype diverges from the more common species-based taxonomy that commonly serves as the biological unit of conservation planning, this work builds upon examples in other taxa and geographies where Indigenous knowledge has helped shape the priority units of biological diversity for conservation. For example, both the Indigenous knowledge of the Sahtú Dene and Métis communities and genetic approaches guided the novel identification of caribou (*Rangifer tarandus*) population structure in Canada's North to inform conservation measures (Polfus et al., 2016). Collectively, approaches like these add to an emerging global pattern of reconciling Indigenous values and scientific approaches to improve conservation and management outcomes (Ban et al., 2018).

AUTHOR CONTRIBUTIONS

C.N.S., C.T.D., P.C.P., C.P., and D.N. conceived the ideas and designed the work. C.N.S., L.H., D.N., and M.S.A. collected the data. C.N.S., M.B., L.H., and M.S.A. analysed the data. C.N.S. and C.T.D. led the writing. All authors contributed to every draft and approved the final version for publication.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

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