

# Niche differentiation between coat colour morphs in the Kermode bear (*Ursidae*) of coastal British Columbia

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One of the most distinctive colour polymorphisms of any mammal occurs in black bears (*Ursus americanus kermodei* Hornaday) of the Great Bear Rainforest of coastal British Columbia. We use carbon and nitrogen stable isotope values and C/N ratios along segments of hair shafts obtained from 14 white and 12 black individual bears to quantify dietary niche of the morphs as a test of the multi-niche model for a polymorphism. On Gribbell Island, where the white bear reaches 30%,  $^{15}\text{N}$  is significantly (GLM repeated measures) more enriched (more marine-derived nitrogen) in the white morph than in the black morph in each season (spring, summer, autumn). On the adjacent Princess Royal Island, where the white morph is less common, both morphs are highly enriched during autumn ( $\sim\delta^{15}\text{N} = +11\%$ ), but there are no isotopic differences between morphs in any season. On both islands, C/N ratios ( $\sim 3.1$ ) of the black morph decrease from spring to autumn, converging on the lower average values for the white morph. Our data suggest that niche of the white morph involves increased use of a marine-associated diet and that ecological segregation between the morphs has facilitated the historical persistence of the polymorphism.

ADDITIONAL KEYWORDS: C/N ratios – Great Bear Rainforest – hair shaft – marine-derived nutrients – multi-niche polymorphism – salmon – Spirit bear – stable isotopes – *Ursus americanus kermodei*.

## INTRODUCTION

Coat colour in North American black bear (*Ursus americanus*), although uniformly black throughout most of its range, exhibits a highly distinctive ‘white’ morph in coastal regions of British Columbia. This morph (referred to as the Kermode or Spirit bear) co-exists with the black morph (Cowan & Guiguet, 1956) and is arguably the most distinctive and conspicuous of all coat colour polymorphisms in carnivores (review in Caro, 2005). A similar polymorphism has recently been described in brown bear (*Ursus arctos*) from the southern Kuril Islands of Japan (Matsubayashi *et al.*, 2016).

The genetics of the Kermode colour polymorphism has been investigated. The white morph is determined by a recessive mutation at the melanocortin 1 receptor gene (*Mc1r*), the same locus associated with coat colour variation in other mammals (Ritland, Newton & Marshall, 2001). This leads to three genotypes of which the heterozygote is indistinguishable from the

dominant black homozygote. Based on genotyping hair collections, the highest frequencies of the white bear occur on Gribbell Island (43%) and Princess Royal Island (17%) (Ritland *et al.*, 2001). This appears to represent a historically stable polymorphism rather than a recent transient polymorphism, as the prevalence of the Kermode bear on the two islands is deeply rooted in the oral history of First Nations in the region (McCrorry, 2012). Phylogenetic analyses place the Kermode bear within a common lineage of coastal subspecies that probably persisted in ice-free areas on the continental shelf during the last glacial advance of the Pleistocene (Byun, Koop & Reimchen, 1997).

Balanced polymorphisms have been described in a diversity of taxa and can be maintained through one or more processes such as superior fitness of heterozygotes, inverse frequency dependence, gene flow, disassortative mating and niche differentiation of the morphs (reviews in Ford, 1964; Futuyma, 1997). The Kermode polymorphism is enigmatic, as many of the parameters influencing the island populations should destabilize any equilibrium, leading to the disappearance of the white morph. For example, rather than heterozygote excess, there is a deficiency of heterozygotes

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on Gribbell Island and Princess Royal Island (Ritland *et al.*, 2001; Marshall & Ritland, 2002; Hedrick & Ritland, 2011), and this would destabilize the polymorphism. Gene flow could promote persistence of the polymorphism yet on these islands, potential migrants would largely be homozygous for the black allele, and this should further destabilize the polymorphism (Hedrick & Ritland, 2011). General demographic factors are also incompatible with long-term persistence of this polymorphism, as population size of bears is estimated at ~50 on Gribbell Island (Blood, 1997; Klinka, 2004) and ~400 on Princess Royal Island (Hedrick & Ritland, 2011), well below the minimum viable population size of 2500 derived from taxonomically broad meta-analyses of population persistence (Traill, Bradshaw & Brook, 2007). An inverse relationship between frequency and fitness might promote the maintenance of the polymorphism (Punzalan, Rodd & Hughes, 2005) although there is no evidence for this in the Kermode bear polymorphism.

An alternative mechanism that can favour a polymorphism occurs if morphs occupy different niche space with fitness of each morph coupled to the appropriate niche. Such 'adaptive variation' or 'multi-niche' models have received both theoretical and empirical support (e.g. Levene, 1953; Van Valen, 1965; Reimchen, 1979; Smith & Skulason, 1996; Galeotti & Rubolini, 2004). Field observations of the white and black morph on Gribbell Island (Klinka & Reimchen, 2009a) showed that the white morph had significantly higher salmon capture efficiency than did the black morph during daylight but a lower efficiency during darkness. Although the two morphs differed in several aspects of their foraging strategies, such as movement profiles, some or all of the increased capture efficiency of the white morph during daylight was a consequence of salmon behaviour. Exposing spawning salmon in the stream to a white- vs. black-costumed observer as a simulated predator showed ~50% reduction in salmon evasive behaviour to a white model relative to a black model during daylight, possibly due to the reduced visual contrast against the background of skylight, but during darkness, no difference was observed in fish responses to the model (Klinka & Reimchen, 2009a). Because salmon are the major yearly sources of protein for coastal bears (Gilbert & Lanner, 1995; Hilderbrand *et al.*, 1996, 1999a, b; Reimchen, 2000), the greater potential capture success of salmon by the white bear could facilitate the persistence of this colour polymorphism.

In the present study, as a test of the multi-niche models, we assess the dietary niche of the white and black coat colour morph of the Kermode bear initially by examining  $\delta^{15}\text{N}$  and  $\delta^{13}\text{C}$  stable isotope values in hair shafts. These dual isotopes comprise an important ecological tool for differentiating multiple parameters

of the diet such as trophic-level (elevated  $\delta^{15}\text{N}$ ) and terrestrial- vs. marine-derived diet (elevated  $\delta^{15}\text{N}$  and  $\delta^{13}\text{C}$ ) (Frey, 2006). Dietary intake is reflected in the isotopic ratios of new hair growth, and as such, variation along hair shafts can be used to identify temporal variation in trophic niche if dietary items vary isotopically (Hobson, McLellan & Woods, 2000; Darimont & Reimchen, 2002). In coastal bears, new hair shafts begin growth in spring and on average continue through to late autumn (Schwertl, Auerswald & Schnyder, 2003; Jones, Heard & Gillingham, 2006). Second, we examine percent carbon (%C) and percent nitrogen (%N) atomic ratios (C/N) along the hair shafts. Although C/N ratios in hair have rarely been used in ecological studies, arthropods and primates, these can differ among individuals (e.g. Denno & Fagan, 2003; Oelze, 2016) and potentially offer insight to individual or morph attributes that are additional to isotopic proxies. We assume here that the combination of isotopic and C/N data are proxies for individual niche space.

Because of the reduced evasiveness of salmon to the white morph, we predict greater isotopic enrichment compared with the black morph during autumn spawning season. For hair growth during spring and summer, we have no a priori predictions with respect to relative enrichment. As coastal bears can be observed foraging in the intertidal, riparian zones and subalpine zones, it is possible that the foraging habitats used by the colour morphs are not identical and if so, isotopic signatures could indicate dietary or ecological segregation, consistent with the multi-niche models.

## MATERIAL AND METHODS

Hair samples from 26 *Ursus americanus kermodei* (12 black, 14 white) were provided by K. Ritland (University of British Columbia) who obtained these using hair snags placed on bear trails near river mouths from the central coast of British Columbia (Great Bear Rainforest) during the autumn salmon spawning migration (September and October, 1997, 1998, 1999) as part of a study on the genetics of the Kermode bear (details of field methodology and genotyping in Ritland *et al.*, 2001; Marshall & Ritland, 2002). Because all samples were collected in autumn, hair shafts from each bear on average comprise growth since their spring moult. All hair shafts with a follicle (allowing polarity to be identified) and of similar lengths were cut into three equal segments (base, mid, tip), roughly corresponding to spring, summer and early autumn growth. These were washed and rinsed with a 2:1 mixture of chloroform and ethanol to remove surface debris and oils. After drying at 60 °C for at least 48 h, we powdered the hair in a Wig-L-Bug

grinder (Crescent Dental Co., Chicago, IL, USA). Approximately 1 mg was subsampled for continuous-flow isotope ratio mass spectrometry analysis at the stable isotope facility, Department of Soil Sciences, University of Saskatchewan, Saskatoon, Canada, using a Europa Scientific ANCA-NT gas–solid–liquid preparation module coupled to a Europa Scientific Tracer 20-20 mass spectrometer (PDZ Europa, Cheshire, England). This provided isotopic values for carbon and nitrogen and  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  for all samples. A single white bear was sampled on two separate years, and as this represents new hair growth each year, the samples are processed as separate individuals but designated as such in the results. A single sample (bear #20) had 30% less N and 30% less C than all other samples and consequently was treated as an outlier and removed from the C/N analysis.

Isotope values are expressed in  $\delta$  notation as ratios relative to Vienna Pee Dee Belemnite (carbon) and atmospheric  $\text{N}_2$  (nitrogen) standards as follows:  $\delta X = (R_{\text{sample}}/R_{\text{standard}}) - 1$ , where  $X$  is  $^{13}\text{C}$  or  $^{15}\text{N}$  and  $R$  is the corresponding ratio  $^{13}\text{C}/^{12}\text{C}$  or  $^{15}\text{N}/^{14}\text{N}$ . The precision of mass spectrometry measurements on hair shafts in a concurrent study averaged  $0.05 \pm 0.04$  SD for carbon and  $0.06 \pm 0.05$  SD for nitrogen (Darimont, Paquet & Reimchen, 2008).

The amount of isotopic enrichment in the hair will depend on the length of time that bears had been able to forage for salmon during autumn. We tested (correlation coefficients) whether  $\delta^{15}\text{N}$  values were correlated with sampling date, predicting those sampled early in the salmon spawning period would have lower  $\delta^{15}\text{N}$  values compared with those sampled later.

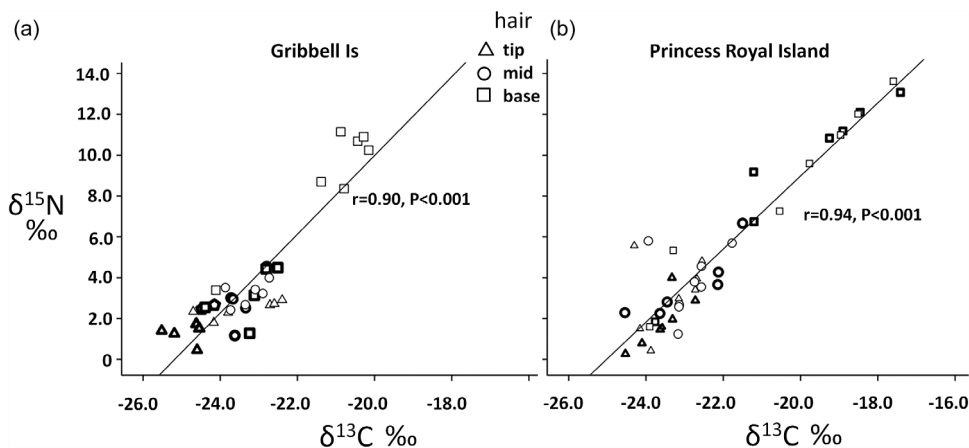
Stable isotope values and C/N ratios from hair shafts for each bear were compared (unpaired Mann–Whitney tests) between islands (Gribbell vs. Prince Royal) and between coat colour morphs (white vs. black) separated for seasons (spring, summer, autumn).

Because the values for season for each bear are not independent of each other, we also used general linear models (GLM) with repeated measures as this integrates multiple measurements for each individual.  $\delta^{15}\text{N}$  and  $\delta^{13}\text{C}$  were highly correlated with each other and for each statistical comparison involving island, colour and season, we present results principally for  $\delta^{15}\text{N}$ . To examine any unique effects of  $\delta^{13}\text{C}$  values that were not correlated with  $\delta^{15}\text{N}$ , for each island we saved the standardized residuals from a regression between  $\delta^{13}\text{C}$  against  $\delta^{15}\text{N}$ , the latter as an independent, and compared these residuals between morphs. For C/N ratios, we used Kolmogorov–Smirnov tests and GLM repeated measures separated for island. We also examined isotopic distances between colour morphs in relation to the allele frequencies for each island (extracted from Ritland *et al.*, 2001). All analyses were carried out using SPSS version 24.

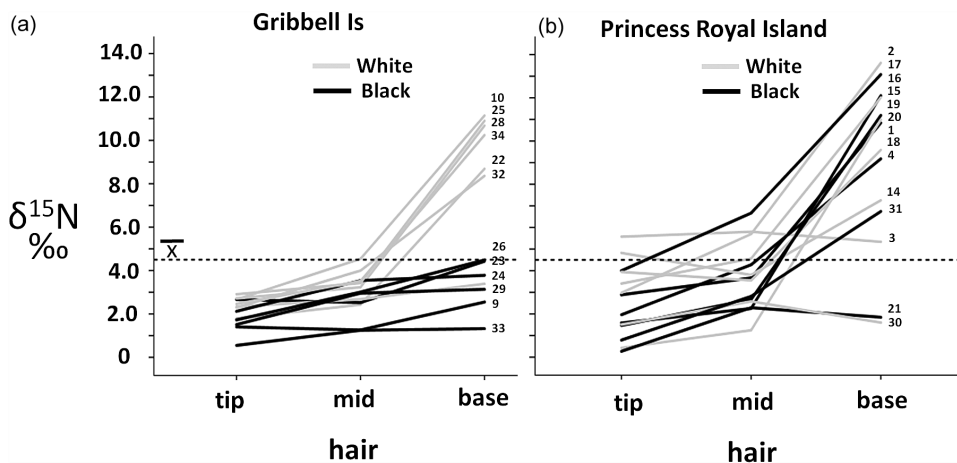
## RESULTS

Isotopic values along the hair shafts and among individuals were variable with  $\delta^{15}\text{N}$  ranging from 0 to 14‰ ( $\bar{x} = +4.5$ ) and  $\delta^{13}\text{C}$  ranging from  $-26$  to  $-17$ ‰ ( $\bar{x} = -22.6$ ) (raw data in Appendix 1). Both isotopes are highly correlated with each other ( $r > 0.9$ ) with similar slopes for Gribbell and Princess Royal Islands (Fig. 1).

Segmental analyses of the hair shafts show that isotopic values differ among seasons and this is associated with coat colour and island (Fig. 2). For Gribbell Island, spring hair  $\delta^{15}\text{N}$  values were slightly higher in the white morph ( $\bar{x} = +2.5$ ‰,  $N = 7$ ) than in the Black morph ( $\bar{x} = +1.6$ ‰,  $N = 5$ ; M-W,  $U_{5,7} = 4.0$ ,  $P < 0.03$ ). A similar difference also occurred in summer (white:  $\bar{x} = +3.4$ ‰,  $N = 5$ ; black:  $\bar{x} = +2.2$ ‰,  $N = 5$ ; M-W,  $U_{5,7} = 5.0$ ,  $P < 0.05$ ). In autumn, six of the seven white bear showed an approximate 6‰



**Figure 1.** Dual isotope plot of hair obtained from 27 Kermode bears on (a) Gribbell Island and (b) Prince Royal Island.

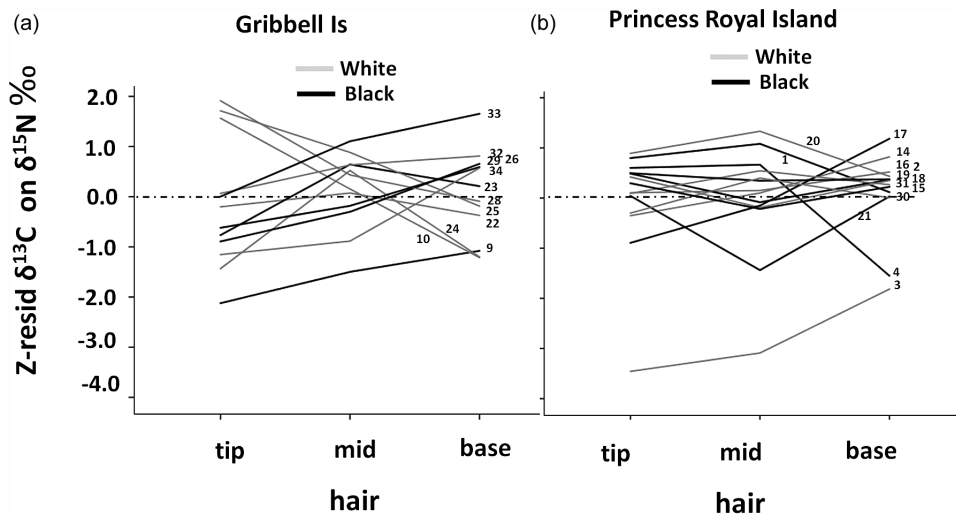


**Figure 2.** Plot of  $\delta^{15}\text{N}$  values for tip (spring), mid (summer) and base (autumn) hair segments obtained from Kermode bears on (a) Gribbell Island and (b) Princess Royal Island. Lines represent each bear with ID. A single white bear on Gribbell Island was sampled twice (25 September 1998 – #28 and 18 September 1999 – #10).

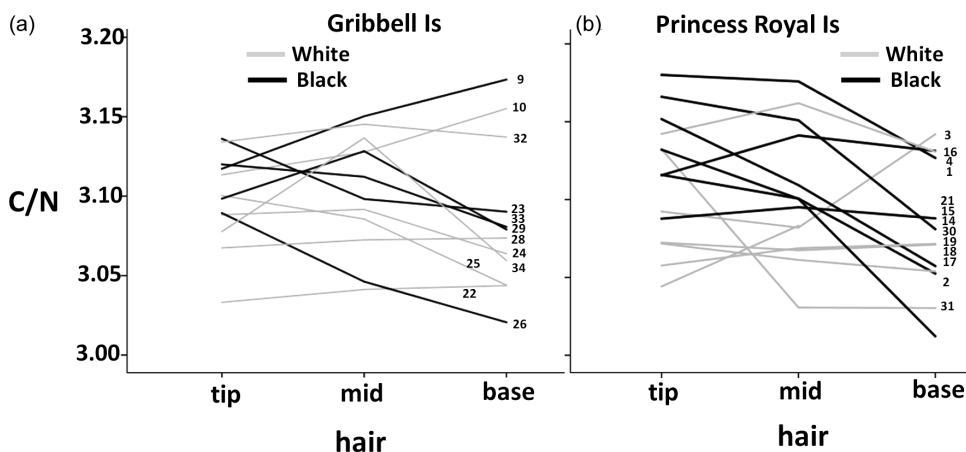
enrichment relative to all black bear although there was a single white bear (#24) with values similar to the black morph in all seasons (white:  $\bar{x} = +9.1\%$ ,  $N = 7$  vs. black:  $\bar{x} = +3.2\%$ ,  $N = 5$ ; M-W,  $U_{5,7} = 2.0$ ,  $P = 0.01$ ). GLM with repeated measures shows a significant within-subject effect for Seasons ( $F_{2,20} = 39.6$ ,  $P < 0.001$ ) and for Season  $\times$  Colour interaction ( $F_{2,20} = 16.2$ ,  $P < 0.001$ ). The between-subject effects (i.e. between the colour morphs) was highly significant ( $F = 18.6$ ,  $P < 0.002$ ). Two hair samples of white bear (#10, #28), collected in separate years, were genotyped as the same individual and had almost identical isotopic values between years. Princess Royal Island bears show no difference between the morphs in each season (Fig. 2b; spring: white –  $\bar{x} = +3.2\%$ ,  $N = 7$ ; black –  $\bar{x} = +1.9\%$ ,  $N = 7$ ; M-W,  $U_{7,7} = 13.0$ ,  $P = 0.14$ ; summer: white –  $\bar{x} = +3.9\%$ ,  $N = 7$ ; black:  $\bar{x} = +3.5\%$ ,  $N = 7$ ; M-W,  $U_{7,7} = 20.0$ ,  $P = 0.6$ ; autumn: white –  $\bar{x} = +8.6\%$ ,  $N = 7$ ; black:  $\bar{x} = +9.3\%$ ,  $N = 7$ ; M-W,  $U_{7,7} = 22.0$ ,  $P = 0.7$ ). Unlike the trend at Gribbell Island where the black morph did not increase in autumn, on Princess Royal Island, the majority of bears (both morphs) showed an approximate 8‰ enrichment between spring and autumn, although three bears (#3, #21, #30), comprising two white and one black, showed no enrichment between spring and autumn. GLM repeated measures for Princess Royal Island indicate a significant Season effect ( $F_{2,24} = 31.4$ ,  $P < 0.001$ ) but no Season  $\times$  Colour interactions ( $F_{2,24} = 0.9$ ,  $P = 0.35$ ) and no Colour effect ( $F = 0.13$ ,  $P = 0.72$ ). There was no significant relationship between autumn isotope signatures and the sampling date (from onset of spawning run) at which the hair samples were obtained (Gribbell Island:  $r = -0.06$ ,  $P = 0.43$ ; Princess Royal Island:  $r = -0.24$ ;  $P = 0.21$ ).

We examined whether  $\delta^{13}\text{C}$  was depleted or enriched relative to that expected for particular  $\delta^{15}\text{N}$  values given the high correlation between these isotopes (see Fig. 1). For Gribbell Island (Fig. 3a), three white bears in spring had high positive residuals relative to the remaining bears, but each shifted towards average or negative residuals in summer and autumn (Season  $\times$  Colour;  $F_{2,30} = 2.8$ ,  $P < 0.08$ ). For Princess Royal Island (Fig. 3b), there were no differences for Colour ( $F_{1,32} = 0.69$ ,  $P = 0.4$ ) or Season  $\times$  Colour interaction ( $F_{2,32} = 0.4$ ,  $P = 0.71$ ) apart from a single white bear (#3) that exhibited the largest negative residuals in each season. This bear also had higher than average  $\delta^{15}\text{N}$  values and was one of the few bears that did not show an autumn enrichment (Fig. 2b).

Total carbon and nitrogen in hair shafts were evaluated (Fig. 4). %N averaged 15.3% and was marginally higher (0.3%) in autumn than in spring ( $F_{2,65} = 7.5$ ,  $P < 0.01$ ) and did not differ between Morphs ( $F_{1,65} = 0.52$ ,  $P = 0.47$ ) and between Islands ( $F_{1,65} = 0.00$ ,  $P = 0.98$ ) with no interactions (all  $P > 0.4$ ). C/N ratios were also variable. On Gribbell Island (Fig. 5), the white morph and black morph did not differ in any season (spring: M-W,  $U_{5,7} = 8.0$ ,  $P = 0.12$ ; summer: M-W,  $U_{5,7} = 14.0$ ,  $P = 0.57$ ; autumn: M-W,  $U_{5,7} = 13.0$ ,  $P = 0.47$ ), while on Princess Royal Island (Fig. 5), the white morph had lower ratios than the black morph in spring and summer but not in autumn (spring: M-W,  $U_{7,7} = 9.0$ ,  $P < 0.05$ ; summer: M-W,  $U_{7,7} = 6.0$ ,  $P < 0.02$ ; autumn: M-W,  $U_{7,7} = 20.0$ ,  $P = 0.89$ ). Correlation matrices of C/N ratios with %C, %N,  $\delta^{15}\text{N}$  and  $\delta^{13}\text{C}$  separated for island and morph indicate that the dominant influence on C/N ratios for both islands and both morphs is the inverse relationship with %N (Gribbell Island:  $r = -0.7$ ,  $P < 0.001$ ; Princess Royal Island:  $r = -0.8$ ,  $P < 0.001$ ) with no effect for %C (Gribbell Island:  $r = -0.03$ ,  $P = 0.90$ ; Princess Royal Island:  $r = -0.05$ ,  $P = 0.74$ ). C/N ratios also were inversely correlated with isotopic values



**Figure 3.** Plot of residuals of  $\delta^{13}\text{C}$  extracted from regression line for  $\delta^{15}\text{N}$  by  $\delta^{13}\text{C}$  relationship (Fig. 1) for tip (spring), mid (summer) and base (autumn) hair segments obtained from Kermode bears on (a) Gribbell Island and (b) Princess Royal Island. Lines represent each bear with ID. A single white bear on Gribbell Island was sampled twice (25 September 1998 – #28 and 18 September 1999 – #10).



**Figure 4.** Plot of %C to %N (C/N) ratios for tip (spring), mid (summer) and base (autumn) hair segments obtained from Kermode bears on (a) Gribbell Island and (b) Princess Royal Island. Lines represent each bear with ID. A single white bear on Gribbell Island was sampled twice (25 September 1998 – #28 and 18 September 1999 – #10).

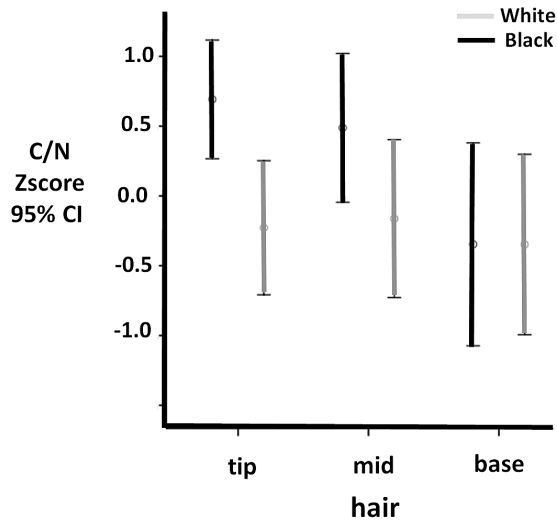
only for the black morph for each isotope on both islands (Gribbell Island,  $\delta^{15}\text{N}$ :  $r = -0.45$ ,  $P = 0.09$ ;  $\delta^{13}\text{C}$ :  $r = -0.62$ ,  $P < 0.02$ ; Princess Royal Island,  $\delta^{15}\text{N}$ :  $r = -0.46$ ,  $P < 0.04$ ;  $\delta^{13}\text{C}$ :  $r = -0.42$ ,  $P < 0.06$ ). GLM with repeated measures supports a significant effect of Season ( $F_{2,22} = 5.1$ ,  $P < 0.02$ ) and a weak Season  $\times$  Colour interaction ( $F_{2,22} = 3.4$ ,  $P < 0.06$ ). Gribbell Island shows no influence for Season ( $F_{2,20} = 1.9$ ,  $P = 0.18$ ), Colour ( $F_{1,10} = 0.4$ ,  $P = 0.54$ ) or Season  $\times$  Colour ( $F_{2,20} = 0.55$ ,  $P = 0.58$ ).

Although number of comparisons is very limited, the extent of mean isotopic differences between the colour morphs (white minus black) is associated with allele frequencies on each island (Fig. 6). In spring and summer, when most bears have a terrestrial or

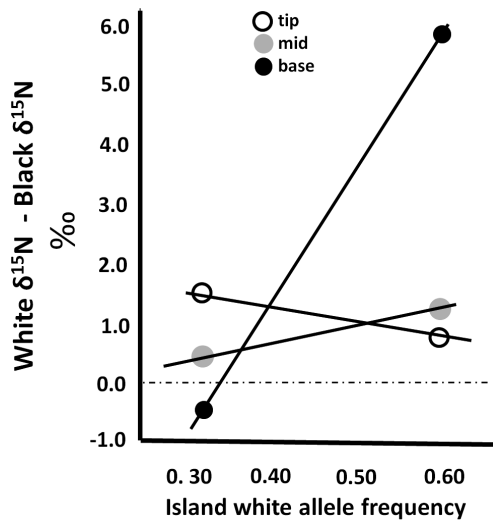
low trophic-level diet (i.e. low isotopic values), there is a slight enrichment in the white morph relative to the black morph at both low and high white allele frequencies. In contrast, in autumn, when most bears are foraging on salmon and show a very large enrichment, the differential between white and black morphs only occurs on the island where the white allele is most common (Gribbell Island).

## DISCUSSION

In bears of the coastal North Pacific, tissue  $\delta^{15}\text{N}$  and  $\delta^{13}\text{C}$  values are a useful proxy for trophic level and the



**Figure 5.** Residuals of C/N ratios ( $\pm$  95% confidence interval) for tip (spring), mid (summer) and base (autumn) hair segment for black morph and white morph. Residuals computed separately for Gribbell and Princess Royal Islands.



**Figure 6.** Isotopic difference between morphs ( $\delta^{15}\text{N}$  white minus  $\delta^{15}\text{N}$  black) for tip (spring), mid (summer) and base (autumn) hair segments against allele frequencies for Princess Royal Island (0.34) and Gribbell Island (0.57). Allele frequencies extracted from Ritland *et al.* (2001).

relative contributions of terrestrial- vs. marine-derived nutrients (Hilderbrand *et al.*, 1996).  $\delta^{15}\text{N}$  values of Alaskan grizzly bears ranged from 0 to 3‰ for a terrestrial diet through to 10 to 14‰ for a diet of mainly salmon (Hilderbrand *et al.*, 1999; Ben-David, Titus & Beier, 2004). Comparable enrichment in salmon watersheds also occurs in coastal wolves (Darimont, Paquet & Reimchen, 2009), mesocarnivores such as marten (Ben-David, Flynn & Schell, 1997), insectivorous birds

(Christie, Hocking & Reimchen, 2008) and predatory insects (Hocking & Reimchen, 2002) through direct or trophic-level use of salmon tissues. Our isotopic data on bears from coastal British Columbia are consistent and show low trophic-level and terrestrial-dominated diet in spring and summer and major enrichment during the autumn salmon spawning period. Yet these seasonal shifts in diet differ between the colour morphs and between islands. On Gribbell Island, the white bears in autumn were 6‰ more enriched than the black morph, consistent with our previous field observations on reduced evasive responses of salmon (Klinka & Reimchen, 2009a). This isotopic enrichment of the white bears indicates a substantive competitive advantage because such enrichment in other coastal bears is associated with improved body condition, larger body size, larger litter size (Hilderbrand *et al.*, 1999a) as well as improved denning survival and body growth of cubs (Ben-David *et al.*, 2004).

While relative isotopic enrichment during autumn salmon spawning season clearly differentiates the coat colour morphs on Gribbell Island, we also observed isotopic differences prior to the autumn appearance of salmon. During spring and summer, all bears had minimal enrichment ( $^{15}\text{N}$ : 0 to 3‰;  $^{13}\text{C}$ : -25 to -21‰), similar to late spring values of Alaskan grizzly bear where the diet is dominated by sedges, grasses and herbivores such as rodents and deer (Ben-David *et al.*, 2004). Our data showed that even with such low enrichment, the white morph was marginally but significantly  $^{15}\text{N}$  and  $^{13}\text{C}$  enriched relative to the black morph in both seasons on both islands but more so on Gribbell Island. This suggests spring and summer spatial differences in foraging between the colour morphs. Isotopic values for intertidal as well as riparian taxa adjacent to salmon streams are more enriched relative to those at higher elevations with no exposure to marine-derived nutrients (Ben-David, Hanley & Schell, 1998; Mathewson, Hocking & Reimchen, 2003; Wilkinson, Hocking & Reimchen, 2005; Fox *et al.*, 2014). Consequently, any increased tendency for white bears to use the marine-terrestrial interface compared with the black morph would result in enrichment. The high residuals of  $^{13}\text{C}$  relative to those expected based on the  $^{13}\text{C}$  and  $^{15}\text{N}$  correlation in three of the white bear on Gribbell Island are consistent with a greater marine-derived diet in spring and summer although this effect was minimal on Princess Royal Island.

Reduced evasiveness of salmon to the white bear (Klinka & Reimchen, 2009a) and the isotopic differentiation on Gribbell Island in each season relative to the black morph would predict comparable enrichment in other islands with salmon watersheds. On the adjacent and much larger Princess Royal Island, while the C/N ratios differed between the morphs, there were no significant isotopic differences and both

morphs became enriched to a similar extent during the salmon spawning periods. Several factors might contribute to these inconsistent results. For example, on Gribbell Island, only two salmon streams are present (Manzon & Marshall, 1981) and spawning areas are greatly restricted resulting in simultaneous aggregations of bears (2–7) and increased high-intensity interactions (Klinka & Reimchen, 2009b), the white morph dominating the black morph during daylight and vice versa during darkness (Klinka, 2004). In contrast, on Princess Royal Island, there are 30 salmon streams (Leaney, Manzon & Marshall, 1982), which might reduce competitive interactions between morphs and limit the relative competitive foraging advantage of the white morph and may also contribute to the low frequencies of the white morph on this island. A second factor could be that the streams on the two islands differ in some unique spectral attributes. Klinka (2004) observed that the black morph, but not the white morph, exploited the shadows of overhanging vegetation thereby reducing their visual contrast against the shadowed background. Island differences in such spectral landscapes could be expected to modify relative foraging success of the colour morphs but currently, there are no data to evaluate this possibility.

An alternate or additional mechanism that can produce a balanced polymorphism is negative frequency dependence, the inverse relationship between fitness and frequency (Clarke, 1964; review in Punzalan *et al.*, 2005). Such a mechanism could be appropriate in the Kermode bear coat colour polymorphism, for example, if salmon were less evasive to the white bear when these bears were uncommon. Although this could be occurring, our autumn isotope data indicate that the white morph had the largest advantage on the island where it was most common but no obvious advantage on Princess Royal Island where the morph was less common, inconsistent with negative frequency dependence.

Apart from isotopic data, C/N ratios in hair shafts of bears could allow additional insight into life histories. Among invertebrate taxa, C/N ratios from whole body extracts are a general proxy of diet, with low ratios having high-protein intake through to low ratios with high lipid intake (Fagan *et al.*, 2002; Denno & Fagan, 2003; Post *et al.*, 2007), while among vertebrates, such as fish, higher trunk muscle C/N ratios (more lipids) are a proxy for 'better condition' rather than differences in diet (Wilder, Raubenheimer & Simpson, 2016). C/N ratios of mammalian hair have received only limited attention in ecological investigations. Hair is predominantly protein (> 90% hard keratin) with some additional lipids, water and minerals (Rogers, 2004; Khan *et al.*, 2014; Farag *et al.*, 2015). Forensic studies on human hair show individual and temporal variation in C/N ratios along the

shaft (range 2.9–3.8), yet these are not influenced by differences in the diet, weathering or amount of melanin (O'Connell & Hedges, 1999). A similar range (3.0–3.8) occurs in infant wild primates (Oelze, 2016). We observed a much narrower range of C/N ratios (3.01–3.18) in both coat colour morphs of the bears but even within this range, we detected shifts in ratios associated with diet and colour morphs. The black morph showed a consistent inverse relationship on both islands between C/N ratios and either  $\delta^{15}\text{N}$  or  $\delta^{13}\text{C}$ , with higher ratios (low %N) occurring during spring and summer when terrestrial diet predominates, through to lower ratios occurring during the autumn dietary shift to salmon. This reduction in autumn ratios of the black morph converges to those of the white morph whose ratios did not change seasonally in any systematic manner despite the autumn shift to a diet of salmon. We speculate that these differences are a further reflection of niche or habitat differences between the morphs, although the reasons for the C/N ratio changes are not known. At low temperatures, mammals with wetted costs incur major thermoregulatory stress (Webb & King, 1984), and this would be particularly common in coastal bears foraging on salmon. Some adaptations to such cold stress have been identified including fur density, fur length, changes in lipid content and keratin-associated proteins (Khan *et al.*, 2014) and modification of cuticular scales on the hair shafts to improve cross-linking of the hairs and insulation (Meyer, Schnapper & Hulmann, 2002; Liwanag *et al.*, 2012). Although we cannot infer that our observed seasonal changes in C/N ratios between the morphs reflect thermal adaptations, the ecological context to this variation may be an additional axis for assessing niche or physiological differences between individuals in monomorphic or polymorphic species.

Despite the presence of numerous salmon watersheds and extensive opportunity for niche partitioning, the low frequency of the white morph on the coastal mainland implicates significant fitness costs relative to the black morph. One of these costs could result from competitive exclusion by the much larger Grizzly Bear (*U. arctos*), which are prevalent on the mainland but are rare or absent on most small islands (Cowan & Guiguet, 1956). Where both species overlap on the mainland, black bear have greatly reduced access to salmon compared with Grizzly bear (Jacoby *et al.*, 1999; Service *et al.*, 2014). This could be particularly costly for the white morph given their high utilization of salmon on the islands. As well, the conspicuous coat colour of the white morph could impose additional risks as Grizzly bear and wolves (*Canis lupus*) are known to predate and consume black bear (Smith & Follmann, 1993; Boyd & Heger, 2000; Darimont *et al.*, 2008).

Hedrick & Ritland (2011) model a theoretical range of parameters that could account for the origin and maintenance of the Kermode coat colour polymorphism on the offshore islands. These include mutation rate, genetic drift, isolation and gene flow and strong selective advantages of the white morph to counteract the destabilizing effects of immigration of the black allele from the mainland. Because of the apparent heterozygote deficiency of the coat colour locus on each of the major islands, an equilibrium could not be readily achieved without high incidence of white–white assortative mating. While this is possible, mating preferences of these bears in the wild are unknown, apart from the occurrence of mother–cub sightings, which shows all coat colour combinations. Our field and isotopic data allow us to re-evaluate some of the basic parameters used in the current models to account for the persistence of this polymorphism (Ritland *et al.* 2001; Marshall & Ritland, 2002; Hedrick & Ritland, 2011).

We infer from our isotopic and C/N data that the coat colour morphs are non-randomly distributed on the landscape, with the white morph on average being found closer to marine habitat and the black morph on average in forested habitat. If this inference is reasonable, it limits reliable estimates of island-level allele frequencies. Hair snags placed only near the mouths or lower reaches of salmon streams, as undertaken in Ritland *et al.* (2001), increase the probability of detecting a white morph. This has two consequences. First, it overestimates the island-wide white allele frequency. We suspect this has occurred, as during three autumn field seasons throughout the length of the major salmon stream on Gribbell Island, Klinka & Reimchen (2009a) observed that of 41 individual bears, 11% were white, which is one quarter the frequency of white bear (43%) based on hair samples of 23 bears (Ritland *et al.*, 2001). Second, overestimating island-wide white allele frequency results in an apparent deficiency of heterozygotes assuming random mating structure. Such a deficiency, generally known as the Wahlund effect, is a simple consequence of non-random sampling of a substructured population (e.g. Rousset & Raymond, 1995) and does not provide evidence for any actual heterozygote deficiency at the population level.

Our empirical results from isotopic data suggest a simpler mechanism for the historical persistence of this striking coat colour polymorphism. We propose that the morphs are ecologically segregated and that their frequencies reflect the amount of available niche space in which the fitness of each morph approaches equality in the appropriate niche. Similar themes have been recently demonstrated in polymorphic lacertid lizards (Scali *et al.*, 2016). Given the very low population numbers of bears on these islands, it seems that inbreeding effects would have compromised long-term persistence

without occasional migration from the mainland (Hedrick & Ritland, 2011) as well as fitness differentials between the morphs (Klinka & Reimchen, 2009a). Such a multi-niche polymorphism does not directly lead to a stable equilibrium, yet even modest influences of stabilizing processes such as density-dependent fitness effects in alternate niches (Reimchen, 1979) or the widely studied heterosis (Ford, 1964; Futuyma, 1997) could promote a balanced polymorphism.

In summary, our study provides new evidence for ecological differences between the coat colour morphs in the Kermode bear, and despite the effects of small population size and destabilizing effects of immigration, the historical persistence of these dimorphic bears indicates high resiliency of this polymorphism. Multiple anthropogenic influences including the 90% reduction in salmon numbers returning to rivers of western North America over the last 100 years (Gresh, Lichatowich & Schoonmaker, 2000), the continued deforestation of watersheds on the islands of the white bear (McCrory, 2012) and the recent colonization and spread of Grizzly bear onto Princess Royal Island (Service *et al.*, 2014) limit the long-term prospects for this remarkable polymorphism.

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**Appendix 1.** Raw data for nitrogen and carbon analyses for hair segments of bear (*Ursus americanus kermodei*) from coastal British Columbia, Canada

Island	Site	Date	Bear ID	Morph	$\delta^{15}\text{N}$ tip	$\delta^{15}\text{N}$ mid	$\delta^{15}\text{N}$ base	$\delta^{13}\text{C}$ tip	$\delta^{13}\text{C}$ mid	$\delta^{13}\text{C}$ base	CN tip	CN mid	CN base
Grib	IR10	18 September 1999	9	Black	+1.4	+1.3	+2.5	-25.5	-25.2	-24.4	3.1	3.2	3.2
Grib	IR10	18 September 1999	10	White	+2.7	+4.5	+11.1	-22.7	-22.8	-20.9	3.1	3.1	3.2
Grib	IR10	27 September 1998	24	White	+2.3	+2.7	+3.4	-24.7	-23.4	-24.1	3.1	3.1	3.1
Grib	IR10	27 September 1998	25	White	+2.7	+3.2	+10.7	-22.6	-22.9	-20.4	3.1	3.1	3.0
Grib	IR10	27. September 1998	26	Black	+1.7	+3.0	+4.5	-24.6	-23.7	-22.5	3.1	3.0	3.0
Grib	IR10	25 September 1998	28	White	+2.9	+3.4	+10.9	-22.4	-23.1	-20.3	3.1	3.1	3.1
Grib	IR10	25 September 1998	29	Black	+1.5	+3.0	+3.1	-24.5	-23.7	-23.1	3.1	3.1	3.1
Grib	IR10	1 October 1997	32	White	+2.3	+4.0	+8.4	-23.8	-22.7	-20.8	3.1	3.1	3.1
Grib	IR10	1 October 1997	34	White	+2.5	+3.5	+10.2	-24.5	-23.9	-20.2	3.1	3.1	3.1
Grib	Riordin	25 September 1998	22	White	+1.8	+2.4	+8.7	-24.2	-23.7	-21.4	3.0	3.0	3.0
Grib	Riordin	25 September 1998	23	Black	+2.7	+2.5	+4.4	-24.2	-23.3	-22.8	3.1	3.1	3.1
Grib	Riordin	2 October 1997	33	Black	+0.5	+1.2	+1.3	-24.6	-23.6	-23.2	3.1	3.1	3.1
PRI	Arnoup	3 October 1998	20	White	+0.4	+1.2	+11.0	-23.9	-23.2	-19.0	3.0	3.1	3.1
PRI	Arnoup	1 October 1998	21	Black	+0.3	+2.3	+1.8	-24.5	-24.5	-23.8	3.1	3.1	3.1
PRI	Canoona	21 September 1998	30	White	+1.5	+2.6	+1.6	-24.2	-23.1	-23.9	3.1	3.1	3.1
PRI	Canoona	18 September 1998	31	Black	+0.8	+2.8	+6.7	-24.1	-23.5	-21.2	3.1	3.1	3.0
PRI	Chapple	25 September 1998	3	White	+5.6	+5.8	+5.3	-24.3	-23.9	-23.3	3.1	3.1	3.1
PRI	Chapple	25 September 1998	4	Black	+2.0	+4.3	+9.2	-23.3	-22.1	-21.2	3.1	3.1	3.1
PRI	Nias	4 October 1998	1	Black	+2.9	+3.7	+10.8	-22.7	-22.1	-19.3	3.2	3.2	3.1
PRI	Nias	4 October 1998	2	White	+3.0	+5.7	+13.6	-23.2	-21.8	-17.6	3.1	3.0	3.0
PRI	Whalen	5 September 1997	14	White	+4.8	+3.8	+7.3	-22.5	-22.7	-20.5	3.1	3.1	3.1
PRI	Whalen	6 September 1997	15	Black	+1.6	+2.3	+12.1	-23.6	-23.6	-18.5	3.2	3.2	3.1
PRI	Whalen	5 September 1997	16	White	+3.4	+4.6	+12.0	-22.7	-22.6	-18.5	3.1	3.2	3.1

**Appendix 1.** *Continued*

Island	Site	Date	Bear ID	Morph	$\delta^{15}\text{N}$ tip	$\delta^{15}\text{N}$ mid	$\delta^{15}\text{N}$ base	$\delta^{13}\text{C}$ tip	$\delta^{13}\text{C}$ mid	$\delta^{13}\text{C}$ base	CN tip	CN mid	CN base
PRI	Whalen	5 September 1997	17	Black	+4.0	+6.7	+13.1	-23.3	-21.5	-17.4	3.1	3.1	3.1
PRI	Whalen	8 September 1997	18	White	+3.9	+3.5	+9.6	-22.7	-22.6	-19.8	3.1	3.1	3.1
PRI	Whalen	6 September 1997	19	Black	+1.5	+2.7	+11.2	-23.6	-23.1	-18.9	3.2	3.1	3.1

Island (Gribbell Island; Prince Royal Island), site (streams within each island), date (day of hair collection), morph (black; white), isotopic and CN ratios for hair tip (spring growth), hair mid (summer growth) and hair base (autumn growth). Hair samples provided by K. Ritland, University of British Columbia.