

## RESPONSE

**Metapopulation or predictable pattern of extinction?**H. van Oort<sup>1</sup>, B. N. McLellan<sup>1,2</sup> & R. Serrouya<sup>1,3</sup><sup>1</sup> Columbia Mountains Caribou Project, Revelstoke, BC, Canada<sup>2</sup> British Columbia Ministry of Forests and Range, Research Branch, Revelstoke, BC, Canada<sup>3</sup> Department of Biological Sciences, University of Alberta, Edmonton, AB, Canada**Correspondence**

R. Serrouya, Columbia Mountains Caribou Project, Revelstoke, BC, Canada V0E 2S0.

Email: serrouya@ualberta.ca

doi:10.1111/j.1469-1795.2011.00467.x

In our research paper (van Oort, McLellan & Serrouya 2011), we investigated the spatial structure of an endangered herbivore, the mountain caribou of southeastern British Columbia. These animals are in decline and were recently found in 18 seemingly isolated subpopulations (Wittmer *et al.* 2005), of which 16 remained in 2010. Using radio telemetry on 358 adult and 26 juvenile animals, we found two females and no juveniles moved between subpopulations. We also used an objective method to define summer ranges within subpopulations and then calculated rates of dispersal between these occupied patches. We found (1) that the mountain caribou populations are considerably more fragmented than previously recognized; (2) that dispersal between population units is likely insufficient to provide demographic rescue for small or extirpated subpopulations. Although the geographical distribution of these animals, with relatively larger subpopulations towards the north and much smaller and more isolated subpopulations towards the south, may suggest a metapopulation, we concluded that it is more likely the predictable pattern of the extinction process.

Our study was not specifically concerned with determining how caribou dispersal decisions are made or why dispersal rates were observed to be so low. Range shifting and expansion (and sometimes amalgamation with other herds) is likely the primary method of 'dispersal' (Hinkes *et al.* 2005; Boulet *et al.* 2007), as was documented for the Mulchatna herd (Hinkes *et al.* 2005). Range shifting may not constitute classic dispersal as defined by the three phases (Ims & Hjermann 2001) mentioned by Morales (2011). Indeed, we are not certain if the process of range shifting and expansion should be called dispersal at all – individuals may disperse from where they were born to another location but do not leave their natal population, although this process can provide gene flow between previously isolated populations. We suggested that complete dispersal behaviour, where individuals leave both the location of their birth and their natal population, is unlikely to be common in

animals such as caribou that have adapted to living in very large social groups. As such we speculated that the low dispersal rate (changing area and social group) is characteristic of this species.

As pointed out by Forester (2011) and Beckmann (2011), caribou dispersal rates may be density dependent and our result may simply reflect the diminished size of our subpopulations. This agrees with the view that dispersal only occurs when herds are sufficiently large enough to expand their range (Hinkes *et al.* 2005). Our paper dealt with diminishing populations (not expanding), but we did observe two cases of classic dispersal, where females left their (presumed) natal subpopulation, moved to a new area and became established in a different social group. It is possible that the dispersal rates measured for this mode of dispersal change when caribou density increases. To avoid inbreeding, dispersal could be greater in small populations but conversely, dispersal could be larger for high-density populations to avoid resource competition. Research into the details of density dependent dispersal is best addressed where caribou are abundant, but is more academic where numbers are small and they are going extinct.

An assumption made by Beckmann's (2011) critique is that caribou populations have been fragmented by habitat degradation. Apps & McLellan (2006) used landscape features and occupancy indices at two spatial scales to compare (1) where caribou remain to their historic distribution; (2) the relative intensity of occupancy within occupied subpopulations. Beckmann's assumption is partially supported at the scale of subpopulations (see Apps & McLellan 2006), but less so at the scale of summer/fall composite ranges. Summer/fall composite ranges were generally located in subalpine habitat where there is little or no forestry or other human impacts. Most summer/fall composite ranges of mountain caribou ranges are, not surprisingly, in mountains and these ranges are naturally severed by valleys >1000 m lower but some are also separated by pristine subalpine habitat that is no longer occupied. In many cases,

our observations suggest that caribou population structure is not clearly related to habitat or landscape attributes; indeed, some of their population structure is likely a manifestation of culturally transmitted movement patterns as suggested by Beckmann (2011).

Forester (2011) and Morales (2011) are correct to raise the issue of low sample size and uncertainty regarding dispersal of calves. Since van Oort *et al.* (2011), we have been using 18 microsatellite loci on 14 remaining subpopulations (184 samples) to further investigate population structure. Six subpopulations are showing an unanticipated level of genetic structure (global  $F_{ST} = 0.074$ ), a high amount for an organism often known for broad-scale movements. From more abundant northern to less abundant southern subpopulations, an assignment test showed only one migrant out of 47 since 1992 (R. Serrouya, unpubl. data). These results further support the lack of movement we documented using radio telemetry.

Of broader relevance, Beckmann (2011) concluded by suggesting that without a before, during and after design (BDA), researchers are 'left guessing' about the impacts of an ecosystem perturbation on population structure. Given the global pervasiveness human-induced habitat fragmentation and the challenges associated with studying endangered species, we reject this conclusion as it may discourage other valid and informative avenues research. Although we agree that a BDA design with replication is powerful, a design that exploits spatial contrasts by controlling for confounding factors in a multi-variate and multi-scale context can also be illuminating (e.g. Apps and McLellan 2006), and is often the only option. In another example of spatial contrasting, Proctor *et al.* (2005) used genetic analyses of grizzly bears *Ursus arctos* in two valleys of similar size and vegetation, but one with and one without a human settlement corridor. The valley with settlement showed complete demographic isolation on either side, the other, panmixia. M.F. Proctor, D. Paetkau, B.N. McLellan, G. Stenhouse, K. Kendall, R. Mace, W. Kasworm, C. Servheen, C. Lausen, M. Gibeau, W. Wakkinen, M. Haroldson, G. Mowat, L. Ciarniello, R. Barclay, M. Boyce, C. Strobeck, C. Schwartz, unpublished data, repeated this approach across many valleys, with 798 radio-marked and 3134 genetic samples of bears from Yellowstone, through British Columbia, to Alaska – results were consistent. By addressing limiting factors (human attractants and people with firearms), bears have begun moving across the fracture identified in Proctor *et al.* (2005), increasing the chance of rescuing a critically small population (M. F.

Proctor *et al.* unpubl. data). We hope that most managers would not be 'left guessing' when presented with evidence that is based on spatial contrasts alone.

## References

- Apps, C.D. & McLellan, B.N. (2006). Factors influencing the dispersion and fragmentation of endangered mountain caribou populations. *Biol. Conserv.* **130**, 84–97.
- Beckmann, J.P. (2011). Understanding the role of behavioral mechanisms and impacts of habitat fragmentation on structuring small declining populations. *Anim. Conserv.* **14**, 229–230.
- Boulet, M., Couturier, S., Côté, S.D., Otto, R.D. & Bernatchez, L. (2007). Integrative use of spatial, genetic, and demographic analyses for investigating genetic connectivity between migratory, montane, and sedentary caribou herds. *Mol. Ecol.* **16**, 4223–4240.
- Forester, J. (2011). Dispersal from the frying pan into the fire. *Anim. Conserv.* **14**, 225–226.
- Hinkes, M.T., Collins, G.H., van Daele, J.L., Kovach, S.D., Aderman, A.R., Woolington, J.D. & Seavoy, R.J. (2005). Influence of population growth on caribou herd identity, calving ground fidelity, and behavior. *J. Wildl. Mgmt.* **69**, 1147–1162.
- Ims, R.A. & Hjermann, D.Ø. (2001). Condition-dependent dispersal. In *Dispersal*: 203–216. Clobert, J., Danchin, E., Dhondt, A.A. & Nichols, J.D. (Eds). New York: Oxford University Press.
- Morales, J.M. (2011). The metapopulation that was not. *Anim. Conserv.* **14**, 227–228.
- van Oort, H., McLellan, B.N. & Serrouya, R. (2011). Fragmentation, dispersal and metapopulation function in remnant populations of endangered mountain caribou. *Anim. Conserv.* **14**, 215–224.
- Proctor, M.F., McLellan, B.N., Strobeck, C. & Barclay, R.M.R. (2005). Genetic analysis reveals demographic fragmentation of grizzly bears yielding vulnerably small populations. *Proc. Roy. Soc. Lond. Ser. B* **1579**, 2409–2416.
- Wittmer, H.U., McLellan, B.N., Seip, D.R., Young, J.A., Kinley, T.A., Watts, G.S. & Hamilton, D. (2005). Population dynamics of the endangered mountain ecotype of woodland caribou (*Rangifer tarandus caribou*) in British Columbia, Canada. *Can. J. Zool.* **83**, 407–418.