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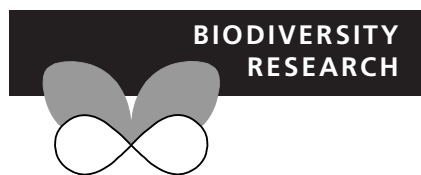
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Range expansion by moose into coastal temperate rainforests of British Columbia, Canada

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ABSTRACT

Ranges of species are dynamic and respond to long-term climate change and contemporary effects such as habitat modification. We report here that moose (*Alces alces*) have recently colonized coastal temperate rainforests of British Columbia, Canada. Contrary to recent publications, field observations of moose and their sign, combined with their occurrence in wolf (*Canis lupus*) faeces, suggest that moose are now widespread on the coastal mainland and occur on at least three islands. Traditional ecological knowledge (information accumulated by aboriginal peoples about their environment) suggests that colonization occurred during the mid 1900s, concomitant with logging of major watersheds that bisect the Coast Mountain Range. Range expansion by moose may have ecological consequences such as alteration of predator–prey dynamics and transmission of disease to native deer (*Odocoileus hemionus*).

Keywords

Alces alces, British Columbia, coastal temperate rainforest, *Canis lupus*, distribution, range expansion, traditional ecological knowledge.

INTRODUCTION

Mammalian distributions during the Pleistocene and Holocene have been dynamic, responding to climate and other environmental variability over time (Lyons, 2003). Ranges of species continue to expand or contract, often rapidly, in part due to anthropogenic effects such as landscape modification, global warming, persecution by humans, and introduction of exotics (Sih *et al.*, 2000; Parmesan & Yohe, 2003; Laliberte & Ripple, 2004; Oden *et al.*, 2004). Changes in species' distributions can alter important ecological interactions, including disease, competition, herbivory, and predation (Vermeij, 1991). In the case of wildlife species that are commonly hunted by humans, range contractions or expansions may also have economic, management, and safety implications.

Moose (*Alces alces*) are a circumpolar mammal undergoing worldwide expansion since the late Pleistocene, largely mediated by climate change (Lister, 1993). There is no palaeontological evidence for their presence in North America before the late Wisconsinian (Kurtén & Anderson, 1980). Recent genetic data suggest that moose colonized North America less than 15,000 years ago (Hundertmark *et al.*, 2002). Since then, their range boundaries were constrained by limitations imposed by climate and vegetation, which changed over time (Karns, 1998). In recent decades, however, moose of North America have expanded into areas considered previously unoccupied (Telfer, 1984; Karns, 1998). Similar range expansions (or contractions)

have not been reported in Eurasia to our knowledge. In North America, vegetation and snow cover are thought to restrict northern distribution, whereas a hot climate may limit range to the south (Fig. 1; Kelsall & Telfer, 1974; Renecker & Hudson, 1986; Karns, 1998; but see Crichton (2000) for new northern records to 67°31' N in Canada). Although there is information within reports from southeast Alaska (Klein, 1965; Alaska Department of Fish & Game, 1973; MacDonald & Cook, 1996), workers have not commented in depth on observed range expansion into coastal North America. We report here the recent arrival of moose to the west coast temperate rainforests of British Columbia (BC), Canada and speculate on the potential causes and consequences. We estimated current range of moose by noting observations of moose and their sign, and by identifying moose remains in wolf faeces. Further insight into distribution and timing of expansion was gained through traditional ecological knowledge (Huntington, 2000; Pierotti & Wildcat, 2000; Turner *et al.*, 2000; Usher, 2000), shared by coastal First Nations peoples during informal interviews.

METHODS

We collected interview and ecological data on the central and north coast of BC, an area comprising more than 60,000 km² (Fig. 1). Extensive fjords and tidal waters separate mainland landmasses and islands, which range in size from < 1 km² to > 2200 km². Inter-island and mainland–island distances range

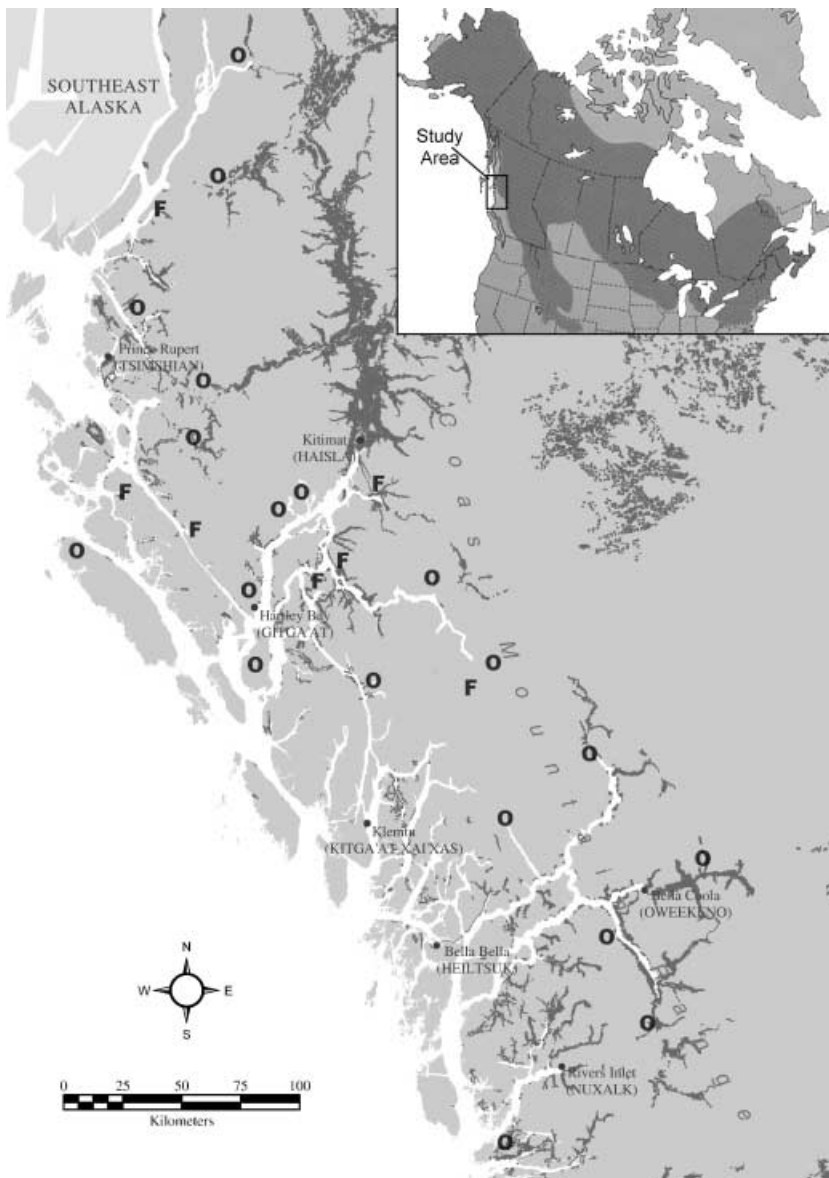


Figure 1 Study area on British Columbia's (BC's) coast. Shown are locations where moose or their sign are observed commonly by coastal First Nations peoples or by the authors during fieldwork (O), and where moose remains have occurred in the faeces of wolves, *Canis lupus* (F) collected during summers 2000 and 2001 (Darimont *et al.*, 2004). Note that, owing to limited interviews and fieldwork, data likely represent a subset of moose range on BC's coast. Dark grey shading indicates areas modified by logging. Coastal villages and associated First Nations groups from which interview data were derived are also shown. Geographic data in BC Albers projection. Inset shows moose distribution in North America in dark grey (from Karns, 1998).

from several metres to approximately 13 km. Most of the low-elevation forest is within the Coastal Western Hemlock biogeoclimatic zone (*sensu* Krajina, 1965), characterized by a wet and temperate climate. Annual precipitation exceeds 350 cm in most areas.

During early stages of ecological studies of wolves and their prey (Darimont & Paquet, 2000, 2002), we conducted informal interviews with First Nation peoples (mostly elders; $n = 7$), who constitute most of the human population in this remote region. We also interviewed naturalists ($n = 2$) with extensive experience on BC's coast, who have written on the area's flora and fauna (McAllister *et al.*, 1997). Discussions varied but always included asking where interviewees commonly see moose and about their first observation of moose on the coast. Additionally, we noted locations of moose sign (tracks, pellets) and visual observations of animals during fieldwork ($n = 32$). Finally, we conducted an analysis of prey remains in wolf faeces ($n = 595$) collected along

BC's coast during the summers of 2000 and 2001 (Fig. 1; Darimont *et al.*, 2004). We followed standard dietary analysis methods using dissecting microscopes with voucher hair specimens and dichotomous keys (Ciucci *et al.*, 1996). Although wolves may deposit faeces with moose remains in areas far from where moose are killed, we consider this possible bias negligible given the spatial scale of the study area. For Fig. 1, we overlaid moose occurrence data on BC provincial base data using BC Albers projection in a Geographic Information System (ArcView 3.2, Environmental Systems Research Institute Inc.). A data layer showing areas modified by logging was obtained from the Sierra Club of British Columbia (<http://bc.sierraclub.ca/>).

RESULTS AND DISCUSSION

Moose are now widespread along the mainland of BC's coastal temperate rainforests and occur on at least three islands (Fig. 1).

This distribution exceeds that described in recent BC government and museum publications, which suggest that moose are generally absent west of the Coast Mountain Range, except in some small localized areas along rivers and heads of inlets (Nagorsen, 1990; Shackleton, 1999; Blood, 2000). Data we report here may represent expansion since these publications. More likely, the discrepancy may reflect the paucity of field investigations conducted along the remote BC coast, coupled with the low density and elusive nature of moose. All interviews and field observations suggest that moose occur at low densities on the coast. Researchers in nearby southeast Alaska (Fig. 1) have noted moose in major mainland river valleys and on several nearby islands, and estimated arrival in the early 1900's (Klein, 1965; Alaska Department of Fish & Game, 1973; MacDonald & Cook, 1996).

Interviews were valuable in establishing that moose were absent on BC's coast in recent history and in estimating the timing of arrival. Moose are not known to be part of historical ceremonial tradition or subsistence use in all First Nation groups contacted. Cecil Paul, a Haisla elder, offered a representative statement regarding moose expansion, 'moose were not here or ever a part of stories when I was a child'. Records from European explorers, traders, and travellers also suggest that moose distribution to mid-nineteenth century did not include coastal BC, (Spalding, 1989). Interviewees indicated that range expansion first occurred in the mid 1900s. For example, Frank Hanuse of the Oweekeno Nation estimates the earliest arrival of moose in the 1940s, with sightings becoming more frequent in subsequent years.

Migration hypotheses, as well as independent genetic and palaeovegetative data, imply that moose could have occupied coastal British Columbia before maintained oral or written history. Bubenik (1998) speculated that moose may have migrated through and existed in glacial refugia of Alaska en route to the Canadian tundra from Siberia during the Wisconsinian glacial period. During the same time, vegetative and genetic data from other mammals suggest that similar refugia existed to the south on the continental shelf off the BC coast (Warner *et al.*, 1982; Josenhans *et al.*, 1993; Byun *et al.*, 1997), which may also have supported moose. The persistence of Dawson Caribou (*Rangifer tarandus dawsoni*) on Haida Gwaii, coastal BC, from the early Holocene until the early 1900s (Cowan & Guiguet, 1956; Byun *et al.*, 2002) and the current widespread coexistence of moose and caribou in North America suggest that the coastal habitat of BC may have been suitable for moose at least during the early to mid-Holocene. After extensive inquiry, however, we did not find supporting archaeological evidence.

Habitat modification has been implicated as a factor in recent moose expansions in other areas of North America (Karns, 1998) and we suspect the same in western Canada. The timing coincides with the first large-scale logging of major mainland watersheds that bisect the Coast Mountain Range, which began during the early to mid 1900s (Drushka, 1992, 1998; Fig. 1). The new travel routes along roads and the availability of emergent vegetation post-logging would have facilitated an expanding moose population. Notably, most interviewees independently postulated a similar or identical hypothesis when asked why they believed moose have arrived on the coast. Alternatively, moose

may have migrated south from coastal Alaska during the twentieth century. This is unlikely, however, given earlier accounts of moose presence only in localized areas near the Coast Mountain Range (Nagorsen, 1990; Shackleton, 1999; Blood, 2000).

We can only speculate on the possible ecological consequences of this immigration. Our wolf dietary data suggest that moose have already altered the historical wolf- and black-tailed deer (*Odocoileus hemionus*) association on the coast. Across a large study area, moose now represent nearly 10% of mammalian biomass consumed by wolves during spring and summer (Darimont *et al.*, 2004). Likewise, all First Nation respondents indicate that moose are now (lightly) hunted for food. Notably, moose may influence parasite dynamics in deer. For example, moose are thought to be the most important hosts of winter ticks, *Derma-centor albipictus*, a parasite that also affects deer (Welch *et al.*, 1991). Conversely, parasite-mediated competition with deer (e.g. Bogaczyk *et al.*, 1993; Schmitz & Nudds, 1994) or other biotic factors may limit moose densities or permanence on the coast. For example, un-manipulated coastal temperate rainforests contain vegetation communities and successional dynamics that do not fit the traditional definitions of moose habitat (Telfer, 1984). These ancient coastal forests, however, are being rapidly converted to tree farms by large-scale logging (Darimont & Paquet, 2000, 2002; Moola *et al.*, 2004), which offer extensive areas of new plant growth of variable age classes throughout the landscape over time. If the volume harvested and current logging practices continue, these anthropogenic changes will likely further facilitate moose presence and distribution on BC's coast.

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