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In the Great Bear Rainforest

island-hopping gray wolves give new insights into island biogeography

by Paul Paquet, Chris Darimont, Chris Genovali, and Faisal Moola

THE GREAT BEAR RAINFOREST (see sidebar) is naturally fragmented by a network of waterways and mountains. To preserve the area effectively, conservationists are compelled to understand how this marine-dominated landscape influences wildlife patterns and movement. Therefore, research and protection efforts must consider connectivity—before resource extraction, mostly logging, starts to degrade and further fragment these precious forests.

Our research efforts have focused on wolves. Among regions of North America where wolves still roam, the North and Central Coasts of British Columbia and the associated archipelago of offshore islands are ecologically unique. It seems likely that this remote ocean archipelago shelters North America's most pristine wolf population (Darimont and Paquet 2002).

The complex physiography of the North and Central Coasts creates many different kinds of habitats in close proximity. Landmasses that limit movements of fish and marine mammals provide habitat and connectivity for populations of terrestrial mammals. Likewise, the waterways and open ocean that provide habitat and travel corridors for aquatic species often inhibit travel of mammals and birds. But for some species—like coastal wolves, known to swim up to 13 kilometers in the open ocean—land and water combine to provide travel linkages between islands. Small islands or non-productive islands act as ocean-bound stepping-stones, providing pathways that connect the larger landmasses. Some stepping-stones may be used as brief rest stops, whereas others that provide good foraging may be occupied for several days. Collectively, these linked islands can support the lifetime requisites of land-hopping wildlife. But changes in sea level on long timescales and tides and currents on short timescales conspire to produce tenuous and often ephemeral linkages. Many ecologists believe that oceanic archipelagos harbor species that are highly vulnerable to disturbance and prone to extinction because landscape connections there are chaotic.

Connectivity, theory, and archipelagos

Our understanding of wolves in the Great Bear Rainforest draws on the long series of ecological studies addressing birds, small mammals, and insects that have formed contemporary conservation theory. Central to these studies, and the subject of intense debate over the past two decades, has been the role of connectivity in determining animal distribution, abundance, and persistence (Connor and McCoy 1979, Gilpin and Hanski 1991). This discussion has been fueled by the global impoverishment of natural systems through human-induced fragmentation and isolation of habitat. Accordingly, the equilibrium theory of island biogeography (MacArthur and Wilson 1967) and metapopulation theory (Gilpin and Hanski 1991, Hanski and Simberloff 1996) have postulated mechanisms explaining animal distribution and persistence of populations in patchy landscapes. These ideas provide much of the theoretical foundation for conservation biology. Although the original concept of a metapopulation as "a population of populations" has expanded to include other spatial population structures, including mainland-island (Hanski and Gilpin 1991) and source-sink metapopulations (Pulliam 1988, 1996), the focus remains on connectivity.

According to these theories, fragmentation decreases accessibility, availability, and productivity of secluded habitats, the remnants of which are often arranged across the landscape as island-like patches. Although island attributes such as size, distance from mainland, and accessibility to colonizing organisms clearly influence species composition, community structure, and community processes, the consequences of these for ecosystem functioning are little understood. If, however, we are to establish biological priorities for conservation, we need a firm understanding of how geography interacts with species to shape the evolution of species, ecological relationships, and landscape processes.

Very few studies have evaluated the response of large terrestrial predators to naturally discontinuous landscapes. In part, this is due to a lack of pristine sites to carry out such research. Nevertheless, clarifying the relationship between the geographic structure of true island systems, connectivity, and distribution of large mammals is a needed link between theory and application (Burkey 1995, Alcover et al. 1998). In that regard, the Great Bear Rainforest provides a valuable opportunity for scientists to study evolutionary and landscape processes in a true island environment under natural conditions. Documenting the responses to a naturally fragmented island environment provides a reference for comparison with similar studies conducted on land.

Coastal wolves and connectivity

Our ongoing studies of the behavior and ecology of coastal gray wolves are helping conservation biologists evaluate and refine prevailing theories about connectivity. The wolf is the most vagile (capable of dispersal) of all large terrestrial predators. On land, they can travel distances of 50 kilometers in a

The Great Bear Rainforest

Where the land meets the sea on British Columbia's wild North and Central Coasts stands the Great Bear Rainforest. The Pacific Ocean overwhelmingly defines and influences this environment, which is rich in human culture and natural history.

Encompassing the mainland and adjacent archipelago, the rainforest spans from the northern tip of Vancouver Island to the Alaskan Panhandle. The region is approximately 60,000 square kilometers, of which 19,300 square kilometers is land (see map). This nearly roadless and mostly unsettled region is bounded by the Coast Mountains to the east and Pacific Ocean to the west, creating a unique ecological and evolutionary environment largely free from industrial development. The few human settlements consist primarily of First Nations communities. Climate is temperate and wet with most areas receiving more than 350 centimeters of annual precipitation, primarily as rain. The wet, remote, and biologically productive mountainous mainland, topographically complex inner islands, and flatter outer islands are separated by equally productive open ocean and waterways. Island sizes range from 5 square kilometers (Moore) to 2,295 square kilometers (Princess Royal), and inter-landmass distances range from 250 meters to more than 7 kilometers.

Coastal temperate rainforest dominates the mainland and islands. This type of rainforest is extremely rare globally, covering only a fraction of a percent of the Earth's surface on the coasts of Chile, Norway, Scotland, Tasmania, New Zealand, and the U.S. Pacific Northwest, Alaska, and British Columbia. The temperate rainforest of the Pacific coast once stretched from northern California to Alaska. Today, only Alaska and British Columbia still contain large undisturbed tracts. The Great Bear comprises the largest

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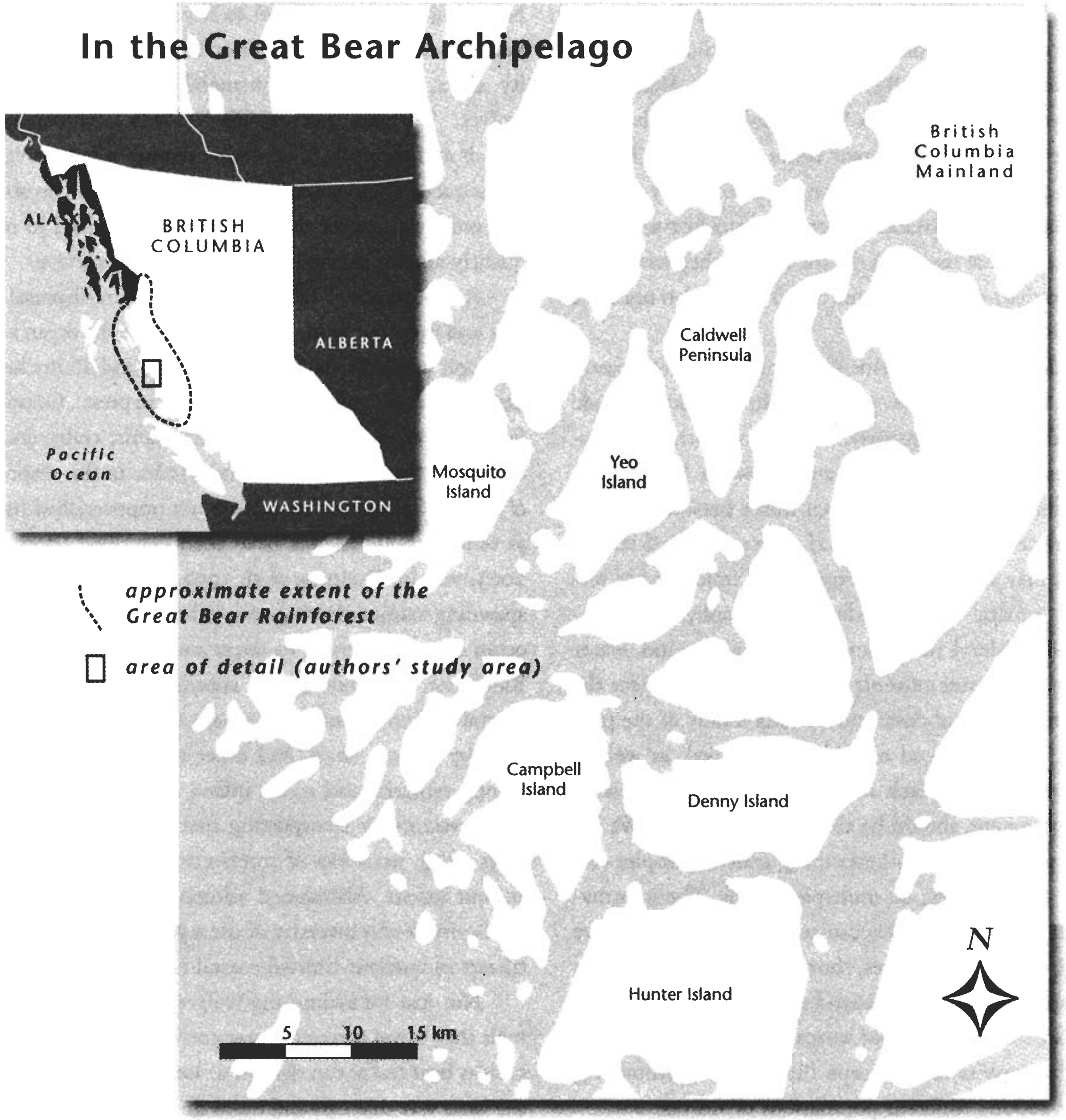

remaining expanse of temperate rainforest in the world (Schoonmaker et al. 1997).

The North and Central Coasts show great variation and distinctiveness at the genetic, species, community, and ecosystem levels. Genetic analyses have identified distinct coastal and continental black bear lineages, which may have been isolated from each other for 360,000 years (Byun et al. 1997). Together with southeastern Alaska, the region supports the highest endemic species concentration for the temperate rainforest region of Pacific North America (Cook and MacDonald 2001). Mammalian distribution on nearby Alexander Archipelago of Southeast Alaska has been well described (MacDonald and Cook 1996) and notable patterns of biogeography (Conroy et al. 1999) and endemism (Cook and MacDonald 2001, Fleming and Cook 2002, Small et al. 2003) have emerged.

The North and Central Coasts are important to wide-ranging species such as grizzly bears, gray wolves, killer whales, humpback whales, salmon, and migratory birds, many of which are now exterminated from much of their former ranges. All these species depend on terrestrial and marine corridors for dispersal, reproduction, transport and distribution of food and nutrients, and communication among subpopulations.

single day. Dispersal distances of several hundred kilometers are common and movements more than 1,000 kilometers have been documented (Fritts 1983, Boyd et al. 1995, Mech et al. 1995, Paquet and Carbyn 2003). Wolves use different habitats within their territories at different times of the year (Paquet and Carbyn 2003). Depending upon the availability of prey they may move long distances, through corridors with few resources, to seasonal use areas. In the spring they move to a den site. Activities and movements center on the den until the pups can travel with the pack.

Well adapted to the marine environment, many coastal wolves are island dwellers whose territories can include groups of islands. Consequently, movement within territories requires traveling on land and between landmasses, which can mean swimming in open ocean between distant islands (Darimont and Paquet 2002). Dispersing and traveling animals may need to cross expanses of inhospitable terrestrial and aquatic habitat. Island topography, island-to-island distance, island size, island productivity, wind, water temperature, and water currents likely combine to affect the frequency and success of these movements. Many of the prey species that wolves depend on for their survival, as well as other carnivores (e.g., black bears and grizzly bears) with which they compete, should be similarly influenced. We are currently testing these hypotheses using genetic samples collected from wolves living on multiple islands. The information derived from the samples can tell us which islands are being used by which wolves, how frequently dispersers reproduce successfully, which island populations are related, and which are isolated. In other words, we can begin to evaluate the effectiveness of landscape linkages in maintaining connectivity among different populations of wolves.

As with other large carnivores, the energetic needs of wolves are substantial, particularly while raising young. Thus, demands for food could influence island-hopping behavior as much as the physical landscape. Movements might be regular and predictable, depending upon the species and the season, or random, depending upon varying climatic conditions and availability of food or other resources. We believe the relationship between use of food resources and connectivity is important but poorly understood. On isolated islands, our wolf foraging data suggest that predator-prey dynamics are inherently unstable and can result in declines in prey populations (Darimont et al. in press). Sitka black-tailed deer, the main prey of coastal wolves, cannot immigrate to remote islands fast enough to replace individuals killed by wolves. Reduced numbers of prey invariably lead to fewer predators. Because connectivity is restricted, these islands become temporary mortality sinks, resulting in ephemeral populations of deer and wolves. Without wolves, deer slowly recolonize isolated islands and the cycle of depletion repeats when wolves return. Consequently, and contrary to predictions based on abiotic factors only, we suspect that wolves are compelled to move frequently among isolated landmasses just to survive.

Although water barriers may constrain dispersal of predator and prey, our work also suggests that the ocean augments the food available on land (Darimont and Reimchen 2002, Darimont et al. 2003, Darimont et al. in press). Coastal wolves feed on deer, moose, goat, salmon, clams, crabs, and marine carrion such as beached seals and whales. In this respect, many of British Columbia's islands are not impoverished fragments, as other oceanic islands have been described (Brotons et al. 2003, see also Dunning et al. 1992, Fahrig 1997). In the fall, spawning salmon, having traveled thousands of kilometers in ocean corridors, return to rivers and creeks of the Great Bear Rainforest, and constitute a considerable part of the diet of coastal wolves. Notably, these are the same rivers and creeks used by wolves, bears, and other terrestrial species to travel among estuaries and access inland forests. Like bears, wolves act as vectors by transporting marine nutrients from waterways along networks of intersecting trails into the region's ancient forests. Abandoned salmon carcasses, wolf feces, and wolf urine feed a diversity of users and become important fertilizers in nutrient-limited coastal ecosystems.

Not just for swimming wolves, but for all coastal mammals that travel through water corridors, human disturbances such as boat traffic can disrupt or impede movements in much the same way that cars and trains do on land. Waves from large boats can overturn swimming animals, and humans harass and kill wildlife as the animals travel between islands. (Killer whales, which have been documented preying on moose and deer swimming between islands, can also pose a lethal threat.) More specifically, we believe that geography that allows islands to serve as useful habitat predisposes wildlife to exploitation by humans. Guide outfitters in the Great Bear Rainforest commonly use jet boats for river access to otherwise remote and secure wildlife habitat (Paquet and Darimont pers. obs.). In essence, coastlines and river systems are analogous to roads, providing humans access to remote areas and opportunities for disrupting connectivity. In southeastern Alaska, for example, humans who gained access by boat to areas otherwise secure were responsible for more than 50% of all wolves killed by hunters and trappers (Person 2001). In this respect, long, narrow islands pose greater risk for wildlife than round islands of equal size. The latter provide more security because the interior of the island is more difficult to reach and the exposed coastline is proportionally less than narrow islands.

Because of its remoteness, unique landscape, and pristine condition, the Great Bear Rainforest is a valuable place for conservation research and protection. Insights gained here about the role of connectivity in sustaining the natural environment, and about those species whose survival depends on the intactness of that environment, can contribute to the design of conservation reserves worldwide. In the face of the ongoing threats of industrial logging, oil and gas extraction, aquaculture, mining, sport hunting, recreational activities, and marine traffic, we hope that caution prevails until knowledge is sufficient to make informed decisions about the destiny of the Great Bear Rainforest. Unfortunately, the putative land-use plans now being proffered by the government of British Columbia would protect a meager 24% and 21% of the North and Central Coasts, respectively. Full protection, within the context of outstanding aboriginal land claims, should be among the preferred options. Our hope is that the Great Bear Rainforest, sometimes called "the Last of the Best," can remain naturally fragmented and wholly wild. ☾

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