Forest Ecology and Management 409 (2018) 190–201

Contents lists available at ScienceDirect

Forest Ecology and Management

journal homepage: www.elsevier.com/locate/foreco

Resource selection by coastal wolves reveals the seasonal importance of seral forest and suitable prey habitat

Gretchen H. Roffler[a,*], David P. Gregovich[a], Kristian R. Larson[b]

[a] Alaska Department of Fish and Game, Division of Wildlife Conservation, 802 3rd Street, Douglas, AK 99824, USA
[b] Alaska Department of Fish and Game, Division of Wildlife Conservation, 2030 Sealevel Drive, Suite 205, Ketchikan, AK 99901, USA

ARTICLE INFO

Keywords:
Canis lupus
Habitat selection
Odocoileus hemionus sitkensis
Successional forest
Temperate rainforest
Thinning treatment

ABSTRACT

Wolves (*Canis lupus*) in Southeast Alaska inhabit temperate rainforests characterized by patchworks of old-growth and harvested forest stands in various stages of regeneration. Investigating wolf space-use patterns in this landscape may yield information on their tolerance of anthropogenic disturbance in forest ecosystems. Furthermore, identifying shifts in habitat selection throughout the year can provide insights into wolves' ability to exploit seasonally available resources. We examined seasonal habitat selection of wolves on Prince of Wales Island, Alaska with respect to forest structure, succession, land cover, topography, road densities and habitat predicted to support Sitka blacked-tailed deer (*Odocoileus hemionus sitkensis*) and salmon (*Onchorynchus* spp.), the primary and a secondary prey species. We used GPS locations from 13 wolves during 2012–2016 to develop resource selection functions (RSFs). Within their home ranges, wolves selected low elevation, flat terrain with open land cover and low-volume old-growth forests across seasons. During fall and winter wolves preferred clearcuts ≤30 years old, but avoided clearcuts > 30 years old and thinned young-growth relative to medium-volume old growth. Habitats with predicted high deer carrying capacities were selected during late summer and fall, and areas close to anadromous streams were important only during summer when salmon were spawning. Areas of high road densities were avoided during denning season and summer, but strongly selected during winter. Our study reveals the potential of coastal wolves to seasonally target prey habitat and adjust to altered landscapes, but successional forests had a limited period of use (< 30 years), thus forestry practices could reduce availability of wolves' preferred habitat.

1. Introduction

Wolves in coastal Southeast Alaska and British Columbia inhabit temperate rainforests distributed across island archipelagos (except for Admiralty, Baranof and Chichagof islands) and a narrow region of the mainland coast separated from the continental interior by mountains and icefields. Coastal wolves are considered distinct from continental populations due to morphological (Goldman, 1944; Nowak, 1983), genetic (Weckworth et al., 2010, 2011; Cronin et al., 2014), and ecological characteristics (Weckworth et al., 2005; Muñoz-Fuentes et al., 2009). Sitka black-tailed deer (*Odocoileus hemionus sitkensis*) constitute the primary prey of coastal wolves throughout most of their naturally fragmented range, in addition to marine resources such as salmon (*Onchorynchus* spp.) and marine mammals (Szepanski et al., 1999; Darimont et al., 2004). This ecosystem has supported wolves for approximately 12,000 years when glacial ice retreated and opened colonization routes from southern Pleistocene refugia (Nowak, 1995). In contemporary times, large-scale industrial logging has transformed forested sections of this landscape into a mosaic of productive old-growth forest and clearcuts in various stages of succession (i.e., young-growth). Intensive industrial-scale logging has occurred since the 1950s, and the resulting forest alteration, habitat fragmentation, and development of a network of roads have raised concerns about the impacts on wildlife populations (Schoen and Kirchhoff, 1988; Cook et al., 2006; Albert and Schoen, 2013).

Temperate rainforests transition through stages of succession post-logging and the consequences to resident wildlife are best understood for deer (Doerr et al., 2005; Hanley et al., 2005; Farmer et al., 2006; Farmer and Kirchhoff, 2007), and affect coastal wolves directly through habitat changes and indirectly through their deer prey. Old-growth forests are heterogeneous in stand age and canopy structure, allowing sufficient light to penetrate to the forest floor and support diverse understory species including shrubs, forbs, and lichens that are important deer forage (Alaback, 1982). Understory shrubs regenerate in young clearcuts (age 0–25–30 years), particularly during summer and mild winters (Alaback, 1984; Farmer and Kirchhoff, 2007; Cole et al., 2010),

* Corresponding author.
E-mail address: gretchen.roffler@alaska.gov (G.H. Roffler).

https://doi.org/10.1016/j.foreco.2017.11.025
Received 18 August 2017; Received in revised form 9 November 2017; Accepted 10 November 2017
Available online 20 November 2017

but during severe winters, early successional forests lack a canopy capable of intercepting snow (Kirchhoff and Schoen, 1987), allowing shrub burial (White et al., 2009) and increasing energetic costs of deer movement (Parker et al., 1999). Older clearcuts (> 25–30 years) grow into even-aged stands with dense canopies which block sunlight and impede growth of deer forage (Alaback, 1982; Schoen et al., 1988, Farmer and Kirchhoff, 2007). This is also known as the stem-exclusion phase and may last > 100 years (Wallmo and Schoen, 1980; DellaSala et al., 1996). These second-growth forests are unproductive for many old-growth associated wildlife species, and the delayed effects of past timber harvest (termed "succession debt") predicts long-term and large-scale declines of deer, and subsequently wolves (Person, 2001).

Wolves in Southeast Alaska have been a focal point of conservation concerns since the 1990s, with heightened attention to the negative consequences of timber harvest on wolf and deer habitats, and increased access from roads built to support the timber industry resulting in higher wolf harvest by humans (Person et al., 1996, 2001; Swanston et al., 1996; Wolf Technical Committee, 2017). In 1993 and 2011 the U.S. Fish and Wildlife Service (USFWS) was petitioned to list Southeast Alaskan wolves under the Endangered Species Act. The most recent petition outlined specific concerns for wolves on Prince of Wales Island (POW), reflecting increased alarm over the effects of continued old-growth logging, as the most intense logging activity in Southeast Alaska occurs on POW (Albert and Schoen, 2013). After completing status reviews, the USFWS determined that listing was not warranted in 1995, in 1997 (after the finding was remanded), and again in 2015. Despite the recent finding, concerns were raised in the species status assessment about the sustainability of POW wolves due to reductions in habitat capability of deer resulting from timber harvest management (USFWS, 2015; FR 32473, 5 Jan 2016).

The majority of the land in Southeast Alaska is within the Tongass National Forest managed by the U.S. Forest Service (USFS). Recently, the USFS developed habitat and access management recommendations to the Tongass National Forest Land and Resource Management Plan (USFS, 1997; USFS, 2008) to maintain long-term, sustainable wolf populations (Wolf Technical Committee, 2017). The key recommendations relating to habitat included enhancement of the deer populations by increasing forage, maintaining corridors to facilitate movement, and increasing heterogeneity within young-growth forest stands, especially in winter habitats (Wolf Technical Committee, 2017). One management action proposed to accomplish these objectives is treating young-growth forest with thinning, with the intended effects of delaying the development of stem exclusion and hindrance of understory forage growth from shading (Hanley, 2005; Cole et al., 2010). The USFS recently implemented a strategy to transition harvest from old-growth forest to young-growth forest with the goal of establishing ecologically, economically, and socially sustainable management practices (81 FR 88657, 8 Dec 2016). The first large-scale effort towards this transition began on POW in 2017; old-growth logging will constitute the majority of the harvest for the first decade of the transition, followed by an increasing proportion of young growth until reaching nearly 100% by the end of the 16 year period.

Wolves are considered habitat generalists (Mladenoff et al., 1995; Fritts, 2003), able to survive in a broad range of ecological conditions, limited mainly by prey availability and mortality risk (Fuller et al., 2003). Furthermore, wolves demonstrate marked dietary plasticity (Peterson and Ciucci, 2003), which suggests the possibility of weak habitat selection patterns and the potential for resilience despite changing habitat conditions. However, patterns of habitat preference may be revealed at finer scales (within the home range; Ciucci et al., 2003) and may shed light on thresholds of tolerance or avoidance of habitat types. Previous research of coastal wolf habitat selection has focused primarily on den sites (Person and Russell, 2009) and the pup rearing period (Person, 2001). Wolves did not demonstrate distinct patterns of habitat selection outside of the denning season (Person, 2001); however, this research relied on VHF radio collar locations at course time intervals. Furthermore, as most attention has been paid to wolves' use of deer habitat, little is known about seasonal changes in wolf habitat selection reflecting use of other prey in temperate rainforests.

Wolves are expected to display preferences for different habitat types among seasons because of variation in behavior throughout the year. For example, during denning season, wolf activity is focused around the den site (Ruprecht et al., 2012) generally located in protected areas because of pup vulnerability (Mech and Boitani, 2003; Sazatornil et al., 2016), whereas territorial behavior increases during winter requiring more movement (Jędrzejewski et al., 2001; Smith et al., 2015) and potentially different habitat selection patterns (Ehlers et al., 2014). Foraging behavior may change throughout the year as wolves have been demonstrated to shift habitat selection seasonally, reflecting variability in prey availability or vulnerability (Peterson et al., 1984; Metz, 2012; Latham et al., 2013). Investigations of variation in seasonal foraging patterns have proved important for understanding predator-prey dynamics (Sand et al., 2008; Knopff et al., 2010; Metz et al., 2012) including apparent competition (Latham et al., 2011) and prey-switching behavior (Latham et al., 2013). Indeed, research using stable isotope ratios suggests coastal wolves switched dietary preference to salmon, a seasonally available resource, when deer became less abundant (Szepanski et al., 1999), or during periods of availability (during late summer and fall), regardless of ungulate abundance (Darimont et al., 2008).

Considering the concerns for coastal wolf viability, determining how wolves select specific forest successional stages is necessary to understand the effects of logging practices, and can inform evaluation of measures taken to mitigate negative consequences of timber harvest and enhance wolf habitat. Moreover, identifying differences in use of primary and alternate prey habitat throughout the year can reveal seasonal targeting of prey species. To address these issues, we investigated seasonal habitat selection of wolves on Prince of Wales Island, Alaska. To understand shifts in patterns of landscape preference throughout the year, we modeled the relative probability that certain resources were selected in relation to the distribution of forest type, land cover classes, topographical variables, road density, and availability of primary and alternate prey. We specifically tested for preferences in selection of productive old-growth forest classes, age of successional forest, and forests that had been treated to enhance deer habitat. We hypothesized that wolves would select habitats that best support deer, including old-growth forests and young successional clearcuts, and would avoid habitats that are unproductive for deer including clearcuts > 30 years old, particularly during winter. Second, we predicted that use of areas near salmon streams would increase with seasonal (late summer) availability of this alternative prey resource. Finally, we predicted that wolves would avoid areas of high road densities during the denning season because pups are vulnerable and less mobile at that time (Person and Russell, 2009; Benson et al., 2015). Conversely, we predicted that wolves would select high-density roaded areas during winter because of increased movement during this period, as roads have been demonstrated to facilitate movement and prey acquisition by wolves (Whittington et al., 2011; Dickie et al., 2016). Greater knowledge of variation in seasonal resource selection is important for understanding coastal wolf ecology and will help evaluate their potential to adjust to altered landscapes.

2. Materials and methods

2.1. Study area

The study area covered 3570 km^2 of temperate rainforest on POW, the largest island (6670 km^2) in the Southeast Alaska Archipelago (Fig. 1). The POW Island complex (9025 km^2) is characterized by an extensive coastline with long fjords, rugged mountains ≤1160 m, and multiple watersheds. A variety of habitat types are represented in this