

to movement and genetic flow for at least 13,000 years (Mercer and Roth 2003), as discussed further below.

Significance

Under our DPS policy, once we have determined that a population segment is discrete, we consider its biological and ecological significance to the larger taxon to which it belongs. This consideration may include, but is not limited to (1) evidence of the persistence of the discrete population segment in an ecological setting that is unique for the taxon; (2) evidence that loss of the population segment would result in a significant gap in the range of the taxon; (3) evidence that the population segment represents the only surviving natural occurrence of a taxon that may be more abundant elsewhere as an introduced population outside its historic range; and (4) evidence that the discrete population segment differs markedly from other populations of the species in its genetic characteristics.

Ecological Setting. The western gray squirrel in the Puget Trough of western Washington persists in a transitional ecological setting, where it occupies habitat composed of Oregon white oak in an ecotone (transitional) between upland Douglas-fir forests and prairies, in comparison with the subspecies' populations elsewhere in its range (Ryan and Carey 1995; Bayrakçi *et al.* 2001). Consequently, existence of the western gray squirrel in the Puget Trough is more intimately tied to the success of Oregon white oak: Oregon white oak is the only native oak in Washington (Stein 1990) and provides an essential winter food item for this squirrel (Sumner and Dixon 1953; Kruckeberg 1991; Carraway and Verts 1994). Acorns and pine seed are critical high-energy foods needed for overwintering (Ryan and Carey 1995a). In western Washington, western gray squirrels have adapted to a more homogeneous environment with fewer and less reliable food resources (Oregon white oak, Douglas-fir, and some ponderosa pine), particularly relying on the acorn of a single tree species as its essential storable winter food resource, thus occupying a less suitable, marginal habitat. Elsewhere in the subspecies' range, Oregon white oaks occur in communities having a wider range of mast-producing tree species, including a variety of oak and pine species, which allows western gray squirrels to use different food resources when one food resource has a poor year for mast production.

The North Cascades population found east of the Cascade Mountains also persists in an ecological setting which

differs from the Puget Trough and the South Cascades. In this population, western gray squirrels expanded their distribution into areas beyond the native range of Oregon white oak. The presence of western gray squirrels in Chelan County early in the twentieth century (Couch 1928; Booth 1947; Larrison 1970; Stream 1993; WDFW 2002) indicates adaptations to using other food resources. The continuous distribution of Oregon white oak extended into Yakima County, with only a spotty distribution into Kittitas County (Stein 1990). The range expansion northward from Yakima County required occupying habitats lacking oaks that provided the main winter food for the subspecies, relying on ponderosa pine as the primary food.

The Washington populations of western gray squirrels are found in differing ecological settings within the State. However, it is not clear that they should collectively or independently be considered as unique ecological settings for the taxon. For example, while the grasslands and oak woodlands of the Puget Sound area have different vegetation complexes compared to the grasslands and oak woodlands where western gray squirrels are found in northern California or southern Oregon, these differences are not so great that we consider the habitat of the Puget Sound population to be a unique or unusual ecological setting for western gray squirrel. The South Cascades population shares many habitat features common to the habitat for western gray squirrels found in Oregon. The North Cascades population's habitat is notable in its absence of oaks, the main source of winter foods for this subspecies in most of its range. This population appears to rely on the seed of pine trees and bigleaf maples (*Acer macrophyllum*).

Throughout their range, however, western gray squirrels consume a variety of types of tree seeds, including many conifer species. In summary, we do not find that the Washington populations individually or collectively are located in an ecological setting unusual or unique for the taxon, such that they meet the significance criterion of the DPS policy.

Gap in the Range. The Washington population segment of the western gray squirrel is at the northern portion of the historic and current distribution of the subspecies. Within the Washington population segment, the Puget Trough population represents the northwestern extension, and the North Cascades population represents the northeastern extension of the subspecies' range.

Within the distribution of every species there exists a peripheral

population, an isolate or subpopulation of a species at the edge of the taxon's range. The population is the basic evolutionary and ecological functional unit. The local population is where responses to environmental challenges occur, where adaptations arise, and where genetic diversity is maintained and reshuffled each generation. A species can continue to exist even though many of its populations are destroyed, resulting in a loss of biodiversity and what may be unique genetic or phenotypic traits (Meffe *et al.* 1997). Peripheral populations are often located at a species' ecological limits where unique genetic combinations are exposed to and tested by environmental circumstances that may not be found elsewhere in the range of the species. When a peripheral population is isolated from gene flow from other populations, the isolated peripheral population may become highly adapted to local conditions. Distinctive traits found in peripheral populations can be important for the survival and evolution of a species as a whole (Meffe *et al.* 1997).

Long-term geographic isolation and the loss of gene flow between populations is the foundation for genetic changes in populations resulting from natural selection or chance. Evidence of changes in peripheral populations may include genetic, behavioral and/or morphological differences from populations in the rest of the subspecies' range. Ecological differences were described above, and genetic differences in western gray squirrels are discussed below. We also considered information regarding morphological and behavioral differences in regard to adaptations that may be occurring in the western gray squirrel in Washington.

The secretive behavior of the western gray squirrel in Washington has been frequently noted and might represent an adaptation of a population on the periphery of its range. Bowles (1921) wrote, regarding western gray squirrels in Pierce County, Washington, that "although extremely numerous, we may walk for days in the country they inhabit and never see one." Scheffer (1923) indicated that in the more heavily timbered country in Washington, the gray squirrel was only occasionally seen. Couch (1926) noted that, although western gray squirrels are hard to see, the presence of western gray squirrels in the lower Puget Sound region is evident in the peeled bark of Douglas-fir. Larrison (1970) wrote that western gray squirrels in Washington are "rather shy and do not mix well with civilization," and in the few places