Thoughts on R-Selected vs. K-Selected Life Strategies for the Covered Species

The City of Austin in its HCP indicates in at least one place (line 1956) that the Covered Species are "K-selected", states in another place (line 1856) that the populations range about an "equilibrium" level, and suggests in at least one other place (line 1863) that the populations manifest "density-dependence". Taken together, these assertions indicate that the City apparently considers the populations as having dominant "equilibrium" as opposed to dominant "opportunistic" life strategies, although no specific assessment or rationale for that belief is offered.

The District in Section 5.3.1 (Assessment of Population Impacts) in its Proposed Draft HCP states the following:

> "Populations of organisms exhibit typical behavior governed by life-history strategies that are in an area along a continuum between two end-members. Both of the Covered Species appear to have generally more "opportunistic" than more "equilibrium" life strategies, as the end-members are known. These opportunistic strategies have developed in an evolutionary sense in response to the not infrequent occurrences of disturbances like droughts and floods in their springflow-dominated endemic environment, which cause rather indiscriminant, density-independent mortality from the temporally variable availability of resources in their habitats (Pianka, 2000). Such opportunistic populations grow in bursts and have evolved to reproduce in relatively larger numbers and more continuously, whenever the resources (including clean substrates and sufficient DO) allow. Equilibrium species characteristically reproduce more selectively, have just a few offspring, and provide post-natal care to attempt to produce more effective competitors, as would be advantageous in an environment that is less erratic in its resource availability and where competition is keen. These latter characteristics do not describe the Covered Species or their habitat.
>
> Equilibrium species are also characterized by having a maximum population size that is defined by the "carrying capacity" of its resources, with populations that are density-dependent and that tend to fluctuate only a little about that carrying capacity. Conversely, opportunistic species are characterized by -- *and adapted to*-- cyclic changes in population size and composition defined by episodic to catastrophic changes in availability of resources such that the populations are density-independent. Describing the size of the latter populations requires use of a more probabilistic metric than simply a single number. During less constrained resource availability, opportunistic species put more energy into reproduction efficiency and develop larger numbers of individuals to accommodate the next down-cycle related to the minima of resource availability. Opportunistic strategies seem to characterize better the observed behavior and characteristics of the salamander populations at Barton Springs.

> Opportunistic species generally may accommodate larger adverse effects related to constrained resources without jeopardizing the species than could equilibrium species. However, regardless of they are more equilibrium or more opportunistic, some large stochastic or random event at an inopportune time could extirpate these small populations."

The District's assessment of the following observed characteristics and attributes of the Covered Species suggests that they are dominantly "opportunistic", mainly with r-selected life strategies emphasizing population growth rates:

- Fluctuations in its aquatic resources, including DO, which affect the salamanders both directly physiologically and possibly indirectly with respect to prey impact;
- Relatively continuous and high rate of reproduction, and relatively large numbers of offspring, whenever energy levels allow (i.e., playing a numbers game);
- Lack of parental care for young to reach maturity that would generally be required to ensure development of efficient competitors in an environment requiring such competition (i.e., unlike the springs, one with relatively stable but finite resources that leads to density-dependence);
- Mortality that is not dependent on prevailing density, rather on large swings in resources;
- "Invertevore" predator characteristics, that makes them less selective as to food supply and less susceptible to reductions in energy sources that might accompany resource-constrained time periods; and
- Small overall population size but with relatively large fluctuations in the actual sizes over short time periods, indicating that the population is not indexed to or controlled by a "carrying capacity" with small variations about it, but one that varies substantially with environmental conditions.

These seem compelling, in aggregate. Perhaps the primary characteristics to the contrary that would suggest the Covered Species are not located at the extreme r-selected end of the opportunistic-equilibrium spectrum are their relatively slow development to reproductive-age maturity, a rather long life span, and their relatively large body size, which are typical of vertebrates. These are generally more characteristic of K-selected species, and perhaps the reasons that the City apparently has considered the salamanders an equilibrium species. However, it is important to note that some (not all) other salamanders and vertebrates are considered mainly opportunistic with r-selected life strategies. And despite the City's assertion, there seems to be no evidence of an actual equilibrium size evidenced in either of these populations, just a lot of cyclic variability whose range is controlled by environmental conditions such as DO and substrate conditions.

The District concludes its impacts of take assessment in Section 5.3.1 with the following:

> "Whether the Covered Species are more opportunistic or equilibrium species affects the consequential impacts of the incidental take more than the take estimate. In this setting, those impacts are by definition less for opportunistic, r-selected species that have evolved to utilize those strategies than they would be for equilibrium, K-selected species whose evolutionary strategy would not be as effective in the spring-outlet environments. Simply put, the Covered Species are genetically configured to bounce back from the smaller population sizes imposed by long-term drought effects.
>
> Indexing incidental take caused by springflow reductions from pumping to related DO-concentration reductions seems entirely appropriate for these more density-independent, opportunistic Covered Species. Another potential source of incidental take is the small reductions in the wetted habitat area that might otherwise be attributable to the Covered Activities ("small" especially relative to reductions attributable to "natural drought" conditions). However, the City's ongoing habitat restoration efforts preclude making a quantitative assessment of how much, if any, of the "new" wetted habitat, which is the baseline for the District's HCP, could be attributable to pumping-induced springflow reductions at the reconfigured perennial springs during extreme drought. In any event, these effects would more likely be an important factor to a density-dependent K-selected species than to these dominantly r-selected species where habitat size is less of a concern than habitat conditions."