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INDICES USED TO ASSESS STATUS OF SEA OTTER POPULATIONS: A REPLY

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Abstract: The California sea otter (*Enhydra lutris*) population, after increasing for more than half a century, stabilized and probably declined from the mid-1970's to the mid-1980's. Estes et al. (1986) suggested that the stabilization and decline were not due to food limitation. Garshelis et al. (1990) challenged this suggestion, although in doing so they misrepresented arguments made by Estes et al. (1986), provided no evidence for alternative hypotheses, and offered no constructive recommendations for a better means of population assessment. While acknowledging some of the points made by Garshelis et al. (1990), I believe the collective evidence presented by Estes et al. (1986) provided a reasonable basis for rejecting the food-limitation hypothesis, and point out that recent increases in the California sea otter population following a legislated reduction in net entanglement mortality is strong evidence against the food-limitation hypothesis.

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I will preface my response to Garshelis et al. (1990) with a brief history of the sea otter population in California and a summary of the arguments my colleagues and I made concerning the status of that population in the mid-1980's. The California sea otter population was hunted to the brink of extinction and may have contained as few as 50 individuals at the beginning of this century (Ralls et al. 1983). Protection was provided in 1911, and the population subsequently increased. Although the growth characteristics of the California population are poorly known through the 1940's, there were an estimated 500-600 individuals in 1950. Thereafter, the population increased steadily at about 5% per year and in 1976 contained an estimated 1,789 otters (U.S. Fish Wildl. Serv. 1982). Although further increases were expected, the population then ceased growing and probably declined somewhat (Estes 1990). However, the extent to which this lack of growth was due to limiting resources versus disturbances was uncertain. My colleagues and I concluded that further population growth probably was not food limited (Estes et al. 1986) because (1) diurnal activity budgets of the California population were similar to those of other sea otter populations known to be below equilibrium density; (2) estimated entanglement mortality from fishing gear was roughly equivalent to an expected growth increment, given the estimated population size at that time and the earlier observed rate of increase of about 5% per year; (3) the diet of the population was similar, in that piscivory was lacking, to other populations known to be below carrying capacity; and (4) suitable

habitat for increased expansion existed at both ends of the population's range. This last point is especially problematic to the resource-limitation hypothesis because several other sea otter populations in the North Pacific Ocean have grown to sizes far exceeding that of the California population, with no measurable decline in growth rate (Estes 1990).

Although no single line of reasoning was very strong, we thought the collective evidence was compelling. Garshelis et al. (1990) have disagreed. However, despite their censure and our reply, the argument now is immaterial. In 1985 the State of California limited the set-net fishery in central California, thus reducing the number of sea otters lost to entanglement. The sea otter population has since increased at a rate of about 7% per year, a trend that has persisted through 1989 (R. J. Jameson and J. A. Estes, unpubl. data). I consider this to be nearly definitive evidence that the observed lack of increase in the California sea otter population from the mid-1970's to the mid-1980's was not food limited, although conceivably my colleagues and I drew the right conclusion for the wrong reasons.

Garshelis et al. (1990) were highly critical of our data and our reasoning, challenging each of our major arguments and even points we did not make. I agree with many of their technical comments, some of which were acknowledged in our original paper (Estes et al. 1986). I even agree with them that our evidence was inconclusive, a point also acknowledged in our original paper. However, I differ with them on 2 main issues. First, although the evidence we presented admittedly was insufficient to permit

a definitive population assessment of sea otters in California, I believe it was strong enough to make a qualified argument, which is what we did. The alternative was to disregard the ideas and evidence as meaningless, a choice that would have contributed nothing to the progression of knowledge. Second, I believe that Garshelis et al. (1990) misrepresented most of our arguments, overstated their case, failed to evaluate the collective evidence in a fair and reasonable way, and failed to offer any constructive suggestions. The following points exemplify these charges.

1. Garshelis et al. (1990) correctly pointed out several problems with activity data obtained from diurnal scan samples. However, they incorrectly recounted our logic in interpreting these data by stating that it was based simply on the fact that sea otters at Amchitka Island spent more time feeding than did sea otters in California. They then argued that this comparison was largely meaningless because other differences besides population status between these distant regions might account for different diurnal time budgets. This recounting of our data and argument is incomplete, and thus misleading. We first compared the diurnal activity budgets of sea otters between 2 islands in the western Aleutians; one (Amchitka) had been at or near equilibrium density for several decades and the other (Attu) was unquestionably well below equilibrium density. The comparison showed that sea otters at Amchitka spent 51–58% of daylight hours foraging, whereas otters at Attu spent 16% of daylight hours foraging. Next, we obtained activity data from sea otters that had been relocated from Amchitka Island to the southern coast of Oregon where food was not a limiting resource, and we found that the animals in Oregon spent 17% of daylight hours foraging. The California study was conceived on the basis of these results. We reasoned a priori that because large differences existed in diurnal time budgets between sea otter populations at or near equilibrium density and those below equilibrium density, and because this character was flexible within populations (as demonstrated by the relocation to Oregon), similar measures from the population in central California would help clarify whether the observed lack of growth was due to food limitation. Our finding that sea otters in California spent 21–28% of daylight hours foraging seemed most consistent with the interpretation that food was not limiting further pop-

ulation growth. All these data were gathered by similar methods so that biases against foraging were not a factor in the comparisons. Furthermore, Garshelis et al. (1990) presented no evidence for regional constraints on foraging time in sea otters that are peculiar to central California (and Oregon).

2. Garshelis et al. (1990) discounted our contention that piscivory in sea otters is related to population status by pointing out that the evidence for increased piscivory at Amchitka Island through time is thin. I agree that the evidence is not strong, but this was not the sole basis for our contention. Garshelis et al. (1990) failed to mention the striking difference in fish consumption between Attu and Amchitka islands (0.2 vs. 11.6% of the foraging observations, respectively [Estes et al. 1981]). This finding was cited in Estes et al. (1986) and has been the principal basis for my contention that the extent of piscivory in sea otters may be related to population status.

3. Garshelis et al. (1990) discounted our scan sampling data by correctly pointing out that estimates obtained by this technique are inherently biased against foraging and lack information from the hours of darkness. We acknowledged the latter point in Estes et al. (1986). However, the inherent bias against foraging activity in scan sampling, which did not become evident until after Estes et al. (1986) was published (Estes and Jameson 1988, Siniff and Ralls 1988) is largely irrelevant to our reported comparisons because we used the same methods at all sites. Garshelis et al. (1990) used both telemetry and scan sample data in an effort to demonstrate that sea otter time budgets in California and at Amchitka Island could be similar. This comparison, by their own detailed account, is inappropriate and misleading.

Garshelis et al. (1990) went to great lengths to point out reasons why each line of evidence presented by Estes et al. (1986) might be incorrect. However, they have not demonstrated in a single instance that our interpretations were incorrect, they provide no evidence for the alternative hypothesis that food was limiting population growth and, what is worse, they offer nothing positive in the way of alternative approaches or suggestions for what we should have done or what might be done in the future. This is indeed unfortunate because it relegates a number of otherwise legitimate points to a paper of little constructive value.

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SEASONAL CYCLES AND DAILY ACTIVITY PATTERNS OF ROCKY MOUNTAIN ELK

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Abstract: We measured monthly and daily activity patterns of free-ranging female elk (*Cervus elaphus*) for 22 months using radio telemetry. Feeding, resting, and moving activities were identified with telemetry signal pulse rate and fluctuations in signal strength. Feeding dominated elk activity (51 ± 4 [SE]%) followed by resting ($36 \pm 3\%$), and moving ($11 \pm 3\%$). Significant seasonal cycles in elk feeding and resting behavior were documented and described by sine functions. Feeding declined by 10% from summer to winter while resting increased by 10%. Diurnal feeding decreased 70% when elk migrated from summer to winter ranges. Nocturnal feeding changed in proportion to the relative length of night. Major daily feeding periods coincided with sunrise and sunset. Elk alternately fed and rested throughout the day on summer range. On winter range, elk rested for extended periods during daylight, but fed and rested during the night.

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Elk in the Rocky Mountain region live in a seasonal environment. Annual changes in temperate weather regimes cause seasonal fluctuations in availability and quality of forage (Hobbs et al. 1981, Baker and Hobbs 1982). Elk energy and nutrient requirements also change seasonally in response to reproductive, foraging, and thermoregulatory costs (Fancy and White 1985, Oftedal 1985, Parker and Robbins 1985). Knowledge of daily and seasonal activity patterns should improve our understanding of elk foraging strategies and of how foraging constraints may dominate behavior patterns (Hanley 1982). Quantitative estimates of elk activity

also are needed to calculate energy expenditures for integration into nutritional carrying capacity models of seasonal ranges (Hobbs et al. 1982, Robbins 1983, Swift 1983, Hudson and White 1985).

Elk maintenance requirements are composed of 3 major cost components: basal metabolism, thermoregulation, and activity. Activity cost can be a major part of energy and nutrient expenditures (Robbins 1983, Fancy and White 1985), but activity is most directly controlled by the animal. Adjustments in activity result in either reduced maintenance costs or increased energy and nutrient intake. This is important in seasonal environments where a negative balance of energy and nutrients during 1 season must be compensated for by increasing rates of acquisition during another season. In temperate climates, ruminants can not continue eating to

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