DALE TOWEILL - A WORKING HYPOTHESIS FOR CALIFORNIA BIGHORN SHEEP MANAGEMENT

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Abstract: California bighorn sheep vary in appearance between herds, with variations due to ecotype. California bighorn sheep are typlified by smaller body size (rams from 180-205 pounds; ewes 106-145 pounds) than Rocky Mountain bighorn sheep, darker coloration, less white in the facial pattern, and (among rams) horns that flare away from the face as the horn curl drops along the jawline. Most show a continuous black or brown dorsal stripe dividing the white rump patch to the tip of the tail. Like other bighorn sheep, California bighorn sheep are 'k-strategists' adapted to exploiting climax plant communities, particularly grassland communities of foothills ranges, low isolated mountains, and rocky canyonlands surrounding the Great Basin and extending nothward into Canada between the Cascade Range and Rocky Mountains. Most populations that currently exist have resulted from transplants into formerly-occupied range since 1975, and demonstrate the 'dispersal phenotype' described by Geist (1971). Because of limited suitable habitat in canyonlands and isolated ranges, most populations have adapted to year-around occupancy of suitable habitat. Few herds demonstrate seasonal migrations, although exploratory movements and distress dispersal into unoccupied habitat are not uncommon. Critical habitat components include forage and free water in proximity to steep rocky rims, terraces, lava beds, steep clay hills or other terrain features that afford opportunity to escape from potential predators. Potential predators include mountain lions, coyotes, and bobcats; large raptors may kill lambs. Weather is rarely a factor affecting California bighorn sheep populations. Susceptibility to disease (except following contact with domestic sheep) seems to be less than documented for Rocky Mountain bighorns, although extensive die-off among California bighorns following contact with domestic sheep has been recorded. There are only limited data suggesting competition between California bighorn sheep and cattle. Where populations are hunted, harvest should not exceed about eight percent of the total number of rams, or 15 percent of the legal rams if harvested under a 3/4 curl rule. California bighorn may exhibit avoidance of habitats due to human disturbance.

The California bighorn sheep (*Ovis canadensis californiana*) is one of seven subspecies of bighorn sheep in North America (Valdez and Krausman 1999, Shackleton et al. 1999). The remaining six subspecies include the Rocky Mountain bighorn (*O. c. canadensis*), the extinct Audubon's bighorn (*O. c. auduboni*), and four desert bighorns—Nelson's (*O. c. nelsoni*), Mexican (*O. c. mexicana*), peninsular (*O. c. cremnobates*) and Weem's (*O. c. weemsi*). Current taxonomic classification follows Cowan (1940), and will likely be reviewed based on development of new taxonomic tools including analysis of chromosomal material. Ramey (1993, 1995) has presented arguments that mitochondrial DNA analysis fails to support currently recognized subspecies. Bighorn sheep, like other Old World species that invaded North America during the Ice Age, are still evolving to fit North America's environments (Geist 1999). Bighorn sheep, elk, moose, and the reindeer/caribou complex, radiated into a wide variety of vacant habitats following the collapse of Ice Age faunas during the past 12,000 years or so (Geist 1999, Toweill and Geist 1999). Like Roosevelt's elk (*Cervus elaphus roosevelti*), the distinctions that set California bighorn sheep apart from other subspecies overlap the ranges of variation for other subspecies and more precisely reflect adaptations to environment and allopatry than strict genetic separation. Unfortunately, because of the rapid extermination of California bighorn herds, little comparative material is available with which to

analyze the range of variability of California bighorns. Their habitats were those most accessible to humans and most desirable for the grazing of domestic livestock, so California bighorns were quickly and completely eliminated from all but two areas of their former range—California's Sierra Nevada and southern British Columbia's interior plateau (Sugden 1961).

California bighorn sheep entered the annals of modern science on December 8, 1825, when one of the hunters attached to Peter Skene Ogden's brigade of fur trappers killed a ram in the Mutton Mountains of eastern Oregon, near the Deschutes River about 45 miles south of the The Dalles. Nine months later, naturalist David Douglas secured the horns of another from an Indian about 6 miles east of The Dalles, and described the species based on those horns and a shirt made from the skin of that animal. Originally named the lava-bed or rimrock bighorn, the name California bighorn was applied by Cowan (1940) in his revision of wild sheep taxonomy because the best-known of the original stocks survived only in California's Sierra Nevada Mountains.

In coloration and body form California bighorns look much like Rocky Mountain bighorn sheep—and for that matter, desert bighorn sheep. Many of the observed variations are due to ecotype, just as Nelson's desert bighorns living in alpine environments quickly assume the look of Rocky Mountain bighorns. While appearance can vary somewhat between herds, Cowan (1940) suggested that smaller body size, darker coloration, less white in the facial pattern, and an open curl among rams (i.e., horns flaring away from the side of the head) were distinguishing characteristics (Hebert and Evans 1991).

California bighorns are less blocky than most Rocky Mountain bighorns, with proportionally longer ears and legs and typically smaller size. Adult rams typically weigh from 180-205 pounds, while adult ewes typically weigh from 106-145 pounds. However, body coloration is somewhat variable. Most California bighorns show a continuous black or dark brown stripe extending forward dorsally from the tip of the tail, dividing the white rump patch. Unlike the horns of Rocky Mountain bighorn rams, which, when viewed from the front, tend to drop nearly straight down from the top of the curl along the face (or even pinch inward), horns of California bighorns typically flare away from the face. As an example, a ram killed by John Muir in California's Modoc lava beds near Mt. Shasta had horns 33 inches in length, but showed a very wide tip-to-tip measurement of 29 1/2 inches (Clark 1964).

Ecological Niche: As glacier followers, all bighorn sheep evolved as prime examples of 'k-strategists'—species adapted to exploitation of climax plant communities, species which exhibit a precise strategy for exploiting all available suitable habitat in both space and time as climatic conditions change. Like all good 'k-strategists', bighorn sheep populations maximize their population size through maximizing the maternal investment in a few young animals, individual longevity, and complex social behavior. Individual longevity and social behavior interact, allowing bighorn populations to maintain social stability while also providing a mechanism whereby populations can pass along traditions of habitat usage through time (Geist 1971), allowing animals to effectively adapt to changing climatic conditions (Geist 1999, Toweill and Geist 1999).

Our understanding of sheep evolution in North America is incomplete, especially since North America's wild sheep evolved as animals adapted to Ice Age habitats, i.e., 'glacier followers' (Geist 1971, 1975, 1999). Glacial and even montane habitats are notoriously poor sites for preservation of fossil material; what little does survive under conditions favorable for fossilization is likely to be pulverized by glacial advance or destroyed by glacial outwash or the combined actions of freezing, thawing, and seasonal precipitation (Horner 1997). Although fossils indicate that bighorn sheep existed in southern California as long as 350,000 years ago and in Wyoming during the interglacial of about 110,000 years ago (Martin and Gilbert 1978, Wang 1984), bighorn sheep were rare habitat specialists until near the end of the late

glacial period of 20,000 to 12,000 years ago. During this period bighorn sheep spread rapidly throughout western North America (Harris and Mundel 1974). With the collapse of the Rancholabrean Ice Age megafauna (which began about 12,000 years ago and continued several thousand years, with a peak at 11,000 years ago and another at 9,000 years ago; see Guthrie 1984), bighorn sheep likely invaded vacant or near-vacant habitats (Geist 1999). It is likely that the California bighorns originated as a result of bighorn sheep invading near-vacant low-elevation habitats following extinction of many Ice Age competitors and predators, during a period of rapidly-fluctuating climatic variation.

However they evolved, California bighorn sheep are animals of the foothills, isolated mountains, and rocky canyonlands. Clark (1964) called them lava-bed or rimrock bighorns, a name that really conveys the habitats selected by the subspecies, and Bailey described their habitat as including "... every canyon, cliff and lava butte as well as many of the rough lava beds ... east of the Cascade Mountains ..." (Bailey 1936).

Restoration of California bighorn sheep to historic habitats has been one of North America's great wildlife conservation success stories. California bighorns were almost completely exterminated by 1930. Despite protection in California, by 1960 only an estimated 390 existed in the United States, with about 1,200 additional animals in British Columbia (Buechner 1960). Although native California herds have continued to struggle (fewer than 170 animals remain), transplants from British Columbia stocks beginning in 1954 have resulted in over 10,000 California bighorns in North America today. In 1999, these populations are distributed among seven states in addition to British Columbia (see Table 1, *from* Toweill and Geist 1999).

Half a century of management aimed at restoration of California bighorns into historic habitats has demonstrated two facts fundamental to California bighorn sheep management:

1. The single best predictor of successful restoration of bighorn sheep in historic California bighorn sheep habitat has resulted from using California bighorn sheep stocks from other areas. Conversely, most failures to re-establish bighorn sheep herds in formerly occupied habitats (either California or Rocky Mountain bighorns) have resulted from transplant wherein an inappropriate source of transplant animals was selected

2. Every state and province where California bighorns now thrive have recognized the distinctive habitat and behavioral requirements of the subspecies. Every state and province manages California bighorns in a manner which will maintain the integrity of the subspecies, a management goal recommended by the California Bighorn Sheep Workgroup chaired by Raymond Demarchi in 1974 (Demarchi 1975).

WORKING HYPOTHESIS: Population Biology: California bighorn sheep are a climax species adapted to typically low-elevation semi-arid environments. Populations are increasing or stable in Canada (Krausman 1997, Shackleton et al. 1997, Toweill and Geist 1999). Virtually all herds outside of British Columbia and California are a result of transplants using stock that originated in British Columbia, beginning in 1954; most were established after 1975 (Toweill and Geist 1999). Because these herds were nearly all re-established in suitable habitat formerly occupied by California bighorns, resources (particularly forage) were (and for many herds still are) essentially unlimited. The relationship between unlimited forage and behavior has implications for management of California bighorn sheep.

Briefly summarized, wild sheep in an environment where critical resources are unlimited grow more rapidly, but utilize resources less efficiently, than those animals that occupy an environment wherein resources are limited. As a result, these "dispersal type" bighorns tend to have a shorter life expectancy, on average, than "maintenance phenotype" bighorns found in areas where forage and other

critical resources are in short supply (Geist 1971). This reduced life expectancy is believed associated with reaching sexual maturity at an earlier age, among other factors (Geist 1971). However, because resources are abundant and animals are vigorous, "dispersal phenotype" bighorns are more likely to disperse in unoccupied suitable habitats. Over long periods of time (ten or more generations) "dispersal phenotype" sheep may become "maintenance phenotype" sheep as a result of population growth and associated resource limitation (Geist 1971).

Virtually all herds of California bighorn sheep re-established since about 1975 should be expected to demonstrate the "dispersal phenotype" characterized by rapid body growth, relatively short life span, and relatively high resistance to disease (a result of both high intake of nutrients, promoting resistance to disease, and low incidence of habitats becoming infected with disease-causing organisms). These herds should also demonstrate a relatively high rate of reproduction and lamb survival, based on the prediction that, with food resources abundant, ewes should be expected to give birth to healthy lambs and provide abundant high-quality milk allowing lambs to grow rapidly and wean successfully. Populations of "dispersal phenotype" bighorns should be expected to respond to habitat alteration by exploratory movements into previously unoccupied habitats, as has been recorded for re-established herds of California bighorn sheep in nearly all states where they have been re-introduced.

Managers should, however, be aware that populations of California bighorn sheep established in the 1950s and 1960s might have begun to experience chronic resource shortages, resulting in development of "maintenance phenotype" populations (Geist 1971). Such populations would likely demonstrate:

(1) a reduction in reproductive rates (associated with reduced average body condition of ewes),

(2) increased average longevity (associated perhaps with increased horn mass among older-age rams),

(3) increased susceptibility to disease (as a result of reduced average body condition), and

(4) greater susceptibility to over-harvest (associated with reduced rates of recruitment of young rams, and full occupancy of suitable habitat).

Such changes should not be unexpected, and may require adjustments to long-term management regimes. Appearance of these indicators in California bighorn sheep herds should prompt managers to investigate resource availability.

Range Limitation: California bighorn sheep populations have adapted to year-around occupancy of a limited habitat; i.e., an isolated mountain, series of rimrocks, or rocky canyon system, generally at elevations between 4,000 and 6,500 feet. Although migrational movements of up to 48 km have been recorded in British Columbia (Sugden 1961, Blood 1963) and California's Sierra Nevada (McCullogh and Schneegass 1996), many herds are non-migratory, spending the entire year within a relatively limited range with little elevational gradient, such as isolated desert mountains or canyonlands (Sugden 1961, Toweill and Geist 1999). However, even in these ranges short (<10 km) seasonal movements between wintering areas, rutting grounds, and spring/summer ranges are typical. Rams typically isolate themselves from ewes in bachelor groups, either by utilizing suitable habitats on the unoccupied periphery of ewe/lamb ranges or by moving away from typical escape terrain onto associated flats or rolling hills.

As 'dispersal phenotypes,' California bighorn sheep may demonstrate exploratory movements into unoccupied sheep habitat due to rapid phenotypic development. They may also demonstrate distress dispersal due to catastrophic change in range conditions (Geist 1971). Such movements may result in establishment of 'satellite' herds that may (or may not) return to the site of origin. One example of such a move occurred in the summer of 1986 when 10-12 California bighorn sheep moved as a group from Leslie Gulch in Oregon following a wildfire on their home range. These animals dispersed approximately 65 km to the

southeast, and finally established themselves in a small area of suitable terrain on Reynolds Creek in Idaho (Toweill, file data), where they still persist 13 years later. In addition to catastrophe, such dispersal may also be triggered by drought (Geist 1971) and other changes in climatic conditions.

Habitat Components: Critical habitat components for California bighorn include sufficient quality of forage and free water in proximity to steep rocky rims, rocky terraces, lava-beds, steep clay hills or other features which allow bighorns an opportunity to escape from mammalian predators (Blood 1961, Bodie et al., Drewek 1970, Kornet 1978, Hansen 1982). California bighorn sheep rarely occupy areas where visibility is impeded by large shrubs or trees. The most critical component of suitable habitat seems to be the presence of rocky terraces on which ewes can isolate themselves for parturition, and which affords ewes an ample supply of forage during the first few weeks after birth. These terraces also provide lambs immediate access to escape terrain from predators able to access the terraces which are typically relatively inaccessible to predatory wolves and coyotes. Females with young lambs are generally found within 100 m of such escape habitat, although distances increase from late spring into summer (Hansen 1982). Rams are much more independent of escape cover, ranging as far as several miles away from cliffs and canyonlands (Hansen 1982).

Predators: The primary predators of California bighorn sheep are mammalian, particularly mountain lions (*Felis concolor*) (Harrison and Hebert 1988). Smaller mammalian predators including coyotes (*Canis latrans*) and bobcats (*Lynx rufus*) may occasionally kill adult bighorns, and coyotes (Hebert and Harrison 1988), bobcats, and large avian predators including golden eagles and even ravens may kill lambs.

Weather Influences: Weather is rarely a factor affecting California bighorn sheep populations. Sheep selectively forage during winter on steep slopes nearly free of snow, although deep accumulations may result in losses among California bighorns (Demarchi and Mitchell 1973). Drought that reduces forage quantity and quality can reduce individual fitness and may reduce lamb recruitment rates. Long wet springs may reduce lamb recruitment rates.

Disease: California bighorn sheep appear to have greater resistance to a variety of potential pathogens than Rocky Mountain bighorns. Large-scale die-offs associated with disease occur more rarely among California bighorns that among Rocky Mountain bighorns. California bighorn sheep are noticeably absent in a review of wild sheep die-offs (Schwantje 1988). However, devastating die-offs such as that recorded for California's Modoc lava-beds herd (Hunt 1980, Jessup 1980) have been recorded among California bighorn sheep following exposure to apparently healthy domestic sheep (Martin et al. 1996).

Interactions with Domestic Livestock: Despite extensive evaluation, there is little evidence of competition between California bighorn sheep and cattle (McCullough and Schneegass 1966, Drewek 1970, Kornet 1978, Estes 1979, Ganskopp and Vavra 1987). While cattle significantly avoided slopes >20%, California bighorn sheep used slopes up to 80% in proportion to availability (Ganskopp and Vavra 1987).

Hunting: Harvest of California bighorn sheep can depress populations and when excessive may reduce the amount of suitable habitat utilized. Behavioral evidence (Geist 1971) suggests that mature rams are necessary to pass along traditions relating to seasonal use and travel routes connecting critical areas of suitable habitat.

Harvest should be focused on mature rams, and carefully limited to insure that mature rams always exist in managed populations. More specifically, harvest of mature rams should not exceed 3/4 of the natural replacement rate, or about 8 percent of the total ram population (Geist 1971, 1975). In areas where herds are routinely surveyed, this guideline has been modified to allow tags for harvest of up to 15 percent of the observed 3/4 curl rams (i.e., typically rams aged 4 years and

older). This guideline has proven to provide a safely conservative harvest, since biologists are unable to observe all of the legal rams in a population and not all hunters are successful.

Harvest of ewes may be allowed where the objective is to reduce population size or to reduce the rate of population growth. Annual harvest should not exceed 20 percent of the ewes. If population stabilization is the objective, harvest of ewes to achieve a 1:1 ratio of ewes to rams, or ratios of 40 ewes and 20 lambs per 40 rams, has been recommended on the basis of long-term studies of Rocky Mountain bighorns (Wishart 1999).

Human Disturbance: Evidence indicates that California bighorn sheep may avoid some habitats due to human disturbance associated with hikers in occupied habitats (Dunaway 1971, Wehausen et al. 1977, Hicks and Elder 1979, Wehausen 1980). Excessive disturbance by humans may lead to permanent abandonment of suitable habitat (Dunaway 1971). Although disturbance may result in decreased use of habitats frequented by humans, whether human disturbance on summer range affects reproduction is inconclusive (Wehausen 1980). However, hunting seasons should be designed to disperse hunters as widely as possible through both time and space to minimize risk of abandonment of portions suitable habitat.

FUNDAMENTAL BASIS FOR MANAGEMENT:

1. Locations of California bighorn sheep herds are well-identified and discreet (Toweill and Geist 1999).

2. California bighorn sheep populations are predictably loyal to their home ranges.

3. The number of animals in each population can be estimated with reasonable accuracy (Bodie et al. 1995).

4. Annual fluctuation in adult population size rarely varies more than 15 percent.

5. Annual lamb recruitment typically varies between 10 and 50 lambs per 100 ewes.

6. Predators can significantly affect California bighorn sheep population growth. Mountain lions are effective predators of bighorn sheep of all ages, and coyotes have been implicated in poor lamb recruitment rates.

7. Most herds exist on low-elevation ranges with a continental climate, and weather is rarely a factor influencing population size. Drought is typically a more severe factor than snowfall.

8. Direct contact between California bighorn sheep and domestic sheep may result in catastrophic fatal epizootics leading to the near-complete demise of California bighorn sheep. Other than that, California bighorn sheep appear remarkably resistant to diseases, and disease is rarely a major concern in management of California bighorn sheep.

9. California bighorn sheep may compete with cattle for forage, but there is little indication of behavioral avoidance of cattle.

10. Parasite loads are rarely a factor in California bighorn sheep population growth.

11. Human disturbance is a stressor on California bighorn sheep, and repeated disturbance by human may result in temporary (rarely permanent) range abandonment.

12. The large majority of California bighorn sheep populations have resulted from transplants within the past 25 years, and resultant populations demonstrate 'dispersal phenotypes,' i.e., rapid growth, high rates of lamb production and recruitment, and an average longevity of 7-10 years.

13. Horn growth of rams is reduced relative to Rocky Mountain bighorn sheep populations, particularly those demonstrating 'maintenance phenotypes.' Even old-age rams (aged 8-10 years) rarely exceed 7/8 curl, horn length

greater than 36 inches, or horn base circumferences larger than 14 1/2 inches.

14. Legal harvest of California bighorn sheep can be controlled by permit-based hunting, and evaluated by regulations requiring that horns of all harvested rams be pinned for permanent identification.

15. Illegal harvest does occur in many herds, illegal harvest targets adult rams, and the extent of illegal harvest is rarely known but may equal legal harvest.

16. Harvest of adult (4-years and older, 3/4 curl or larger) rams at a rate less than 3/4 of the ram recruitment rate has little effect on the viability of California bighorn sheep herds.

17. Removal of >20 percent of ewes compromises lamb production and results in population declines.

DISCUSSION: Much like Roosevelt's or Tule elk, successful California bighorn sheep management has been based on a collection of ecotype distinctions which may (or may not) be reflected in mitochondrial DNA or other genetic markers. Fifty years of management experience with California bighorn sheep have proven that California bighorn sheep have some apparently unique behavioral and/or physiological adaptations to semiarid, low elevation habitats. Efforts to re-establish bighorns in such habitats have been most successful when animals for transplant have originated from California bighorn stocks.

Some of the past management successes can no doubt be attributed to the familiarity of individual animals with forage species available on low-elevation ranges, learned behavior associated with securing moisture and escaping predators, etc. Another likely factor is that California bighorn sheep, as a largely non-migratory species, have demonstrated less of a tendency to disperse individually from release sites soon after release, thereby enhancing the potential for rapid establishment of a resident population.

While the genetic status of the subspecies may remain uncertain until a taxonomic revision is completed, ecotypic variation has been and will continue to be a major concern for wildlife managers. State and provincial agencies will almost certainly continue to management California bighorns as an ecotype distinct from Rocky Mountain bighorns, much as they continue to manage Roosevelt's elk as an ecotype distinct from Rocky Mountain elk.

Management of California bighorn offers opportunities not available to managers of Rocky Mountain bighorns. Because California bighorns occupy low-elevation habitats and often do not establish migratory traditions due to climatic influences, populations can often be quickly established in very discreet habitats, such as isolated Great Basin mountains or rocky canyonlands.

California bighorns appear to be more resistant to diseases than Rocky Mountain bighorns, and appear to be able to co-exist with cattle grazing and some degree of human interaction. Predation, especially where mountain lion or coyotes numbers are high, is a concern.

Harvest management must be based on removal of only a portion of the mature animals in the population. Mature rams are critical for the behavioral maintenance of social order (Geist 1971). Harvest of adult rams and harvest of ewes (if allowed) should be carefully monitored to insure that the number of animals harvested by hunters plus the number lost to other causes does not exceed the annual recruitment rate of adult into the population.

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Table 1. Population estimates for California bighorn sheep in North America, 1998 (*from* Toweill and Geist 1999).

Location	1960	1970	1975	1985	1990	1998
British Columbia	1,185	1,764	1,850	3,240	4,645	3,630
California	390	390	195	300	320	170
Idaho	0	90	50	530	1,205	1,460
Nevada	0	8	30	151	484	1,248
North Dakota	0	120	250	--	232	350
Oregon	24	--	210	1,007	1,805	2,890
Utah	0	0	0	0	0	30
Washington	Remnant	303	400	550	586	745
TOTAL	1,609	2,765	2,985	5,778	9,227	10,523

QUESTIONS, ANSWERS AND COMMENTS - DALE TOWEILL PRESENTATION

VERN BLEICH, CALIFORNIA: Dale, why would removal of 20 percent of the ewe cohort compromise lamb recruitment rates?

DALE TOWEILL: Fewer factories, basically.

BLEICH: You mean you just produce fewer lambs?

TOWEILL: Produce fewer lambs and you, in fact, affect the ability of that herd to maintain itself. Again, this is based on our experience in Idaho when we got carried away with our transplant efforts.

BLEICH: I'm sorry. I understood you to say that the recruitment rates were compromised.

TOWEILL: Excuse me. I misspoke. Recruitment rates may be reduced if ram harvest exceeds the replacement rate. Overharvest or removal of ewes compromises lamb production.

TOM RYDER, WYOMING: Dale, I'd be curious to hear your opinion of utilizing California sheep to try and repopulate maybe some distant Audubon ranges in central and eastern Wyoming and like those other folks have already done in Nebraska and South Dakota?

TOWEILL: It's my opinion, based on what I know of California bighorn sheep and Rocky Mountain bighorn sheep ranges, that many of the Audubon sheep ranges tend to be isolated. They tend to be patchy habitats, very good in small areas. They appear to be ideally situated to small populations, so that once you dump them out there, they remain relatively loyal to that habitat.

As we all know, when you transplant animals the first worry is if you have enough animals to interact and start a basal population. The number of animals transplanted goes down and may disappear. Whether they disappear to find something better to live in or whether they become coyote fodder, using a population of animals that does not have a migratory tradition maximizes your opportunity to establish a basal population. minimizes a chance that your desired population is going to wind up some place different than where you intended.

WAYNE HEIMER, ALASKA: Are you aware of any susceptibility to *Pasteurella* toxins?

TOWEILL: I'm not aware of any. There may be some, but I have no personal awareness of those.