These specimens have been identified as *E. junaluska* because similar specimens have been induced to metamorphose by treatment with thyroxin (Sam Sweet, pers. comm.). The large larvae of *E. junaluska* are quite distinct from those of other aquatic salamanders in the area. They have a pattern similar to that of metamorphosed individuals except that in the larvae, there is typically more mottling dorsolaterally, especially on the tail. Many of the larger larvae of *E. junaluska* possess a row of 6-7 large melanophores dorsal to the lateral mottling on the trunk (Fig. 1).

Smaller larvae of *E. junaluska* may be confused with those of *E. bislineata.* However, the pattern typical of the smaller larvae of *E. junaluska* is similar to that of the larger ones, whereas larvae of *E. bislineata* typically have lighter and/or more diffuse mottling than *E. junaluska.* Bruce (1982b) noted that larval *E. junaluska* are more melanistic and more robust than *E. bislineata* larvae. Still, I cannot allocate some small larvae to either species with certainty, and Bruce (1982b) could find no significant differences by microscopic examination in the pigmentation of newly hatched *E. junaluska* and *E. bislineata* larvae. A more detailed description of the larvae of *E. junaluska* is in progress (Bruce, 1982b). It is apparent, however, that in lotic habitats within its range, any *Eurycea* larva $>$ 34 mm SVL is likely *E. junaluska.*

*E. junaluska* may be more common than the few specimens collected would indicate. Despite much fieldwork in the area over the past decade, I have collected fewer than 50 metamorphosed individuals. The most effective way to collect metamorphosed specimens remains road-hunting on rainy nights. On such occasions, *E. junaluska* is one of the most frequently encountered salamanders along the Cheoah River road, and it was one of the most abundant forms in my collection along the Tellico River road. The species should be searched for in other drainages of the Tennessee River in southeastern Tennessee. Many of the larger streams are bordered by blacktop roads that would be suitable for roadhunting. Perhaps the best way of determining the presence of the species in an area would be to search for the larvae in smaller streams. The large and distinctive larvae are quite common at locales such as Santeetlah Creek and Tullulah Creek in North Carolina, where adults are seldom encountered. However, the larvae are not especially numerous in the Cheoah or Tellico Rivers. These larger streams are heavily stocked with trout, and perhaps predation by this and other fish species has an adverse effect on the population size of *E. junaluska* there. Competition with other aquatic salamanders may also be a factor. Trout are numerous in Santeetlah Creek, but few species of salamanders other than *E. bislineata* and *E. junaluska* are common in the main channel of the stream (Bruce, 1982b).

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# INTERRELATIONSHIPS BETWEEN BEHAVIORS IN A BEAVER, *Castor canadensis,* POPULATION

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Interrelationships between behaviors in a population of beavers in the Western United States are illustrated by R-factor analysis. Three of the eight extracted factors interrelate different behavioral categories. One factor associates all repair behaviors, while the other two interrelate types of encounters between beavers. These interrelationships are considered to be important in understanding the organization of the beaver social group.

### INTRODUCTION

The beaver, *Castor canadensis,* is semiaquatic, primarily nocturnal, strictly herbivorous, and the largest native North American rodent (Hall and Kelson 1959). Beavers live in family groups which most often consist of a mated pair of adults, from one to four yearlings, and from one to four young of the year called kits (Bradt 1938, Svendsen 1980).

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Compared to the vast amount of literature that exists on the general life history of the beaver (e.g. Warren 1927, Seton 1928), until recently few quantitative studies of their behavior have been conducted. Brady (1975) and Svendsen (1978, 1980), in Ohio, Hodgdon and Larson (1973) and Hodgdon (1978), in Massachusetts, and Busher (1980), in California, all examined various aspects of the behavior in marked populations of beavers in which the age and sex of each individual was known. In this paper I further describe the interrelationships between behaviors in a marked population of beavers in the Western United States, and argue that these interrelationships are important in the organization of the family group.

## Methods

Research was conducted at the University of California research station at Sagehen Creek, Nevada County, California. The stream, located on the east slope of the central Sierra Nevada, originates from natural springs at an elevation of 2400 m and flows for 13.5 km to the east where it empties into Stampede Reservoir at 1800 m in elevation.

Predominant plants along the stream are four species of willow, *Salix spp.*, and mountain alder, *Alnus tenuifolia,* with patches of quaking aspen, *Populus tremuloides,* lodgepole pine, *Pinus murrayana,* jeffrey pine, *P. jeffreyi,* and white fir, *Abies concolor.* Meadows bordering the stream are primarily composed of members of the sedge family, *Cyperaceae,* and grass family, *Gramineae.* Detailed descriptions of the physiography, climate, and vegetation at Sagehen Creek can be found in Hall (1960), Savage (1973), and Busher (1980).

Research was begun in 1977 and continued through October 1979. Data were collected from May through October each year, for a total of 300 days for the entire study period. Over 1000 hours were spent in observation of behavior.

Beavers were livetrapped in Bailey live-beaver-traps, weighed, measured, sexed by external palpation for the os penis and testes (Osborne 1955) and by examination of blood smears (Larson and Knapp 1971), and marked for individual identification with number 3 monel metal wing bands fitted with a 2-3 cm pieces of colored plastic attached in each ear (Miller 1964). Beavers were assigned to one of four age classes (kits, yearlings, 2-year-olds, adults) based on weight and other physical measurements, and no ambiguity about either age class or sex existed during the study.

Behavioral observations were made with binoculars from platforms 5-10 m high in stream-side trees. Data were tape-recorded and later transcribed onto computer compatible coding forms for analysis. Early evening (1700-2100 hours) and early morning (0530-0700 hours) observation periods were conducted on most days in the field. Night observations using an infrared scope were made less frequently. Focal animal and focal subgroup sampling (Altmann 1974) were conducted, and the number of occurrences of each category of behavior recorded. Durations of selected behavioral categories were also collected. Since beavers were in view for varying periods of time all occurrences of each behavioral category were converted to a rate (number of occurrences/minute). Durations were also converted to a rate (number of seconds/minute). Data for the behavioral categories were analyzed by R-factor analysis with oblique rotation (Nie *et al.* 1970). This analysis, which illustrates correlations between variables in multivariant data, has been used successfully in other behavioral studies (Svendsen and Armitage 1973, Yahner 1978). The initial step in R-factor analysis is to create a correlation matrix, and my original matrix consisted of 114 observation periods (rows) and 18 behavioral categories (columns). From this original matrix a smaller number of factors, which attempt to explain the correlations between the larger number of variables (behavioral categories) were computed. Factors with eigenvalues greater than 1 (which is an indication of the total variance explained by each factor) were extracted. A final matrix of behavioral categories (rows) and factors (columns) was generated and variables with factor loadings (correlation coefficients) greater than 0.35 for an individual factor were considered in interpretation of the data. Behavioral categories with factor loadings greater than 0.35 for the same factor were considered to be interrelated.

## Results

Thirty-seven beavers living in four family groups were studied, and data on 18 behavioral categories (Table 1) collected.

TABLE 1: *Descriptions of the 18 behavioral categories.*

| Behavorial Category | Description |
|---|---|
| Feeding | Eating of willow, grass, and other items. |
| FeedingD | Time spent feeding. |
| Grooming | Cleaning the fur with the fore and hind feet. |
| GroomingD | Time spent grooming. |
| Swimming | Movement through the water, usually from one location to another. The head is held low in the water and movement is rapid. |
| SwimmingD | Time spent swimming. |
| Patrol | State of alertness both moving and stationary. During a moving patrol the head is held high out of the water and movement is relatively slow. Sniffing is common during both types of patrol. |
| PatrolD | Time spent patrolling. |
| Dam Repair | Addition of mud, sticks and other material to a dam. |
| Provision | Carrying food to a rest site (lodge or burrow) where other beavers are known to be. |
| House | Addition of mud, sticks and other material to a lodge, or digging out the entrance to a burrow. |
| Encounter Dom. | A dominant encounter. When two beavers come within one meter of each other and one beaver forces the other to move away from it. Contact may or may not occur. |
| Encounter Sub. | A submissive encounter. When two beavers come within one meter of each other and one beaver moves away from the other. Contact may or may not occur. |
| Encounter Neu. | A neutral encounter. When two beavers come within one meter of each other, but neither forces the other to move away. |
| Encounter Food | An encounter in which at least one beaver has food, and another beaver will attempt to take the food, or feed on it. |
| Encounter Voc. | An encounter during which at least one beaver vocalizes. |
| Tail Slap | Striking the surface of the water with the tail to produce a loud slap. |
| Scent Mound | Building a pile of mud and sticks on which a beaver will secrete scent from the anal and castor glands. |

Eight factors which accounted for 70.3% of the total variation were isolated. Four of these factors associated

the duration of a behavioral category with its rate of occurrence. A fifth factor isolated most neutral encounters by themselves, whereas the remaining three factors interrelated different behavioral categories (Table 2). Because these three factors interrelate different behavioral categories they are considered in further interpretation of the data.

Factor V interrelates submissive encounters and encounters involving food. I call this the "submissive factor" and it accounts for 7% of the total variation. Factor VII, which I call the "Maintenance factor", correlates repair behaviors of dams with repair behaviors of lodges and burrows (House). This factor accounts for 5.8% of the total variation. Factor VIII associates neutral encounters with encounters during which at least one beaver vocalized. This factor, called the "neutral factor" accounts for 5.7% of the total variation.

TABLE 2: *Factor matrix of behavioral categories and four of eight factors which interrelate different categories. Only factor loadings (correlation coefficients) greater than 0.35 are reported.*

| Behavioral | Factor | | | |
|---|---|---|---|---|
| Category | III | V | VII | VIII |
| Feeding | | | | |
| FeedingD | | | | |
| Grooming | | | | |
| GroomingD | | | | |
| Swimming | | | | |
| SwimmingD | | | | |
| Patrol | | | | |
| PatrolD | | | | |
| Dam Repair | | | .61 | |
| Provision | | | | |
| House | | | .41 | |
| Encounter Dom. | | | | |
| Encounter Sub. | | .58 | | |
| Encounter Neu. | .78 | | | .38 |
| Encounter Food | | .63 | | |
| Encounter Voc. | | | | .73 |
| Tail Slap | | | | |
| Scent Mound | | | | |
| Percent Variation Explained | 8.8 | 7.0 | 5.8 | 5.7 |

## *Discussion*

The importance of the interrelationships between behavioral categories most likely lies in their role in the social organization of the beaver.

The submissive factor (factor V), with which submissive encounters and encounters involving food are correlated, is interpreted to suggest that submissive beavers in the population are more likely to be involved in encounters over food. Beavers have been reported to "beg" food (Tevis 1950, Schramm 1968, Hodgdon and Larson 1973) from other beavers and antagonistic interactions during these food begging encounters have been observed (Tevis 1950, Schramm 1968). However, Tevis (1950), and Schramm (1968), do not report any clear correlation between food begging and submissive beavers, whereas Hodgdon and Larson (1973) did not even consider encounters over food in determining dominance within a family group because they found any beaver would give up food to any other beaver. Since an age class dominance hierarchy, with older animals dominant over younger animals, has been reported for beavers in Massachusetts (Hodgdon and Larson 1973), and California (Busher 1980), a general hypothesis based on the present analysis can be formulated. This hypothesis is that the more submissive beavers (for example the younger beavers) in the population will be most likely to beg food, or at least be involved in encounters over food.

The correlation of both dam repair and house repair behaviors with factor VII indicates that the same beavers in the population are involved in both types of repair activities. Hodgdon (1978) reports that females of every age class had higher frequencies of construction and repair behaviors than males, and that adults had higher frequencies than younger animals. Busher (1980) found an opposite pattern with males of every age class having higher frequencies than females, but also found adults to have higher frequencies than other age classes. The present analysis provides further evidence that different types of repair behaviors are related and that they are most likely performed by the same beavers.

Vocalizations by beavers have been studied by Leighton (1933), Tevis (1950), Schramm (1968), Novakowski (1969), Hodgdon and Larson (1973), and Hodgdon (1978). These reports either note the quality and possible meaning of the vocalization, or the specific direction (from one beaver to another) of the vocalization. None of these authors report a relationship between vocalizations and a specific type of dominance-submissive encounter. The extraction of a neutral factor (factor VIII) suggests that neutral encounters and encounters in which at least one beaver vocalized are related. Interpretation of this factor is difficult since the factor loading of neutral encounters is low (0.38) for this factor, while it is higher for another factor (factor III, 0.78). However, since both of these behavioral categories are correlated with one factor some interrelationship between these categories does exist. A possible explanation is that vocalizations are used when beavers encounter each other to create a neutral encounter and avoid a dominant-submissive interaction. This would help promote group unity and reduce intra-family strife, which would be important in a small, closed social group such as a beaver family.

In conclusion, this analysis provides added insight into beaver behavior and suggests that organization of the social group is enhanced by interrelationships between behavioral categories.

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