ARE HOUSE COUNTS RELIABLE ESTIMATORS OF DUSKY-FOOTED WOODRAT POPULATION SIZE?

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ABSTRACT: Dusky-footed woodrat (*Neotoma fuscipes*) abundance is often estimated using house counts; a house typically being described as a large pile of sticks, usually built on the ground, but occasionally on tree limbs. For purposes of the count, it is sometimes assumed that each "active" house represents one woodrat. An active woodrat house is indicated by its appearance; fresh vegetative cuttings at the house and the presence of recently deposited fecal pellets. Results from our ongoing study in the foothills of the Sierra Nevada suggest that, in some habitats, house counts may not be a reliable method for estimating dusky-footed woodrat population size. Woodrats frequently resided in atypical houses, which bore little resemblance to typical houses and were often very difficult to locate, if not altogether overlooked. These included houses within tree cavities, rock crevices, and ground holes. Furthermore, individual woodrats often used and maintained more than one house and, occasionally, more than one woodrat occupied or used a single house. The classical use of total house counts for population estimation of dusky-footed woodrats could potentially cause substantial errors in estimating population size.

Key words: dusky-footed woodrat, house counts, *Neotoma fuscipes*, oak woodland, population estimation, rock outcrops, Sierra Nevada, stick houses, tree cavities

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Dusky-footed woodrats (*Neotoma fuscipes*) are known for their habit of constructing stick houses within which they reside, store food, and bear young (Vestal 1938, Linsdale and Tevis 1951). These houses have commonly been described as conspicuous, conical piles of sticks with many passageways and compartments (English 1923, Gander 1929, Linsdale and Tevis 1951, Cameron 1971, Ashley and Bohnsack 1974). There has been some mention in the literature of "atypical" houses built in hollow limbs and rock crevices, particularly in earlier studies (Gander 1929, Davis 1934, Horton and Wright 1944), however more recent studies have focussed primarily on the "typical" large stick house (Cameron 1971, Hammer and Maser 1973, Sakai and Noon 1993).

Some studies have used counts of houses to estimate dusky-footed woodrat abundance (Vogl 1967, Sakai and Noon 1993, Hamm 1995). Primarily, only active woodrat houses are counted. An active house is one that has evidence of structural maintenance (new sticks added), house entrances and travel paths that are free of debris and spider webs, fresh vegetative cuttings, and recently deposited fecal pellets (Cameron 1971, Barbour and Humphrey 1982, Vestal 1938).

Since woodrat houses are typically recognized as conspicuous piles of sticks, it is usually these houses alone that are counted, while more cryptic, "atypical" houses, if present, are overlooked. House counts are primarily conducted by traveling a transect and visually searching for the houses (Hammer and Maser 1973, Hamm 1995). The width of the transects could greatly affect how many houses, particularly inconspicuous ones, can be located. Hammer and Maser (1973) located houses while traveling along roads and cross-country, stating that dusky-footed woodrat houses were easily discernible. Such an assumption is unlikely to be true for all populations across all habitats.

For counting purposes, each active house is often assumed to contain one woodrat (Gander 1929, Vestal 1938, Vogl 1967). However, the number of houses used by dusky-footed woodrats is variable between individuals and over time. At particular times of the year, there may be temporary cohabitation of woodrats within one house, such as during the breeding season when some male woodrats reside with females (English 1923, Donat 1933) and when females have young they are nursing (Gander 1929, Linsdale and Tevis 1956). In addition, woodrats frequently use and maintain more than one house (English 1923, Linsdale and Tevis 1956, Cranford 1977).

Basing woodrat population size solely on house counts, especially where atypical houses are prevalent, could seriously underestimate woodrat abundance or even allow some sites to appear uninhabited by woodrats. On the other hand, disregarding multiple house use by woodrats could tip population estimates in the other direction. In reference to a Key Largo woodrat (*Neotoma floridana smalli*) study by Barbour and Humphrey (1982), in which house counts underestimated woodrat population size, Humphrey (1988) stated that his observations confirmed that woodrat numbers were correlated

poorly with the abundance of sign (houses, piles of droppings, and burrows). In a dusky-footed woodrat study in California, Hamm (1995) reported that house index was not a precise predictor of current woodrat abundance. Herein, we provide further support for these conclusions by describing the variation in the types and use of woodrat houses on three oak woodland sites in the southern Sierra Nevada, and we discuss the resulting implications for estimating woodrat population size.

STUDY AREA

The study area consisted of three 2.25-hectare oak woodland sites, Pine Flat, Camp 4 1/2, and Secata, in the foothills of the Sierra Nevada in eastern Fresno County. Elevation ranged from 300 to 450 m. All three sites were within 2 km of the Kings River. Pine Flat was the most densely vegetated site, with an overstory dominated by interior live oak (*Quercus wislizenii*) with some gray pine (*Pinus sabiniana*) and ash (*Fraxinus* spp.). It had a dense shrub understory of ceanothus (*Ceanothus* spp.), poison oak (*Toxicodendron diversiloba*), and manzanita (*Arctostaphylos* spp.). Camp 4 1/2 had a moderate overstory of blue oak (*Q. douglasii*), interior live oak, and California buckeye (*Aesculus californica*), with a relatively sparse to moderate understory of poison oak and ceanothus. Secata was the most open site, dominated by blue oak, with small patches of interior live oak and California buckeye. The understory was sparse, consisting of ceanothus, chaparral honeysuckle (*Lonicera interrupta*), and manzanita.

METHODS

Many woodrat houses were located and tagged during the initial establishment of 7 x 7 trapping grids (15 m spacing) in 1993 for a small mammal population ecology study. In 1994, we focused our study primarily on dusky-footed woodrats and enlarged each study site from 0.81 hectares to 2.25 hectares. During the winter of 1994-95, each study site was searched in its entirety for woodrat houses by walking the center of 10 m-wide transects (15 per site). All potential woodrat house sites and all woodrat sign, such as fecal droppings or vegetative clippings, were investigated to determine if a house was present. Two conditions indicated a woodrat house: (1) the presence of one or more piles of sticks and other collected debris, and (2) the presence of woodrat sign, such as fecal deposits and ground paths, very near or at a cavity or cavities. The latter condition applied even when sticks were not present or visible. All houses found were numbered and tagged. Over the course of the study (through 1997), additional houses were incidentally found during summer trapping sessions (1-3 weeks/site/year) when woodrats retreated into previously undetected houses and as new houses were built. The former were primarily cryptic houses located in hollow limbs with no external evidence of their presence, and as such, were not detectable during house searches. Each new house was numbered and tagged as well.

Each house was classified into one of three categories: typical, atypical, or intermediate. The location of the nest and storage chambers within each house type was determined based on the location of entrance-ways, and on several occasions was confirmed visually, when stick houses were found torn open, limbs containing houses split open, or chambers were visible within rock crevices. A typical house is the classical large stick pile. The nest chamber and storage chambers are located within the stick pile. Any use of structures, such as rocks or shrubs, are purely as support or foundation for the house. Due to the large number of sticks used, these houses are easy to locate, assuming the surrounding vegetation is not particularly dense. An atypical house contains very few or no sticks. The nest and storage chambers are located within a cavity or hole, such as a tree hollow, rock crevice, or ground hole. The tree, rock, or ground serve as both the foundation and the framework for the house. Due to the lack of sticks or their visibility, these houses are usually difficult, if not impossible, to locate without intensive searching or following a woodrat to the house.

An intermediate house has characteristics of both typical and atypical houses. It consists of both sticks and one or more other structures, such as rocks or logs. The stick piles do not contain entrance-ways; rather the nest and storage chambers are located in a cavity of the structure being used (i.e., rock outcrop). These houses have a moderate number of sticks, and therefore are relatively easy to locate, assuming the surrounding vegetation is not particularly dense.

To determine house use by woodrats, data were pooled from 2 previous studies on the same sites: (1) a mark-recapture population ecology study (Fargo and Laudenslayer, unpubl. data, 1995-1996), and (2) a microhabitat use study involving direct observation of woodrats and fluorescent powder tracking (Fargo, unpubl. data, 1996-1998). We obtained house use data from the former by trapping at woodrat houses and observing woodrats as they retreated into their houses. House use data was provided by the latter by directly observing woodrats during the evening through use of battery operated light-tags and by tracking woodrats using fluorescent powder. These methods sometimes revealed the locations of "hidden" atypical houses having no external evidence of their presence, particularly those in hollow tree limbs.

During analysis of house use, we excluded houses where more than one woodrat was captured, as the resi-

dent woodrat, if there was one, was not always easy to determine. The purpose of this count was simply to confirm multiple house use by individual woodrats, and therefore it was not necessary to include all houses in the count. Juvenile and subadult woodrats were also excluded from this data, since they generally were either residing with their maternal parent or perhaps attempting to establish their own home range (Linsdale and Tevis 1951).

RESULTS

The types of houses used by woodrats varied both within and between sites, but more substantially between sites (Fig. 1). Pine Flat, the most densely vegetated site, had primarily typical (30; 27%) and intermediate houses (63; 57%). Secata, with the sparsest cover, had primarily atypical houses (25; 61%) and very few typicals (3; 7%). Camp 4 1/2 had a more even number of the three house types: typical (16; 31%), intermediate (20; 39%), and atypical (15; 29%). For all three sites in total, intermediate houses made up 47%, typicals 24%, and atypicals 29%.

Data from previous studies (Fargo and Laudenslayer, unpubl. data, 1995-1996, Fargo, unpubl. data, 1996-1998) showed that some woodrats used up to 4 houses concurrently. The largest number of woodrats (50) were found at 1 house, however 25 were found using 2 houses, 8 were found using 3 houses, and 1 individual was found using 4 houses.

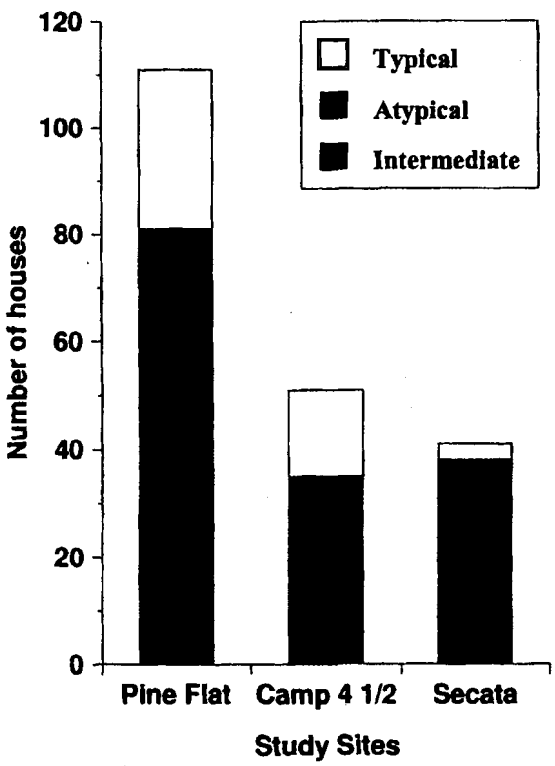

Fig. 1. Numbers of typical, atypical, and intermediate dusky-footed woodrat houses on 3 oak woodland study sites in the southern Sierra Nevada 1993-1997.

DISCUSSION

Our results indicated that cursory house counts may not be reliable estimators of dusky-footed woodrat population size in some habitats. One problem was the presence of inconspicuous atypical houses. Despite the variability in vegetative composition and structure between our 3 oak woodland sites, all 3 contained atypical houses. There was a particularly high percentage of atypical houses on our most sparsely vegetated site, which had a high component of large blue oaks with hollow limbs and many rock outcrops. The atypical houses located in hollow limbs were the most difficult to detect, due, in part, to their having little or no external evidence of woodrat presence. In addition, their location made them less visually accessible and created the potential for woodrats to use travel routes in the higher limbs. This reduced the chance of trapping woodrats on the ground or low in limbs and following them back to their houses. Many of these houses were not detected during the house survey, and were located only when the resident woodrat was captured at a neighboring house and subsequently retreated into the previously undetected one. At least 15 of these "invisible" houses were located in such a manner. This begs the question of how many more were present on our sites that were not detected.

Some other studies on dusky-footed woodrats, particularly earlier ones, have also noted the presence of inconspicuous houses in rock crevices and tree cavities (e.g., Gander 1929, Davis 1934, Horton and Wright 1944, Hammer and Maser 1973). Davis (1934) described dusky-footed woodrat houses in California as varying from a few handfuls of twigs to huge structures on the ground and on large rocks. He also detected one that was merely a nest chamber in a crevice in a large rock. Horton and Wright (1944) also cited the use of rock outcrops and other structures that provided natural cavities for nesting and storage chambers. The Key Largo woodrat (*N. floridana smalli*), known also for its habit of building conspicuous stick houses, was noted by Barbour and Humphrey (1982) to potentially reside within rock crevices in certain habitats, thereby escaping detection in those areas. All else being equal, if atypical houses are more common than believed, then population estimates of woodrats and related biological findings based on house counts may be inaccurate.

Sakai and Noon (1993) estimated dusky-footed woodrat abundance using both house counts and livetrapping at houses and on grids. In only 4 out of 32 cases was there more than one woodrat captured where no

houses were found, thus they concluded that the bias created by undetected atypical houses was negligible. In some areas woodrats are prone to restrict their travel to familiar routes (Linsdale and Tevis 1951, Laudenslayer and Fargo 1997), therefore low capture success in those areas may be due to trap location. If cryptic houses are present, but not found, traps set along a transect or on a grid may not be near enough to those houses or to their associated travel routes to capture resident woodrats. If inconspicuous houses are present but not located and woodrats in those areas restrict their travel to specific paths that emanate from their houses, then trapping in conjunction with house counts may not add to the reliability of the population estimates.

A second, but not necessarily independent, factor affecting the correlation between house counts and population size is variability in house use between individual woodrats. Although infrequent, woodrats sometimes reside together. During the breeding season, some males will reside periodically with the females in their territories (English 1923, Donat 1933). Young woodrats also reside with their maternal parent until old enough to fend for themselves (Gander 1929, Linsdale and Tevis 1956). In addition, socializing between related females, particularly mother-daughter, can produce multiple captures at a single house (Kelly 1989). Through livetrapping and direct observations, multiple woodrats were, on several occasions, detected at a single house, and sometimes were soon after seen travelling to another (Fargo and Laudenslayer, unpubl. data). This study and others (English 1923, Linsdale and Tevis 1956, Cranford 1977, Wallen 1982) have shown that a single woodrat will often use more than one house, and the number and location of houses used by any one woodrat varies between individuals and over time. English (1923) found that dusky-footed woodrats displayed familiarity with many houses within their range. As woodrats were chased from one house, they would retreat to another nearby house, and so on. Using radio-telemetry, Cranford (1977) found that dusky-footed woodrats resided within any one particular house for an average of 34 days (with a range of 26 to 54 days). If only one house was present within a home range, the house was larger and the woodrat resided within it for a longer period.

Wallen (1982) examined variability in house use by dusky-footed woodrats by using repeat livetrapping at houses. He classified houses into those that were occupied by a particular individual, those that were commonly used by more than one individual without any one particular resident, and those that had little use. He found that all types of houses had visitations by multiple woodrats, however the "unoccupied" houses had the highest number of different individuals and the "low use" houses the lowest. Sakai and Noon (1993) captured an average of 1.3 to 1.8 woodrats per house among 3 vegetation types. This may reflect some cohabitation of woodrats, but more likely is primarily a result of "visitation" by woodrats to non-resident houses. In such cases, assuming a 1:1 ratio of woodrats to houses could lead to inaccurate population estimates.

Even assuming that the number of woodrats per house (or houses per woodrat) can be accurately derived from livetrapping, it may not be useful over extended periods. As conditions change over time, so does the assemblage and use of houses. This is true even over short periods, such as within one year. Following breeding, males residing with females are forced out and either take up residence in an unoccupied house or build a new one (English 1923, Donat 1933). Most subadult woodrats are eventually forced out of their natal homes and have to find shelter elsewhere (Linsdale and Tevis 1951). Since building a new house takes time and exposes dispersing animals to predation, they usually take up residence in nearby unoccupied houses, often ones built and maintained by their maternal parent (English 1923, Linsdale and Tevis 1951). New houses are generally built in the fall and winter by woodrats that are already established in the area (Vestal 1938, Linsdale and Tevis 1951). House use by woodrats may also change as they expand their ranges or disperse to a completely new area to occupy houses that may have been abandoned by their previous owners (Linsdale and Tevis 1956). Such situations may or may not show a change in the number of houses, regardless of what is happening with population size. Put simply, a change in the number of houses does not necessarily coincide with a change in the number of woodrats, nor does a change in the number of woodrats necessarily create a change in the number of houses.

RECOMMENDATIONS

To reduce the potential bias created by the presence of atypical houses, one should become familiar with the spatial and structural characteristics of such houses, and the areas where they commonly occur. Based on our results, atypical houses appeared to be more common in areas with low shrub cover and a substantial amount of rock outcrops and/or hollow limbs. We also suggest that thorough searches of the area be conducted, examining each potential house site and all woodrat sign. For study areas with homogeneous structural and vegetative characteristics, a trapping regime in which traps are randomly set at several rock outcrops, hollow logs, and trees with cavities may provide an estimate of the number of atypical houses present that can be applied to the entire area.

Determining house use may be more difficult. At the least, we recommend that trapping be conducted

during times when woodrats are not as likely to be cohabitating. Ideally, livetrapping should be conducted periodically both at houses and on a grid over the course of a year to account for seasonal changes. This should give a better estimate of the number of houses per woodrat, which potentially may be used to assess the accuracy of house count results.

One conclusion that could be easily derived from a study of house counts may be related to habitat quality rather than to woodrat population size; areas with many houses more likely indicate high quality habitats that can potentially sustain a large number of woodrats, even though at any one time, woodrat numbers may be low, and areas with relatively few houses indicate low quality habitats. However, as pointed out by Van Horne (1983), mere numbers of a resource are not always positively correlated with habitat quality; high numbers may indicate a sink situation.

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