AN ANALYSIS OF A METHOD FOR COMPARING RESIDENTS AND COLONISTS IN A NATURAL POPULATION OF MICROTUS OCHROGASTER

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Dueser et al. (1981) described a method for identifying individuals as dispersers or residents in a natural population of Microtus pennsylvanicus. They operationally defined dispersers to be those individuals which, when first captured, weighed at least 30 g. All animals that weighed less than 30 g were defined as residents. They then used standard demographic variables to compare the dispersers and the residents once the residents had grown to at least 30 g. They reasoned that for a very trappable species, trapped very frequently, and with closely spaced traps, the probability of missing an individual until it was at least 30 g was very small and most of these individuals would have been captured had they been born on the grid. This method allowed them to test for differences between these two groups which may relate to different life history strategies involving the costs and benefits of dispersing or remaining in the population (Gaines and McClenaghan, 1980; Johnson, 1984; Johnson and Gaines, 1985). In fact, Dueser et al. (1981) found the disperser group exhibited relatively greater proportions of reproductively active individuals and was predominantly composed of males. The high reproductive activity of dispersers would be necessary for dispersal to be an evolutionarily stable strategy (Johnson, 1984; Johnson and Gaines, 1985), since dispersal has been shown to increase the risk of mortality (Ambrose, 1972; Metzgar, 1967).

Recently, the Dueser et al. (1981) technique has been the subject of some controversy as to its usefulness and justifiability. Tamarin (1984) argues the error rates of misclassifying dispersers are high. He cites studies which indicate that a large percentage of dispersing individuals are under 30 g. These animals would be mistakenly classified as residents. In rebuttal, Dueser et al. (1984, p. 728) state the 30 g criterion is valid since "...the relatively low body weight of 30 g is most likely to err in the direction of identifying residents as 'dispersers', rather than vice versa..." real differences between dispersers and residents will be reduced by misclassification. Thus, their technique is conservative.

The disagreement about misclassification may, in part, stem from Dueser et al.‘s use of the term disperser. Their disperser group is really the post-dispersal subset of the larger set of animals which actually dispersed from a population. Tamarin (1984) cites studies which identify dispersers as animals appearing in vacant habitat. While an individual of any size or physical condition may be able to colonize empty habitat, there is no reason to assume those which successfully colonize in an established population should be similar to those which immigrate into the rather uncommon condition of unoccupied but suitable habitat. There are several reasons to believe that animals colonizing in an existing population may differ substantially. Larger animals have lower energetic costs of transport per unit distance, may be less susceptible to death by exposure and predation, and may have a better chance of establishing a home range in a population of strange and potentially aggressive animals. To avoid misinterpretation, we have relabeled Dueser et al.’s dispersers as colonists and emphasize that the Dueser et al. (1981) technique attempts to monitor dispersers after they have entered an established population.

In this paper, we test the appropriateness of Dueser et al.’s method, keeping in mind that we are comparing colonists (successful dispersers) and residents (nondispersers), not dispersers and residents. Though we cannot quantitatively estimate the accuracy of the resident classification, we can determine if it is correct at least more often than not. The accuracy of the colonist classification can be quantitatively estimated. Using M. ochrogaster, we also compare demographic characteristics of colonists and residents in an attempt to replicate Dueser et al.’s results.

Our data collecting protocol was the same as Dueser et al. (1981). The data were collected as part of another study (Johnson 1984; Johnson and Gaines, 1985) from December 1979 to November 1981. We utilized two 0.8 ha live-trapping grids, one open (A) and one fenced (Y), which were about 500 m apart. Voles could immigrate and emigrate to and from the open grid at all times. Only emigration was allowed from the enclosed grid. Voles dispersed from the enclosure by crossing a 1-m wide mowed strip next to the
Fig. 1.—Frequency distributions for weights at first capture on grids A (open) and Y (fenced).

fence and entering a tube leading to an exit trap (Johnson and Gaines, in press). These traps were set simultaneously with the grid traps in the interior. Animals captured in the exit traps were considered dispersers and removed permanently from the study area.

As Dueser et al. (1981) point out, for this technique to be appropriate, animals must have a high trappability. An average of 90.5% of the animals known to be alive on the fenced grid were captured during each biweekly session. Trappability on the open grid (81.2%) was significantly lower than on the fenced grid (P < 0.05, sign test). This result is most likely due to individuals living on the periphery of the open grid and being caught only occasionally. However, both grids were higher than the highest average trappability of Dueser et al. (77.0%) High trappability reduces the likelihood of resident individuals avoiding capture until large enough to be misclassified as colonists.

All animals not emigrating from the fenced enclosure prior to first capture were born in the enclosure and therefore were true residents. The weights at first capture for these individuals provide a probability distribution for catching a resident for the first time in a given weight class. We use 3-g intervals to construct weight classes. The resulting probability distribution from 384 individuals (Fig. 1) has a mean of 22.83 g. A similar distribution for 422 animals on the open grid was also constructed (Fig. 1). This distribution has a mean of 28.63 g which is significantly higher than the mean for the fenced grid (P < 0.005, Fig. 1). Relative to the open grid, the fenced grid had consistently larger proportions of the total population caught for the first time in weight classes below 27 g and smaller proportions in weight classes of 27 g and larger (Fig. 1). We also tested each sex separately and found the same consistent and highly significant differences between the two grids. There are two possible explanations for the large differences in weights at first capture. The difference in trappability between the two grids (9.3%) implies animals are being captured for the first time at younger ages. That the higher trappability on the fenced grid could lead to the 20% reduction in average weight at first capture seems unlikely. Nonetheless, the possibility cannot be ruled out. Alternatively, since these two grids differ in the presence of immigration, the weight differences may be a result of large, new animals which are successful dispersers, or colonists by our terminology. Supporting this explanation, even though subadults (≤34 g) were overrepresented relative to the entire population (Johnson, 1984), the average weight of emigrants from the fenced grid was 36.2 g (n = 202).

To estimate the accuracy of Dueser et al.’s classification method, we assume the distribution function of weights at first capture for animals on the fenced grid is the true distribution for residents in general, and the distribution on the open grid is the true distribution for an unenclosed population. The large sample sizes and high trappabilities combine to make this a reasonable assumption. We can then calculate how many of the 422 animals on the open grid should be residents which escaped capture until attaining a given weight with the following equation:

\[ E_c = (1 - P_c)N \]

where \( E_c \) is the expected number of animals first captured at or above weight \( X \), \( P_c \) is the sum of the probabilities of first capture below weight \( X \), and \( N \) is the total number of animals on the open grid. Using
Table 1.—Demographic attributes of residents and colonists on the open grid.

<table>
<thead>
<tr>
<th></th>
<th>Residents</th>
<th>Colonists</th>
</tr>
</thead>
<tbody>
<tr>
<td>Frequency reproductive</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Males</td>
<td>0.78</td>
<td>0.88</td>
</tr>
<tr>
<td>Females</td>
<td>0.78</td>
<td>0.73</td>
</tr>
<tr>
<td>Survival rates</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Males</td>
<td>0.80</td>
<td>0.75</td>
</tr>
<tr>
<td>Females</td>
<td>0.82</td>
<td>0.78</td>
</tr>
<tr>
<td>Sex ratio M/F</td>
<td>0.30 (11/37)*</td>
<td>1.44 (62/45)*</td>
</tr>
</tbody>
</table>

*P < 0.05.

The frequencies of reproductive individuals are the proportions of each sex in breeding condition (see text). Survival rates are the average proportion surviving from one biweekly trapping session to the next.

Dueser et al.’s criterion of ≥30 g at first capture for classification of colonists, we expect 90 animals. On the open grid, 185 animals (44%) were first captured at ≥30 g. The difference between the observed and expected numbers can be attributed to immigration of animals onto the open grid. Therefore, if we call these animals colonists, then 51.1% of this group are really colonists and the rest are misclassified residents which avoided capture until they reached at least 30 g. For analyses, we increased the weight criterion to 39 g to improve the accuracy of the disperser classification. Only 10.4% of the residents on the fenced grid were not captured until 39 g. With this criterion, we increase the accuracy of the classification slightly to 57.3% for 105 colonists.

It is not possible to estimate the accuracy of Dueser et al.’s method of defining residents in a quantitative manner such as we have done for colonists. However, if the likelihood of colonization is independent of body size, as implied by Tamarin (1984), those small individuals which disperse from the open grid should be replaced by animals of similar size from the surrounding area, assuming those populations have the same weight distributions. This will give a distribution function identical to that of the fenced grid. However, consistently lower proportions of the population on the open grid, relative to the fenced grid, were first caught in weight classes of 26 g or less (Fig. 1). This suggests that small animals were being lost from the population but not being replaced by equally small immigrants. Therefore, the majority of individuals first caught when still small were probably born there, although we cannot rule out differences in trappability. For our purposes, we have defined residents to be those animals <27 g at first capture. A greater proportion of the open grid population, relative to the fenced grid, was first captured above this cut off criterion (Fig. 1). This group initially contains 192 animals on the open grid. However, to properly compare this group to the colonist group, only those individuals which eventually reach at least 39 g can be used. This reduces the sample size to 48 individuals. The remaining 144 died or emigrated before reaching 39 g. Those animals which were first captured with body weights between 26 and 39 g are excluded from the analysis. By doing this, we increase the differences between the two groups with respect to colonist and resident composition, thereby increasing the power to detect differences between them. Dueser et al. (1981) chose a single criterion of 30 g to differentiate between the groups. Their choice, like ours, was an attempt to eliminate as many misclassifications as possible. It is important to note that our conditions for classifying an individual may not be appropriate for a different species or locality.

To compare reproductive and survival data between colonists and residents, we use the same Chi-square statistics as Dueser et al. (1981). We find no differences between colonists and residents in male or female reproductive activity or survival (P > 0.10 in all cases, Table 1). Because of the low statistical power of these comparisons resulting from misclassifications, we cannot be confident that there are in fact, no differences between colonists and residents with respect to reproduction and survival. We can only say the differences, if indeed they exist at all, are not of sufficient magnitude to be detected by the Dueser et al. technique, even with our modifications.

Sex ratios were significantly biased towards females in the resident group and significantly biased towards males in the disperser category (P < 0.05, Table 1). Dueser et al. (1981) did not find resident sex ratios to be biased towards females. However, their results were similar to ours in that colonists were significantly more likely to be males relative to the resident group.

While we have demonstrated the Dueser et al. (1981) technique to be valid in that it can be used to distinguish colonists from dispersers, the degree of accuracy in these classifications is so low as to permit detection of only very large differences between the groups. While this substantially reduces the usefulness of the technique, Tamarin (1984) is incorrect in stating "The technique of Dueser et al. (1981) can only
distract from our understanding of dispersal in voles.” Statistically significant differences between the two classifications are likely to be ecologically significant as well. Failure to find statistically significant differences should not be interpreted to mean differences do not exist.

Though the technique lacks statistical power, it has several advantages over other methods. Unlike removal or vacuum grids (Johnson and Gaines, 1985; Myers and Krebs, 1971) and marginal habitat dispersal sinks (Tamarin et al., 1984), it allows the study of colonists as they exist in a resident population. Methods such as exit doors in fenced enclosures (Gaines et al., 1979) cannot separate successful from unsuccessful dispersers. This technique involves only successful dispersers. Finally, this technique does not involve expensive and potentially confounding fences or other equipment.

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LITERATURE CITED


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PREFERENCE FOR ESTROUS FEMALE URINE BY MALE KANGAROO RATS (DIPODOMYS SPECTABILIS)

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The banntertail kangaroo rat (Dipodomys spectabilis) is considered a solitary species, and, with rare exception, all adults reside in separate, large dirt mounds (territories) that they defend from all other individuals (Randall, 1984). Most reproduction occurs from February to April (Jones, 1984), and males visit neighboring mounds of adult females at much higher frequencies in the spring than in the summer (Randall, 1984). On three occasions, I observed males going to females' mounds to mate. Thus males might examine odors in female territories for signals indicating estrus. Because female mammals frequently advertise their readiness to mate by olfactory signals in their urine, which probably contains metabolic products reflecting hormonal changes (Johnston, 1983; Nyby, 1983), I tested whether urine could be a source of olfactory signal that communicates changes in reproductive status in D. spectabilis.