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Social Traveling Inferred from Multiple Captures: Testing Assumptions

ABSTRACT: Live-trapping studies in which aspects of social behavior in rodents are inferred from multiple capture data assume that there is no bias introduced by the trapping mechanism. We document differences in springing weights of Sherman traps in the field, and show that more deer mice are captured in traps that have lower springing weights. Multiple captures need not occur as a result of social traveling, but could result from random nonsynchronous entry of mice into insensitive traps.

Introduction

Several recent studies of small nocturnal rodents have offered evidence of social behavior based on analyses of pairs of animals captured simultaneously in standard single-capture live traps (Getz, 1972; Blaustein and Rothstein, 1978; Jenkins and Llewellyn, 1981; Spencer et al., 1982; Novak, 1983). Some controversy has arisen from these studies, particularly concerning the validity of inferring social traveling from such analyses. Getz (1972), using traps designed for multiple captures, set two criteria for inferring social traveling: (1) that significant nonrandomness or association be found with respect to sex/age categories in multiple captures, and (2) that specific pairs of animals representing these associations be recaptured together numerous times. Two subsequent studies have examined double captures in single-capture traps and concluded that social traveling occurred based on the first criterion; however, both have ignored Getz's second criterion. Spencer et al. (1982) state that no multiple recapture was ever observed in their study. Blaustein and Rothstein (1978) do not mention recaptures. Thus, the conclusions of these two studies do not fulfill Getz's (1972) conservative criteria.

Notwithstanding this failure, both studies also assume that the Sherman live trap has optimal sensitivity to sample pairs of animals simultaneously. Numerous studies report that both Longworth and Sherman live traps, because of variable sensitivity of the tripping mechanism, undersample lighter-weight individuals in the population (Dalby and Straney, 1976; Grant, 1970; Beacham and Krebs, 1980). This has direct implications for multiple-capture studies reporting social traveling, since the less sensitive traps may not be sprung by one animal but more likely close after a second animal enters. This scenario is especially likely when a juvenile enters a trap. Grant (1970) demonstrated this sampling bias in Longworth traps by actually measuring the minimum weight required to trip the traps; he found that animals were captured disproportionately in traps with lighter than average springing weights. For some reason, although most multiple-capture studies have mentioned possible effects of this bias, none has tested it directly. Blaustein and Rothstein (1978) professed to have ruled out trap bias by experimentation, but they never tested springing weights either of traps used in the experiment or of traps used in the field study. We must assume that the former is a random sample of the latter in order to accept their conclusions about trap bias. Finally, some studies have examined trap bias indirectly via statistical comparison of weights of mice involved in multiple captures with those involved in single captures (e.g., Novak, 1983). This analysis also assumes that all traps are equally sensitive. In this paper we examine the validity of the assumption of equal sensitivity among Sherman traps in two samples from trapping grids with very different histories, and we discuss the implications of our findings for drawing inferences from multiple capture data.

METHODS

We examined springing weights of Sherman traps (7.5 x 7.5 x 23 cm) in the field. At the start of the experiment, all traps were either new or newly cleaned and repaired. Two 0.36-ha study grids were established in tallgrass prairie habitat near Lawrence, Kansas, each consisting of 25 single-trap stations. We purposely tried to adjust the tripping mechanism of traps so that we could categorize them as either "sensitive" (traps would spring with a light touch of the treadle; springing weight < 25 g) or "insensitive" (traps would only spring when firm pressure was applied to the treadle; springing weight > 25 g). By experience, we chose 25 g as a convenient cutoff at or below the median springing weight, above which we anticipated capture success would be negatively affected. Traps were then randomly assigned to the 50 trap stations with respect to these two categories. Trap dispersion was rerandomized each day and all captures of deer mice (Peromyscus maniculatus) were recorded for 3 days. Additionally, the actual sensitivity of each trap was measured both at the time of setting and at the time of checking by recording the minimum weight which, when applied to the rear of the treadle, would spring the trap. (If a set of premeasured weights is not available, a variety of pocket change and a 100-g spring

scale is a convenient alternative.) A sign test was used to determine whether any systematic change in springing weight occurred between the two times, both in traps which captured and traps which failed to capture animals. If none was detected, future springing weights could be more conveniently measured at the time of checking. To see whether our efforts at manipulating the traps produced an "artificial" distribution of springing weights, we measured the springing weights of 50 Sherman traps on another investigator's grid just after they had been set. These traps were part of a long-term study and had been left on the grid permanently for several years.

RESULTS AND DISCUSSION

No systematic change in springing weights occurred between setting and checking either in traps which captured animals or traps which failed to capture animals (sign tests; all P > 0.1). This indicated that future live-trapping studies could validly measure springing weight at the time of checking, for comparison with animal weights and with probability of single and multiple captures. Trap sensitivity varied greatly (Fig. 1); as much variation in springing weight occurred in the continuously operated trapping grid as in the population of traps we deliberately manipulated to vary in sensitivity. About half the traps were potentially too insensitive to cap-

Table 1.—Summary of springing weights (g) of Sherman traps involved in single and double captures of *Peromyscus maniculatus* in 1983

Capture type	N	$\bar{\mathbf{x}}$	SE
Single Double	89	19.4	1.05
Double	20	29.0	4.27

One-way ANOVA: F = 10.25; P < 0.005

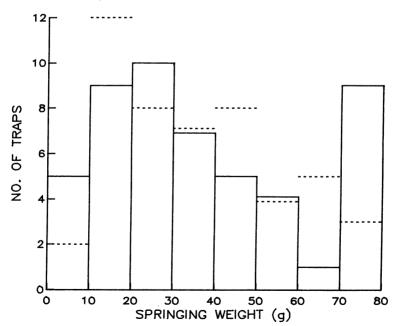


Fig. 1.—Frequency histogram of minimum weight required to spring traps in two samples of 50 Sherman traps (7.5 x 7.5 x 23.0 cm). Solid bars represent traps in an experiment designed to divide traps into "sensitive" and "insensitive" categories. Dashed lines represent traps on another investigator's grid involved in a long-term live-trapping study. A Kolmogorov-Smirnov two-sample test shows no difference (P>0.1) between the two distributions

ture single animals the weight of an adult *Peromyscus* (20-25 g). Both this study and Grant's (1970) measured only dead weight, and of course an active animal would be able to apply additional force, but the probability of capture certainly would decrease as the springing weight approached or exceeded twice the animal's weight. In fact, in the 3-day experiment, significantly more *Peromyscus maniculatus* were captured in sensitive traps than insensitive traps (29 vs. 13; $X^2 = 6.09$; P < 0.02).

Proponents of the social traveling hypothesis have assumed synchronous encounter of the trap by two animals instead of random nonsynchronous encounter. Since the latter assumes nothing about the social behavior of the species, it clearly should be the null hypothesis for such studies. We have shown [as Grant (1970) did for Longworth traps] that Sherman traps with lower springing weights are more likely to capture single mice than traps with higher springing weights. Also, since significant numbers of the traps in any grid are likely to be "insensitive," regardless of their history or condition, multiple captures could often result from the

increased weight and activity of two mice in these insensitive traps.

During the spring and summer of 1983, after the experiment just described had been completed, one of us (BJB) trapped a population of *Peromyscus maniculatus* in the Theodore Roosevelt National Forest in the Front Range of Colorado at ca. 2100 m elevation. The springing weights of traps yielding single and double captures were recorded as described above. Trap sensitivities were not purposely manipulated. Information on recaptures of the same pairs of mice was not available, since the animals were not consistently marked and since several populations were trapped at scattered intervals during the 3-month period (although no pairs were captured twice during the period when the animals were marked). Any hypothesis of simultaneous capture of pairs of mice would predict that single and double captures should occur in traps whose sensitivities are random samples of the population of traps. That double captures occurred in traps with significantly higher springing weights than single captures (Table 1) suggests that at least some multiple captures occur simply because insensitive traps allow nonsynchronous entry of two mice. In this case, one cannot infer social traveling. Of course, social traveling cannot be verified without direct observation, but it can be reasonably evaluated only when alternative falsifiable hypotheses, such as the hypothesis of variable trap sensitivity, are tested directly.

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