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Heterogeneity of recaptures in Chilean small mammals

Heterogeneidad en recapturas de micromamíferos chilenos

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ABSTRACT

Several capture-recapture methods used to estimate population size assume that the probability of recapture is homogeneous among the individuals of a given population. This assumption is empirically falsified in Chilean small mammals. Recapture probabilities are heterogeneous for *Akodon longipilis, A. olivaceus, Oryzomys longicaudatus* and *Phyllotis darwini.* In these species, most of individuals are trap-shy, while a smaller group reacts as trap-prone. The heterogeneity in their trap response precludes the use of capture-recapture methods based on homogeneous probabilities of recaptures. Direct enumeration methods are discussed as a viable alternative for estimating the size of the population in Chilean small mammals.

Key words: Enumeration, population estimates.

RESUMEN

Un gran número de métodos de captura-recaptura empleados para determinar tamaños poblacionales supone que la probabilidad de recaptura es homogénea entre los diferentes miembros de una población. Esta suposición es refutada empíricamente en micromamíferos chilenos. *Akodon longipilis, A. olivaceus, Oryzomys longicaudatus* y *Phyllotis darwini* exhiben probabilidades de captura heterogéneas. Algunos individuos son recapturados un número menor de veces que lo esperado por azar mientras otros son capturados más frecuentemente que lo esperado por azar. Se discuten métodos de enumeración directa como una alternativa viable para estimar tamaños poblacionales en micromamíferos chilenos.

Palabras claves: Enumeración, estimación poblacional.

INTRODUCTION

Capture-recapture methods are commonly used to estimate the size of small mammal populations. These methods use the ratio of marked to unmarked individuals to assess population sizes, and several of them are based on the assumption that all individuals have the same probability of being captured. Heterogeneity of recapture probabilities violates this assumption, biasing the estimates. In general, lower than actual population sizes are obtained when there are unequal capture probabilities among the individuals of a given population (Seber 1982, White *et al.* 1982).

This note documents the heterogeneity in trap response in populations of Chilean small mammals. Basically, it addresses the question of whether recaptures are random among these populations. It is expected that this analysis will allow to select the most appropriate method to assess small mammal populations in Chile.

METHODS

The trap response of *Akodon longipilis* (Waterhouse 1837), *A. olivaceus* (Waterhouse 1837), *Marmosa elegans* (Waterhouse 1838), *Oryzomys longicaudatus* (Bennett 1832) and, *Phyllotis darwini* (Waterhouse 1837) was studied between August 1984 and February 1985 in a shrubland area of Los Dominicos, 20 km E Santiago, central Chile.

Vegetation was typical shrubland, with 55% shrub cover mostly of *Lithraea caustica* (Mol.) H. et Arn. and *Quillaja sapona-*

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ria Mol. These species accounted for 83% of the total shrub cover. Herb cover was extensive. *Vulpia megalura* (Nutt.) Rydberg, *Trifolium glomeratum* L. and *Bromus* spp. dominated the herb stratum growing in the openings between shrub canopies, while *Torilis nodosa* (L.) Gaertn, was common under the shrub canopies.

Four series of live-trappings were carried out for a total of 101 nights, and a total trapping effort of 8,804 actual night-traps: 11 to 14 August and 28 August to 12 September (both winter), 16 October to 27 November 1984, and 8 January to 5 February 1985 (summer). Two adjacent trapping grids were used in all series of live-trappings. These grids consisted of 50 medium-sized Sherman traps, placed in a 5 by 10 configuration with 10 m spacing. The location of the traps was always the same during the four trapping periods. Trapping data from both grids were pooled. All animals caught were marked with individual codes by fur-clipping.

If there is a homogeneous probability of capture among all members of a given population, the frequency of recaptures should fit a Poisson distribution (Eberhardt 1969). The distributions of individuals according to the number of recaptures were determined and compared to an expected Poisson distribution. Goodness of fit of the observed and expected distributions was tested by the log-likelihood ratio test (G test). Frequencies in the tails of the distributions were pooled as needed to avoid expected frequencies less than 1.0. Animals found dead in the traps and those captured for the first time during the last 4 days of each trapping series were excluded from the analysis.

RESULTS AND DISCUSSION

Akodon longipilis, A. olivaceus, O. longicaudatus, and *P. darwini* exhibited heterogeneous probabilities of recapture (Table 1). For each species showing a heterogeneous trap response, a large number of individuals was recaptured less than expected if they were randomly sampled (trap-shy), and a few members of each population were recaptured more frequently than expected by random (trap-prone). Figures were: 50% of the animals were trap-shy and 25% trap-prone in *A. longipilis,* 33% trap-shy and 12% trap-prone in *A. olivaceus,* 56% trap-shy and 15% trap-prone in *O. longicaudatus,* and 56% trap-shy and no trap-prone in *P. darwini.*

The single case in which the null hypothesis of equal trappability was not rejected was for *M. elegans* (Table 1). Roff (1973) has proposed that it may be inappropriate to use the Poisson distribution as a test for trap response heterogeneity, because it may be insensitive to real heterogeneity. That is, it may lead to the commission of Type II error. Indeed, an analysis of the power

TABLE 1

Test of homogeneity for recapture probabilities of small mammals of central Chile. Figures are the frequency of occurrence ($\bar{x}$), sample size (number of individuals studied, n), total number of recaptures (TC), log-likelihood test (G) for the goodness of fit of the observed distribution of recaptures to a Poisson distribution, degrees of freedom (df), and significance level (P).

Prueba para homogeneidad en la probabilidad de recaptura de micromamíferos de Chile central. Los valores son la frecuencia promedio ($\bar{x}$), el tamaño de la muestra (número de individuos estudiados, n), número de recapturas (TC), valor de G para la bondad de ajuste entre la distribución de recapturas observadas y una distribución de Poisson, los grados de libertad (df) y el nivel de significación (P).

	Akodon longipilis	*Akodon olivaceus*	*Marmosa elegans*	*Oryzomys longicaudatus*	*Phyllotis darwini*
$\bar{x}$	3.16	2.91	1.27	3.50	6.00
n	12	33	22	54	9
TC	38	96	28	189	35
G	14.48	56.52	4.85	205.12	12.60
df	4	5	2	7	4
P	< 0.002	$\ll 0.001$	0.08	$\ll 0.001$	0.02

of the G test suggests that this could be the case in *M. elegans*. Only 54% of G tests carried out under the specified conditions (W [effect size] = 0.46, alpha = 0.05, 2 df, and n = 22; see Cohen 1977) are expected to result in the rejection of the null hypothesis, i.e., that recapture frequencies follow a Poisson distribution. A larger sample is required to properly test whether recaptures of *M. elegans* are random events. However, in the four other populations studied, the null hypothesis – i.e., homogeneity – was rejected. Thus, deviation from randomness was so manifest in the distribution of recaptures that even a conservative test is able to detect it.

There are several possible causes of heterogeneous responses to traps in small mammals (see Smith *et al.* 1975 for an overview). Age, sex, and social status may affect trappability. In general, adult males are often captured more frequently than females and juveniles. However, no such pattern was found between trap-prone and trap-shy individuals of the populations studied. Neither sex nor age ratio differed significantly between trap-prone and trap-shy members of a given species (Tables 2A and 2B). A larger sample however, seems desirable.

Trap-proneness may reflect social dominance as higher-ranked animals are more active and have larger home ranges than the subordinate members of the populations. Trap-proneness may also be a trapping artifact, given the proximity of a trap location to the animal's burrows. In the first case, the average distance between successive recaptures of trap-prone individuals should be larger than that of subordinate individuals. In the second case, the opposite should be true. The average distance between recaptures should be shorter for trap-prone individuals, showing that they are being captured close to their burrows. A comparison of the distance between recaptures revealed no significant differences between trap-prone and the other members of the population within each species, rejecting both alternative explanations (Table 2C).

An ethological analysis of the degree of neophobia in the species of small mammals of central Chile might cast light on the causes of their heterogeneous trap response. A marked avoidance of unfamiliar objects could explain the low capture-recapture frequencies (Cowan 1977). Similarly, an analysis of the behavioral response of the small mammals to both entrapment and bait consumption is required. Small mammals may regard captures as punishing, and bait eating as rewarding. Simultaneous reward and punishment – which is the usual case while live-trapping animals lured by bait – may trigger conflicting tendencies to re-enter and to avoid traps (Balph 1968). If punishment overrides the rewarding experience during the period of capture, animals may become trap-shy, which could explain the low frequency of recaptures.

Whatever the underlying causes for the observed heterogeneity, the results strongly suggest that methods that assume equal trappability are inappropriate for assessing the population size of central Chilean small mammals. Enumeration techniques or other capture-recapture methods which do not require an homogeneous probability of capture should be used (Hilborn *et al.* 1976, White *et al.* 1982; but see Nichols & Pollock 1983).

Direct enumeration estimates population size through the assessment of the minimum number of animals known to be alive (MNA). It relies on the assumption that a large proportion of the population is captured during a given trapping season, so that the population size can be estimated with no need for assessing the size of the untrapped-unmarked portion of the population. MNA is a reliable index of populations size only if trappability is high (above 50%; Hilborn *et al.* 1976). Trappability, defined as the number of individuals captured at time i over the MNA at time i (Hilborn *et al.* 1976), was high for the five species studied here. Figures were 100% for *A. longipilis, M. elegans* and *P. darwini,* 96% for *A. olivaceus,* and 94% for *O. longicaudatus.* Southern Chilean populations of *A. olivaceus* also exhibit high trappability (over 75%; González *et al.* 1982). Similarly, northern Chilean populations of *A. longipilis, A. olivaceus,* and *P. darwini* are highly trappable (83% to 100%; Meserve 1981).

The assessment of MNA has indeed been common in studies of Chilean small mammals (e.g. Fulk 1975 [in part], Glanz 1977, González *et al.* 1982, Jaksić *et al.* 1981, Meserve 1981, Simonetti 1983). Given the inapplicability of capture-recapture methods assuming homogeneous recapture probabilities, and the high

TABLE 2

Comparison of trap-prone and trap-shy individuals among Chilean small mammals. A) Age ratio is the proportion of adults as opposed to immatures in each group, both trap-prone and trap-shy. n is sample size, Z_c is the difference between proportions (corrected for continuity), and P the significance level. B) Sex ratio is the proportion of males in the samples. Symbols as in A. C) Movement between recaptures refers to the mean distance travelled between successive recaptures for trap-prone and other members of a population. Figures are mean ± two standard errors, n is sample size, U is the Mann-Whitney statistic (two-tailed test) and P is the significance level.

Comparación de individuos adictos y tímidos a trampas en especies de micromamíferos chilenos. A) Razón de edades es la proporción de adultos en oposición a individuos sexualmente inmaduros en cada grupo, adicto y tímido a las trampas. n es el tamaño de la muestra, Z_c es la diferencia entre las proporciones (corregida para continuidad) y P es el nivel de significación. B) Razón de sexos es la proporción de machos en cada grupo. Símbolos como en A. C) Movimientos entre recapturas es la distancia media recorrida entre recapturas sucesivas para individuos adictos a las trampas y el resto de la población. Valores son la media ± dos errores estándar, n es el tamaño de la muestra, U es el estadígrafo de Mann-Whitney (prueba bilateral) y P es el nivel de significación.

TABLE 2A

	AGE RATIO				
Species	prone	shy	n	Z_c	P
Akodon longipilis	1.00	0.67	9	0.28	>0.50
Akodon olivaceus	0.40	0.36	16	0.42	>0.50
Oryzomys longicaudatus	0.75	0.47	38	1.03	>0.20
Phyllotis darwini	0.50	0.60	9	~0	~1.00

TABLE 2B

	SEX RATIO				
Species	prone	shy	n	Z_c	P
Akodon longipilis	0.67	0.50	9	0.24	>0.50
Akodon olivaceus	0.40	0.36	16	0.42	>0.50
Oryzomys longicaudatus	0.63	0.53	38	0.63	>0.50
Phyllotis darwini	0.50	0.60	9	~0	~1.00

TABLE 2C

	MOVEMENT BETWEEN RECAPTURES					
Species	prone	n	others	n	U	P
Akodon longipilis	10.2 ± 5.3	27	23.6 ± 15.7	11	197	>0.10
Akodon olivaceus	36.8 ± 11.1	43	31.3 ± 8.8	45	912	>0.50
Oryzomys longicaudatus	28.5 ± 4.4	116	23.5 ± 4.2	75	3688	>0.05
Phyllotis darwini	10.4 ± 3.4	39	5.6 ± 2.4	18	438	>0.10

trappability of Chilean small mammals, direct enumeration should be preferred over other methods for estimating population size, as it should allow more adequate comparisons of different studies, as well as providing more accurate population estimates.

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LITERATURE CITED

BALPH DF (1968) Behavioral responses of unconfined Uinta ground squirrels to trapping. Journal of Wildlife Management 32: 778-794.

COHEN J (1977) Statistical power analysis for the behavioral sciences. Revised edition. Academic Press, New York.

COWAN PE (1977) Neophobia and neophilia: new-object and new-place reactions of three *Rattus* species. Journal of Comparative and Physiological Psychology 91: 63-71.

EBERHARDT LL (1969). Population estimates from recapture frequencies. Journal of Wildlife Management 33: 28-39.

FULK GW (1975) Population ecology of rodents in the semi-arid shrublands of Chile. Occasional Papers of The Museum, Texas Tech University 33: 1-40.

GLANZ WE (1977) Comparative ecology of small mammal communities in California and Chile. PhD dissertation, University of California, Berkeley.

GONZALEZ LA, R MURUA & R FEITO (1982) Densidad poblacional y padrones de actividad espacial en *Akodon olivaceus* (Rodentia, Cricetidae) en hábitats diferentes. En: Salinas P (ed) Zoología Neotropical: 935-947. Actas del VIII Congreso Latinoamericano de Zoología, Mérida.

HILBORN R, JA REDFIELD & CJ KREBS (1976) On the reliability of enumeration for mark and recapture census of voles. Canadian Journal of Zoology 54: 1019-1024.

JAKSIC FM, JL YAÑEZ & ER FUENTES (1981) Assessing a small mammal community in central Chile. Journal of Mammalogy 62: 391-396.

MESERVE PL (1981) Resource partitioning in a Chilean semi-arid small mammal community. Journal of Animal Ecology 50: 745-757.

NICHOLS JD & KH POLLOCK (1983) Estimation methodology in contemporary small mammal capture-recapture studies. Journal of Mammalogy 64: 253-260.

ROFF DA (1973) On the examination of some statistical tests used in the analysis of mark-recapture data. Oecologia (Berlin) 12: 35-54.

SEBER GAF (1982) The estimation of animal abundance and related parameters. Second Edition. Macmillan Publishing Company, New York.

SIMONETTI JA (1983) Effect of goats upon native rodents and European rabbits in the Chilean matorral. Revista Chilena de Historia Natural 56: 27-30.

SMITH MH, RH GARDNER, JB GENTRY, DW KAUFMAN & MH O'FARREL (1975) Density estimations of small mammal populations. In: FB Golley, K Petrusewicz & L Ryszkowski (eds) Small mammals: their productivity and population dynamics: 25-54. Cambridge University Press, London.

WHITE GC, DR ANDERSON, KP BURHNAM & DL OTIS (1982) Capture-recapture and removal methods for sampling closed populations. LA-8787-NERP, Los Alamos National Laboratory, New Mexico.