The influence of trap type on evaluating population structure of the semifossorial and social rodent *Octodon degus*

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Trap type may influence captures of individuals in different age-sex categories in small mammal studies, resulting in biased population and demographic information. We deployed 4 live trap types at burrow systems of the rodent, Octodon degus Molina, 1782, in central Chile to determine trap efficacy in capturing individuals of 6 demographic categories. We captured 2672 individuals in 17 709 trap days (15.1% trapping success). Tomahawks were the most efficient trap capturing half of individuals during both years, followed by mesh Sherman traps, large Sherman traps, and medium Sherman traps in 2005. All trap types equally sampled sexes. Large and medium Sherman traps provided similar demographic structure, where half of the individuals captured were pups; Tomahawk traps sampled more adults than pups. Relative captures of pups were similar across different trap types, suggesting that pups are equally sampled by each of the deployed trap types. Relative captures of adults were lower in Sherman traps, suggesting that this age class avoided solid-walled traps. For Octodon degus, the sole use of Tomahawk traps may produce sufficient, unbiased demographic data. Only 4 trap mortalities occurred (0.15%). Researchers may minimize trap mortality without compromising sufficient demographic sampling by trapping during peak animal activity.

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Introduction

Long-term demographic studies of small mammals are important for understanding population dynamics and behavior (Metcalf and Pavard 2007). The success of these studies depends on the researchers' abilities to capture individuals representing all demographic groups present in

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the population. Unequal sampling of demographic groups could result in erroneous estimates of density, survival, sex ratios, and adult-to-offspring ratios. Additionally, biased sampling in a social species can limit researchers' abilities to determine social group size and composition. Evaluating the effectiveness of multiple trap types in capturing individuals from different sex and age classes in a population is critical, yet few studies have addressed this issue.

Many factors can influence small mammal trap success, including those that researchers can control such as trap type (Wiener and Smith 1972, Slade et al. 1993, O'Farrell et al. 1994). Mechanical differences in live traps, such as treadle sensitivity, can influence trap success among age-size demographic groups (Wiener and Smith 1972, Rose et al. 1977, Slade et al. 1993). Additionally, a number of uncontrollable factors intrinsic to the study organism may influence trappability such as behavior (ie, trap shy vs trap prone individuals), age class, and body mass of individuals (Neal and Cock 1969, Gliwicz 1970, Anthony et al. 2005). These factors are particularly challenging to researchers because variability in trap efficacy may introduce biases (Boonstra and Rodd 1982, Maly and Cranford 1985). Therefore, a combination of multiple trap types might be necessary to accurately sample small mammals of variable sizes (Szaro et al. 1988, O'Farrell et al. 1994, Iriarte et al. 1989, Anthony et al. 2005, Santos-Filho et al. 2006).

Two commonly used types of live traps in small mammal studies are the Sherman (H. B. Sherman Inc., Tallahassee, FL) and Tomahawk traps (Tomahawk Live Trap Co., Tomahawk, WI). Although several studies have compared the trap efficacy of Sherman live traps to other trap types in capturing small mammals (Sealander and James 1958, Slade *et al.* 1993, O'Farrell *et al.* 1994, Anthony *et al.* 2005), few studies have compared the relative effectiveness of Sherman vs Tomahawk live traps. Santos-Filho *et al.* (2006) found Tomahawk traps to be essential in sampling a small mammal community in the Neotropics, capturing 6 species that were com-

pletely missed using a suite of Sherman, snap, and pitfall traps. Iriarte et al. (1989) reported differences in medium Sherman live traps vs Tomahawk live traps in a long-term community study in central Chile. Tomahawk traps were poor at sampling small rodents and marsupials and provided lower population density estimates for larger species, including Octodon degus Molina, 1782. No study, to our knowledge, has compared the trap efficacies of multiple trap types, including Shermans and Tomahawks, in sampling individuals of a single species to determine social group and population demography.

Differences in trap design may influence trappability and trap success. Mesh traps differ greatly from solid-walled traps in the amount of light allowed into the trap. The internal, dark nature of solid-walled Sherman traps may resemble a burrow or other refuge. In contrast, mesh traps (eg Tomahawk) allow visibility of the external environment. In a study involving the nocturnal and solitary dusky footed woodrat Neotoma fuscipes, Laudenslayer and Fargo (2002) had more captures using solid-walled Sherman traps than with mesh Tomahawks when trapping at woodrat nest sites, but the opposite was true when trapping on a grid. O'Farrell et al. (1994) found mesh traps to be more effective than solid-walled traps in capturing a number of small mammal species in a variety of habitats and geographical locations. To date, no study has determined the effectiveness of multiple trap types, including mesh and solid-walled traps in sampling individuals of different demographic categories within a species.

The success of different trap types may also depend on the behavior of the study organism. For example, semifossorial rodents spend a considerable amount of time underground, emerging from burrows to forage. Capturing these animals may be difficult, and burrow counts may result in biased population density estimates (Powell *et al.* 1994, Van Horne *et al.* 1997). Trap placement may influence captures in mammals that are microhabitat specialists (Knowles and Burger 2008). For example, Loeb *et al.* (1999) found that trap placement in trees

was necessary to document arboreal species. In contrast, trap placement at burrow openings or along runways may be necessary to efficiently capture semifossorial species. Therefore, knowledge of trap effectiveness for capturing burrowing rodents is especially important for ecological studies.

Degus Octodon degus are medium-sized (adults ~170-300g), caviomorph rodents endemic to Chile (Woods and Boraker 1975). Degus are diurnally active and semifossorial, emerging from burrows at daybreak to forage (Kenagy et al. 2002, Ebensperger et al. 2004, Hayes et al. 2007). Activity patterns are bimodal during the austral spring and unimodal during the austral winter (Kenagy et al. 2002). Degus are social, living in groups consisting of several males and reproductive females, which frequently use the same burrow systems (Ebensperger et al. 2004). These burrow systems are extensive, involving numerous burrow openings (Hayes et al. 2007, Hayes et al., in press, Ebensperger et al. 2009). Thus, efficient trapping methods are required to quantify the size and composition of social groups. Not surprisingly, previous studies involving degus indicated that trap type might influence capture success. Fulk (1976) and Jaksic et al. (1981) questioned the adequacy of medium Sherman traps in sampling larger degus. On the other hand, Iriarte et al. (1989) stated that young degus might be able to escape from mesh Tomahawk traps, resulting in biased density estimates. Therefore, it may be necessary to deploy multiple trap types to accurately sample demography of social groups and populations of this species.

As part of an ongoing study of degu sociality and space use (Hayes *et al.* 2007, Hayes *et al.*, in press, Ebensperger *et al.* 2009), we deployed 4 trap types to determine the efficacy of total captures and captures of individuals from 6 demographic categories. Our objective was to determine what type of trap, or combination of traps, produced an accurate representation of social group and population structure. We specifically tested the null hypothesis that individuals from all demographic categories and total captures were equally likely to be captured by each trap type used.

Material and methods

Study area

Our study took place in central Chile at the Estación Experimental Rinconada de Maipú (33°23' S, 70°31' W, altitude = 495 m), a field station of the Universidad de Chile. Mediterranean-type climate with cool wet winters and warm dry summers characterizes the site. The habitat is Chilean matorral featuring an open landscape with scattered shrubs and a grass and forb herbaceous composition. During the winter of 2005, we established 2 trapping grids [grid 1 = 0.18 ha (30 $\,$ 60 m) and grid 2 = 0.25 ha (50 $\,$ 50 m)] approximately 150 m apart in areas where degus were visually abundant. Since the home ranges of degus at our study site are typically less than 0.5 ha (Hayes $et\ al.\ 2007$), we assumed no exchange of individuals between grids. This was further confirmed by our trapping data.

Trapping and burrow system establishment

We conducted density-trapping sessions on grids 1 and 2 followed by burrow trapping in the general area of the 2 trapping grids. We initially conducted 5 consecutive days of grid trapping during the austral winters (June) of 2005 and 2006 using only large Sherman live traps (30 10 9.5 cm). We set traps baited with dry oats at fixed stations spaced at 5 m intervals [91 (13 7) traps on grid 1 and 121 (11 11) traps on grid 2] in the morning prior to animal emergence. After 2 hrs, we determined the location of all captures and closed the traps. We recorded the sex, body mass, and reproductive status of all animals. Animals were given unique identification by toe-clips and released at their point of capture. We also recorded recaptured animals.

Degus are microhabitat specialists, using heterogeneously distributed burrow systems (Ebensperger et al. 2009). Therefore, our trapping methodology involved targeting burrow systems. In order to determine these burrow systems, we fitted some adult females (n = 19 in 2005, n =27 in 2006) with radio-transmitters (RI-2D, Holohil Systems Limited, Ontario, Canada and SOM-2190A, Wildlife Materials Incorporated, Murphysboro, IL) during grid trapping. Using a handheld, 3-element Yagi antenna and an LA 12-Q receiver (AVM Instrument Co., CA) or FM-100 receiver (Advanced Telemetry Systems, MN), we tracked animals once per night ca 1 h after sunset to determine which burrow systems they used during the austral winter (mid June-September). We marked active burrow systems - a group of burrow openings spanning 2-3 meters in diameter (Hayes et al. 2007) - with wooden stakes labeled with a unique number.

Subsequent to grid trapping and nighttime telemetry, we trapped known active burrow systems during the austral winter to spring transition (September–November) of both years. We placed 10–12 traps in locations free of vegetative impediment at each active burrow system. We deployed 4 trap types to determine their effectiveness in capturing individuals of 6 demographic categories of degus: adult males, adult females, juvenile males, juvenile females, male pups, and female pups. We trapped 34 burrow

systems in 2005 and 68 in 2006. Burrow trapping sessions corresponded with lactation, which enabled us to analyze the trappability of all age classes: pups (25-69.9 g) juveniles (70-129.9 g females, 70-139.9 g males) and adults (>130 g females, >140 g males) (Ebensperger and Hurtado 2005). Two types of traps were solid-walled: the medium Sherman live trap (23 9 8 cm) and the large Sherman live trap (30 10 9.5 cm). The locally produced mesh Sherman-like trap (herein referred to as mesh Sherman) 9.5 cm) and the mesh Tomahawk No. 201 11.5(herein referred to as Tomahawk) live trap (41 14 14 cm) allowed for external visibility from inside the trap. Tomahawks were entirely constructed of wire mesh and were the largest of our traps. The mesh Sherman traps exhibited wire mesh on the sides and rear, with solid metal tops and bases. The 3 Sherman traps had solid metal bases, allowing most of the bait to be retained inside the trap. Tomahawk traps were the only traps with wire bases, permitting bait to fall through the trap. The treadle mechanism was more likely to become impeded by oats in large and medium Sherman traps during consecutive trapping days. We cleaned the oats from these traps assiduously before setting them during each trapping event.

During both years of the study, we used a proportional combination of trap types at each burrow system for each trapping event. We set an unequal number of traps, per trap type, per burrow system, due to the number of traps per trap type available. However, the ratio of traps per trap type remained constant at each burrow system during each trapping period. In order to correct for this sampling bias we divided the number of trap days for each trap type by the number of trap days of the trap type with the lowest number of trap days. We then divided the absolute captures for every trap by the former ratio to obtain relative captures for each year.

In 2006, we increased our trapping intensity more than twofold to incorporate more burrow systems but remained within the same general area of the grids. We set traps baited with dry oats in the morning prior to animal emergence at burrow openings, along runways, or nearby dustbathing sites. At ca 1.5 hrs after degu emergence from burrows, we determined the identity and location of all captures and closed the traps until the next trapping event. We kept animals in the shade during processing. As with grid trapping, we determined the sex, body mass, and reproductive status of all captures. We recorded recaptures and gave each new animal a unique identification using toeclips. After processing, we released the animals at the same burrow system of their capture. Our field procedures were approved by The University of Louisiana at Monroe Institutional Animal Care and Use Committee and are in accordance with Chilean law (permit no. 1-58.205-2711 by Servicio Agrícola y Ganadero).

Statistical analysis

We did not trap degus using a standard grid design, therefore we calculated the population size using a "close capture with heterogeneity model" (Cooch and White 2008) for the areas around grids 1 and 2 for both years. This algorithm considers the heterogeneity of individual recapture

probability explicitly. When individuals vary in their capture probabilities, the most catchable animals are likely to be caught first and more often. This leads to capture probability being over estimated and abundance being underestimated. We used four consecutive days of burrow trapping during the austral winters of 2005 and 2006 to determine animal population size. During the course of this study, we never recorded a single animal from the area around grid 1 to use burrow systems around grid 2 or vice versa. Therefore, we conducted 2 density estimates per year using capture data from burrow systems in the areas around grids 1 and 2. We performed these analyses using the MARK software 5.1 (White and Burnham 1999).

We used statistical log-linear models for multidimensional contingency tables (Zar 1996) to test for differences in frequencies of occurrence of individual degus by trap type (four trap types), by sex (males vs females), by age (pups vs juveniles vs adults), and by year (2005 vs 2006), as main factors (Anthony et al. 2005). We terminated the use of medium Sherman traps in 2006 due to poor trap success in 2005 [8.77 captures/trap day (n = 1,312 trap days) compared to 22.45 captures/trap day (n = 4,231 trap days) with the other 3 trap types]. Since we did not use the medium Sherman trap in 2006, we omitted this trap from the analysis in order to test for interannual differences in trap efficacy. We used standardized residuals from the log-linear analyses to represent the degree of deviance from the null model (see Anthony et al. 2005 for a similar approach). We verified the statistical significance within levels of a factor by examining the components of maximum likelihood, comparing these values with the critical level of significance for 1 degree of freedom (Flaquer et al. 2007). We assumed statistically significant differences at p < 0.05.

Results

The close capture with heterogeneity model indicated that the size of our degu populations comprised of 37.34 ± 1.61 (95% CI = 36.21-44.57) and 37.14 ± 2.75 (95% CI = 36.07 - 53.25) adults in winter 2005 around grids 1 and 2, respectively. In 2006, adult population size around grid 1 increased to 87.25 ± 8.93 (95% CI = 78.41-119.02) and decreased to 22.32 ± 3.96 (95% CI = 19.52– 39.98) in the area around grid 2. Nighttime telemetry identified 21 and 51 active burrow systems suitable for burrow trapping in 2005 and 2006, respectively. Across years and trap types, we captured 2672 individuals in 17709 trap days (15.1% trapping success) during burrow trapping. In 2005, we trapped 1069 individuals in 5543 trap days (19.28% trap success). More than half of these were adults (55%), followed by pups (24%), and juveniles (21%) (Fig. 1 and 2a), and 60% of individuals were

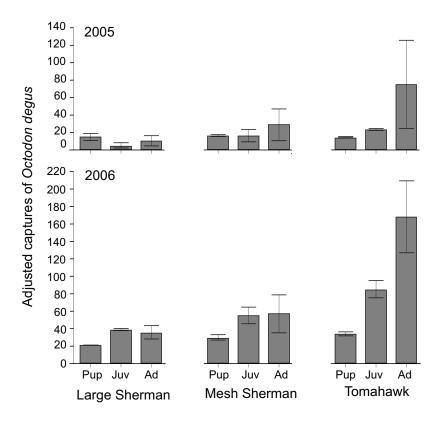


Fig. 1. Mean number of captures (\pm SD) of *Octodon degus* by trap type, age, and year of sampling. Captures were adjusted to control for differences in sampling effort within years between trap types. Ad – adult, Juv – juvenile.

females (Fig. 2b). During 2006, we captured 1603 animals in 12 166 trap days (13.26% trap success), with a similar proportion of adults (54%), but with higher frequency of juveniles (33%), and lower proportion of pups (15%) (Fig. 1, Fig. 2a). In 2006, 53% of individuals captured were females (Fig. 2b). Four trap mortalities occurred (all in 2005) in 2682 total captures (0.15%). These involved 1 female and 1 male pup in medium Sherman traps and 1 male pup and 1 male adult in mesh Sherman traps.

The statistical log-linear model for multidimensional contingency tables allowed us to test the efficacy of the different trap types in catching individual degus depending on sex, age, and year of sampling (Table 1). Automatic selection of the best model via backwards elimination yielded a model involving four, two-way interactions ($G^2_{20} = 24.1, p = 0.23$). Therefore, we rejected the null model testing the independence

of the factors analyzed. We detected one interactive effect associated with trap type (Table 1), confirming that the use of different trap models affected the demographic estimates of degu populations.

A significant effect of trap type ($G^2_2 = 315.7$, p < 0.0001) (Table 1) showed that trap types differed in their efficacy in catching individuals. Tomahawk traps captured approximately half of the individuals during both years (48% in 2005 and 56% in 2006), and hence, proved to be the most efficient method for catching degus, followed by mesh Sherman traps (26% and 27%, respectively), and large Sherman traps (13% and 18%, respectively). Medium Sherman traps showed the lowest efficacy (12% in 2005), but this was similar to large Sherman traps (Fig. 2c). Tomahawks yielded two times more captures than mesh Shermans, and three or four times more captures than large and medium

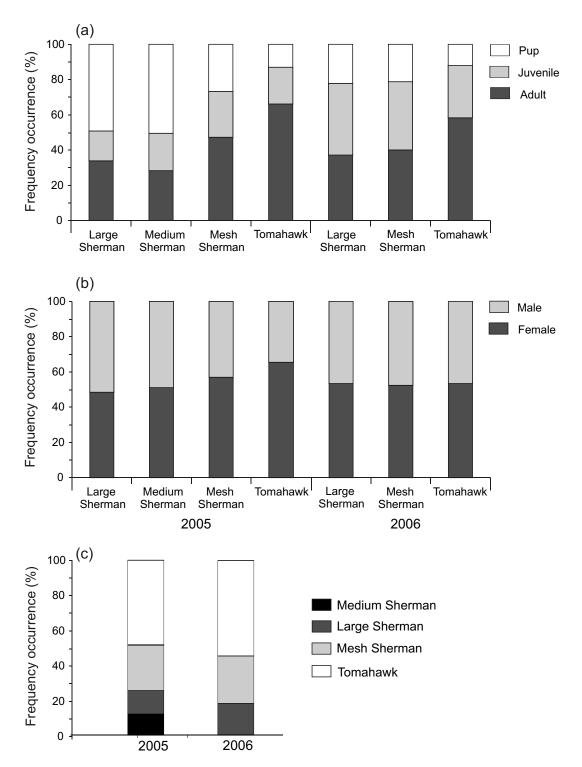


Fig. 2. Frequency of captures of *Octodon degus* by age (a), sex (b), and trap type (c), during the austral winter to spring transition (September–November) 2005 and 2006.

Table 1. Results of the statistical log-linear model for multidimensional contingency tables testing for differences in frequencies of occurrence of individual *Octodon degus* by trap type, sex, age, and year, as main factors, and their interactions.

Factor	Degrees of freedom	χ^2	p
Trap	2	315.73	< 0.0001
Sex	1	15.66	< 0.0001
Age	2	245.42	< 0.0001
Year	1	285.11	< 0.0001
Trap sex	2	0.02	0.99
Trap age	4	72.84	< 0.0001
Trap year	2	2.46	0.29
Sex age	2	41.15	< 0.0001
Sex year	1	4.18	0.04
Age year	2	22.63	< 0.0001
Trap sex age	4	1.72	0.78
Trap sex year	2	2.23	0.32
Trap age year	4	7.41	0.11
Sex age year	2	6.46	0.03
Trap sex age year	4	1.10	0.89

Shermans – a pattern that was similar between years (interaction trap type—year: $G_2^2 = 2.4$, p = 0.29). Throughout our study, wire mesh traps (Tomahawks and mesh Sherman) captured more than the 70% of individual degus (Fig. 2c).

We found all trap types to be equally efficient in sampling sexes. Furthermore, we found no significant sex ratio biases between traps (interaction trap type sex: $G_2^2 = 0.016$, p = 0.99), despite the fact that more females were sampled as a whole (factor sex: $G_1^2 = 15.6$, p = 0.00007) (Fig. 2b). Otherwise, the different trap types showed heterogeneity in sampling the three age classes of degus (interaction trap type age: $G_4^2 = 72.8$, p < 0.0001) (Fig. 2a). Adults were the more frequently trapped age class during both years (factor age: $G_1^2 = 245.4$, p < 0.00001), but age structure of the population changed between years (interaction age year: $G_2^2 = 22.6$, p < 0.000.0001). Large and medium Sherman traps provided a similar picture of the age structure of the population during 2005. Half of the individuals

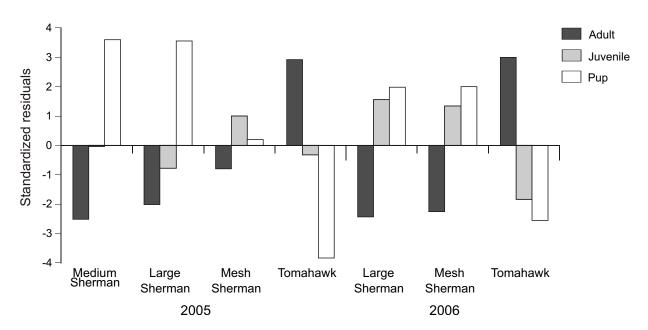


Fig. 3. Standardized residuals after log-linear models testing the interaction between trap type and age class during 2005 ($G_6^2 = 60.7, p < 0.00001$) and 2006 ($G_4^2 = 42.6, p < 0.00001$). Residual deviations higher than ± 1.96 are significantly different from zero.

captured were pups; adults represented about 30% of individuals. This pattern was opposite to that observed by Tomahawk traps, which sampled 65% of adults and 15% of pups. Mesh Shermans showed a similar pattern to Tomahawks during 2005 (with more adults than pups), which was similar to large Sherman traps during 2006. Year of sampling did not modify the age structure of the population determined by every trap model (interaction trap type age year: $G_4^2 = 7.4$, p = 0.11) (Fig. 2a).

Standardized residuals of the significant interaction between trap age after the log-linear models revealed that Tomahawk traps oversampled adult degus and under-sampled pups and juveniles (Likelihood ratio Chi-square L_2^2 = 19.4, p < 0.005) (Fig. 3). The other three trap types showed opposite patterns, and undersampled adults while over-sampling pups and juveniles. During 2005, medium and large Sherman traps showed identical patterns (medium Sherman: $L_2^2 = 15.3$, p < 0.005, large Sherman: $L_2^2 = 17.7$, p < 0.005) (Fig. 3), whereas mesh Sherman traps showed non-significant patterns $(L_{2}^{2} = 1.9, p > 0.05)$ (Fig. 3). During 2006 both mesh and large Sherman traps under-sampled adult degus and over-sampled juveniles and pups.

Discussion

In 2 years, we logged more than 17 700 trap days using 4 trap types during burrow trapping. Trap mortality was low in our study including zero mortality in 2006. Tomahawks were the most efficient traps for capturing individuals, accounting for half of the captures made during both years, followed by the mesh Sherman traps. Large and medium Sherman traps showed lower efficacy. Our results agree with O'Farrell et al. (1994) and Lambert et al. (2005), who suggested that mesh traps are more effective at capturing small mammals than solid-walled traps. Differences in effectiveness may account for biased estimates of density when using different trap types. Tomahawk traps were the largest of our trap types and the only model entirely made of wire mesh used in our study. Preference for Tomahawk traps may be due to the size of the

trap opening, as well as the spaciousness and openness inside the trap, which reflects the external environment in which degus forage. Additionally, animals may easily see food inside the traps, further enticing them to enter.

We found differences in the three age classes sampled by the trap types used. Tomahawks over-sampled adults and under-sampled pups and juveniles during both years. This pattern was contrary to that observed by the other three trap models, which in general, over-sampled pups or juveniles, and under-sampled adults. Nonetheless, relative captures of pups were similar in the different traps throughout the study (Fig. 1), suggesting that different traps can equally sample this age class. Thus, our observations do not support concerns by Iriarte et al. (1989) regarding the ability of Tomahawks in sampling younger degus. We have no evidence to suspect that juveniles or pups are able to escape from the larger mesh Tomahawk traps.

Our study provides insight into questions proposed by Fulk (1976) and Jaksic *et al.* (1981) regarding the effectiveness of medium Sherman traps in capturing *Octodon degus*. We found poor trap success using medium Sherman traps in 2005, and our results provided further evidence that the size of these traps may be a limiting factor in capturing large (adult) degus. Adults were under-sampled by Sherman traps, suggesting that this age class did not enter solid-walled traps readily. Since adult individuals forage above ground, they may be more interested in foraging in open habitat than entering a solid-walled trap that resembles a burrow.

Our trap success decreased substantially from 2005 to 2006 possibly in response to a more than doubling of our trapping effort between years (5543 trap days in 2005; 12 166 trap days in 2006, within the same time frame and area), resulting in an increased trapping effort beyond a saturation point. We also increased the number of trapped burrow systems in 2006 to include some with low activity. The increased trapping intensity from 2005 to 2006 provided us little additional demographic data. The decrease in the degu population around grid 2 from 2005 to 2006 probably had little effect on the overall decrease in trap success since the adult degu population

around grid 1 increased more than 2-fold. Careful consideration of trap density and sampling duration (Conard *et al.* 2008) may increase efficiency when sampling small mammal population structure.

Trap mortality may be of special concern when studying endangered or social species where the anthropogenic induced loss of an individual may disturb social structure. We had 4 trap mortalities in 2005 and zero in 2006. None of these occurred in the larger mesh Tomahawk traps. Overall trap mortality in our study (0.15%) was far less than reported by Anthony et al. (2005), which found mortality rates as high as 20%. Checking traps after morning emergence, during a peak activity period of degus (Kenagy et al. 2002), allowed a maximum of 1.5 hrs the animals spent in traps exposed to the sun and potential predator harassment. Thus, synchronizing trapping effort with animal activity may minimize if not eliminate trap mortality, yet still provide sufficient data regarding population and social group demography. Our attempt at targeting trap effort during animal activity minimized time animals spent in traps, which apparently resulted in very low mortality. This may easily be accomplished with diurnal species whose activity patterns are known. Developing trap-timing devices that record the time of captures (Barry et al. 1989), and thus animal activity periods, may be a cost-effective way to achieve this goal for nocturnal or crepuscular animals.

Previous studies found that choosing the appropriate scale (Bowman et al. 2001) and trap density (Conard et al. 2008) may be crucial in small mammal trapping studies. Studies addressing social group and population demography may result in misleading information if researchers' used a suboptimal trap type. Although we cannot say for certain how the elimination of each trap type would affect the capture success of remaining traps, the exclusive use of the popular medium or large Sherman trap may have provided severely biased results in our study. It is likely that our trap success would have decreased substantially with the sole use of one of these traps, thus resulting in underestimates of species density (O'Farrell et al. 1994) and erroneous demographic information. On the

other hand, achieving the optimal number and type of trap may be economically efficient and effective in sampling small mammal demography in population and sociality studies. In our study animal, *Octodon degus*, the sole use of Tomahawk traps may produce sufficient, unbiased demographic data. Consideration of the appropriate trap type is likely important for sampling demography accurately in other species as well.

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