Tools and Technology Article

Evaluating Abundance Estimate Precision and the Assumptions of a Count-Based Index for Small Mammals

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ABSTRACT Conservation and management of small mammals requires reliable knowledge of population size. We investigated precision of mark–recapture and removal abundance estimates generated from live-trapping and snap-trapping data collected at sites on Guam ($n = 7$), Rota ($n = 4$), Saipan ($n = 5$), and Tinian ($n = 3$), in the Mariana Islands. We also evaluated a common index, captures per unit effort (CPUE), as a predictor of abundance. In addition, we evaluated cost and time associated with implementing live-trapping and snap-trapping and compared species-specific capture rates of selected live- and snap-traps. For all species, mark–recapture estimates were consistently more precise than removal estimates based on coefficients of variation and 95% confidence intervals. The predictive utility of CPUE was poor but improved with increasing sampling duration. Nonetheless, modeling of sampling data revealed that underlying assumptions critical to application of an index of abundance, such as constant capture probability across space, time, and individuals, were not met. Although snap-trapping was cheaper and faster than live-trapping, the time difference was negligible when site preparation time was considered. *Rattus diardii* spp. captures were greatest in Haguruma live-traps (Standard Trading Co., Honolulu, HI) and Victor snap traps (Woodstream Corporation, Lititz, PA), whereas *Suncus murinus* and *Mus musculus* captures were greatest in Sherman live-traps (H. B. Sherman Traps, Inc., Tallahassee, FL) and Museum Special snap-traps (Woodstream Corporation). Although snap-trapping and CPUE may have utility after validation against more rigorous methods, validation should occur across the full range of study conditions. Resources required for this level of validation would likely be better allocated towards implementing rigorous and robust methods. (JOURNAL OF WILDLIFE MANAGEMENT 73(5):761–771, 2009)

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Reliable information about small-mammal population size is often necessary for implementation and evaluation of conservation and management practices. Unfortunately, many species are cryptic, nocturnal, and have spatially and temporally variable densities. Many researchers therefore select sampling and data analysis methods perceived to be fast and inexpensive, such as snap-trapping and indices of abundance, despite concerns about accuracy and precision of these methods (Nichols 1992; Anderson 2001, 2003; Sullivan et al. 2003; White 2005).

Live-trapping and snap-trapping are 2 of the most commonly used small-mammal sampling methods (Williams et al. 2002). During live-trapping, captured animals can be uniquely marked and released, where they are available for recapture during subsequent sampling occasions. In contrast, captured animals are removed from the population during snap-trapping, eliminating the possibility of recapture. Direct comparisons between live-trapping and snap-trapping, or analogous methods for other taxa, suggest that removal of individuals from the population often produces biased data (Rodgers et al. 1992, Jung et al. 2002, Sullivan et al. 2003).

Closed population mark–recapture (live-trapping data) and removal (snap-trapping data) abundance estimators assume that capture probability is appropriately modeled and that the population is subject to no births, deaths, emigration, or immigration during sampling (Williams et al. 2002). Mark–recapture estimators also assume that marked animals are correctly identified upon recapture. Removal estimators are subject to an additional restriction, because captures must decline over subsequent sampling occasions; nondeclining captures result in estimates with poor accuracy and precision (Otis et al. 1978, White et al. 1982).

Many researchers choose to forgo abundance estimation altogether and instead report only count-based indices of abundance, such as captures per unit effort (CPUE; White et al. 1982). Index proponents suggest that indices require less analytical expertise and are subject to fewer or less restrictive assumptions than abundance estimation methods (Engeman 2003, 2005). Careful consideration of indices, however, suggests that they are not without restrictive assumptions (Table 1). For example, the inherent assumption of any index of abundance is that the relationship between the index and true abundance is monotonic, proportional, and constant across space, time, and individuals (Nichols 1992; Anderson 2001, 2003). Unfortunately, few researchers test this assumption, either by evaluating indices against known populations (Conn et al. 2006), double-sampling (Eberhardt and Simmons 1987, Slade and Blair 2000), or through simulation (McKelvey and Pearson 2001). Failure to validate indices limits their utility (Nichols 1992; Anderson 2001, 2003).

We evaluated mark–recapture and removal abundance estimates, with the a priori expectation that mark–recapture

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Table 1. Comparison of the robustness of an index of abundance (captures per unit effort [CPUE]) and 2 estimates of abundance (removal and mark–recapture) to violation of population closure and potential forms of capture probability variation.

Population attribute	CPUE	Removal	Mark–recapture
Closed population	Required; unclear how to recognize violation	Required; difficult to recognize violation	Possible to recognize violation
Capture probability variation by:			
Space	Invalid across space	Valid if modeled	Valid if modeled
Time	Invalid across time	Problematic; reduced accuracy and precision	Valid if modeled
Behavior	Valid; only first capture data are utilized	Valid; only first capture data are utilized	Valid if modeled
Individual heterogeneity	Invalid unless stratified	Problematic, reduced accuracy and precision	Valid if modeled

estimates would be more precise (smaller CV and narrower 95% CI) than removal estimates. We based this hypothesis on the amount of information used to generate estimates (mark–recapture > removal), as well as the anticipated robustness of each metric to violations of critical assumptions (Table 1). We evaluated CPUE as a predictor of abundance, with the a priori expectation that violations of underlying assumptions (Table 1) would likely compromise this index. Finally, we evaluated effects of sampling duration on CPUE, cost and time associated with implementing live-trapping and snap-trapping, and species-specific capture rates of selected live- and snap-traps.

STUDY AREA

We sampled small-mammal populations on Guam, Rota, Saipan, and Tinian in the Mariana Islands, an archipelago of 15 islands arrayed in a north–south arc between 13° N and 21° N and 144° E and 146° E in the tropical northwest Pacific Ocean.

The small-mammal community of the Mariana Islands consisted of ≥5 introduced species, including *Mus musculus*, *Rattus exulans*, *R. norvegicus*, and *Suncus murinus*. Uncertainty exists regarding the identity of an additional *Rattus* species, thought to be either *R. rattus* or *R. tanezumi* (Musser and Carleton 2005). Preliminary genetic analysis of randomly selected samples from Guam ($n = 17$), Rota ($n = 10$), Saipan ($n = 10$), and Tinian ($n = 10$) indicated that all were most closely related to the *R. diardii* group described by Robins et al. (2007; S. J. Oyler-McCance and J. St. John, United States Geological Survey, unpublished data). Although the taxonomic identity of this group is under comprehensive investigation, we refer to them as *R. diardii* spp.

METHODS

Sampling Design

On each island, we identified potential study sites based on habitat type and available area of homogeneous habitat using 1:24,000-scale and 1:25,000-scale United States Geological Survey topographical maps and 1:20,000-scale vegetation maps (Falanruw et al. 1989). We selected sites in 4 habitats: grassland, native limestone forest (hereafter, native forest), secondary forest dominated by the introduced leguminous tree *Leucaena leucocephala* (hereafter, *Leucaena* forest), or mixed habitat (typically a mixture of grassland and *Leucaena* forest). With the exception of mixed habitat, sites contained ≥4 ha of homogeneous habitat. We sampled 7 sites on Guam, 4 on Rota, 5 on Saipan, and 3 on Tinian, including ≥1 grassland, one native forest, and one *Leucaena* forest site per island, between April 2005 and November 2006. During the same period, we sampled 4 mixed habitat sites on Guam ($n = 1$), Rota ($n = 1$), and Saipan ($n = 2$).

At each site, we prepared an 11 × 11 grid with 12.5-m intervals between each trap station (1.56 ha). Sampling activities occurred over 2 weeks and consisted of (in chronological order) a 2-day live-trap acclimation period, a 5-day live-trapping period, a 2-day snap-trap acclimation period, and a 5-day snap-trapping period. During live-trapping, we placed one standard-length folding Sherman live-trap (229 × 89 × 76 mm; H. B. Sherman Traps, Inc., Tallahassee, FL) at each trap station ($n = 121$) and one Haguruma wire mesh live-trap (285 × 210 × 140 mm; Standard Trading Co., Honolulu, HI) at every other trap station (25-m intervals; $n = 36$). Prior to the snap-trap acclimation period, we replaced each Sherman trap with one Museum Special snap-trap (141 × 70 × 15 mm; Woodstream Corporation, Lititz, PA) and each Haguruma trap with one Victor rat snap-trap (175 × 84 × 28 mm; Model M201, Woodstream Corporation).

We used 2 types of live- and snap-traps to maximize captures, based on preliminary testing that indicated that Haguruma and Victor traps targeted *Rattus* spp., whereas Sherman and Museum Special traps targeted *M. musculus* and *S. murinus*. We based trap spacing on home range and movement patterns of *M. musculus*, *S. murinus*, and *Rattus* spp. in the Mariana Islands (Baker 1946; Barbehenn 1969, 1974).

We placed traps on the ground and, whenever possible, next to or beneath clumps of grass, downed woody debris, or rocks to provide shelter from sun and rain. We baited traps with a mixture of peanut butter, oats, and food-grade paraffin and checked them beginning at 0730–0800 hours each day. We closed traps throughout the day to minimize trap mortality, reopened them at approximately 1600 hours, and rebaited as necessary. We did not bait traps during acclimation periods. At each site, we recorded the time required to prepare the trapping grid and complete daily activities associated with each sampling method, including trap baiting, trap monitoring, and animal processing.

During live-trapping, we uniquely marked all captured

animals with numbered metal ear tags (*M. musculus* and *S. murinus*: tags produced by S. Roestenburg, Riverton, UT; *Rattus* spp.: no. 1005-1, National Band and Tag Co., Newport, KY). We examined and measured captured animals to determine species, sex, age, and reproductive status, mass (g), head–body length (mm), tail length (mm), right hind-foot length (mm), right ear length (mm), and testes length (mm; if applicable). Capture, handling, and marking techniques followed guidelines approved by the American Society of Mammalogists (Gannon et al. 2007) and the Animal Care and Use Committee of the United States Geological Survey Fort Collins Science Center. We disposed of animals captured during snap-trapping away from study sites and human-use areas.

Data Analysis

Our data analysis followed an information-theoretic approach involving model selection and multimodel inference. We based model selection on Akaike's Information Criterion corrected for small sample size (AIC_c; Burnham and Anderson 2002). We considered models competitive with the top-ranked model when the difference (ΔAIC_c) was ≤ 2.0 (Burnham and Anderson 2002). We model-averaged parameter estimates based on Akaike weights (w_i; Burnham and Anderson 2002) and included the entire model set except for models with nonsensical β estimates (e.g., $\beta = -18.6$, $SE[\beta] = 475.6$), which we removed prior to model-averaging. Unless otherwise indicated, estimates are presented as mean ± 1 standard error.

We treated live-trapping and snap-trapping data similarly during abundance estimation, with the exception that we constrained recapture probability to zero when modeling snap-trapping data. We generated all abundance estimates in Program MARK 4.3 (White and Burnham 1999) using the conditional likelihood closed capture–recapture model developed by Huggins (1989, 1991). This model uses estimates of capture probability and number of individuals captured to estimate abundance and can account for heterogeneity in capture probability from temporal, behavioral, and individual effects (expressed either as unexplained heterogeneity, i.e., finite mixture distributions [Pledger 2000], or covariate-associated capture heterogeneity [Huggins 1989, 1991]). In this context, mixture distributions are an attempt to deal with individual capture heterogeneity by grouping animals with similar capture probabilities into discrete classes for modeling purposes.

In Program MARK, we coded design matrices to allow sites to be treated either individually or as groups based on common attributes such as island or habitat. We modeled capture and recapture probability across these groups to increase statistical efficiency (i.e., reduce estimate variance) and allow abundance estimates to be generated for sites with few captures or recaptures (Bowden et al. 2003, White 2005). We built models in an iterative fashion, beginning with models allowing capture probability to vary by time (t), behavior (b), individuals (heterogeneity [h]), combinations of these factors, or constraining capture probability to be constant. We specified heterogeneity models as 2-mixture models, based on concerns that our data set would not support a more parameterized model (Conn et al. 2006). If the top model amongst these models included a temporal component, we fit a set of neophobia models to the data set. Neophobia models allowed capture probability to vary during the first (neo1) or first and second (neo2) sampling occasions, while holding capture probability constant for remaining sampling occasions. Motivation for these models came from literature accounts of neophobia for introduced *Rattus* spp. (Temme and Jackson 1979, Inglis et al. 1996, Clapperton 2006). Building on the framework of the top model, we next added a set of models parameterized to model capture probability, recapture probability, or both capture and recapture probability as a function of island, habitat, or site. We hypothesized that capture or recapture probability would differ between Guam (where introduced brown treesnakes [*Boiga irregularis*] occur at high densities) and Rota, Saipan, and Tinian (without established brown treesnake populations), so we coded the island grouping in 2 ways, with island[4] differentiating each island and island[2] differentiating Guam from the combination of Rota, Saipan, and Tinian.

Our final set of models incorporated individual and environmental covariates, beginning with the global model and proceeding through a series of more parsimonious models. We assessed covariate importance by examining β values and 95% confidence intervals, where we considered covariates with 95% confidence intervals not overlapping zero influential on capture probability. Covariates under consideration included sex, age, reproductive status, body condition index, body size, rain previous night, and rain amount. Reproductive status (repstat) was a categorical variable that differentiated reproductive and nonreproductive individuals; we determined repstat based on mass and presence of externally visible sexual characteristics such as descended testes for males or lactation for females. We calculated body condition index (bodycon) as the ratio between the observed and expected mass of an individual, where we determined expected mass from a linear regression of the natural log of mass versus the natural log of head–body length. For each species, we modeled variation in bodycon as a function of island[4], island[2], and habitat in an analysis of variance framework (Proc GLM; SAS Institute, Inc., Cary, NC); we did not consider a site-specific bodycon model because of sparse data for some sites. We included bodycon estimates from the top model (or the model-averaged estimate) for each species in MARK modeling. Body size was a species-specific composite variable created from a principal components analysis (Proc FACTOR; SAS Institute, Inc.) of mass, head–body length, tail length, hind-foot length, and ear length measured for each captured individual. Finally, rain previous night (rainprev) was a categorical measure of the presence or absence of rainfall during each trap-night and rain amount (rainamt) was a quantitative measure of total rainfall (mm) at the center of each trapping grid. Rainamt measurements encompassed a 24-hour period, with the exception of the

Table 2. Number of *Mus musculus*, *Rattus diardii* spp., and *Suncus murinus* captures (CAP) and captures per unit effort (CPUE) during live-trapping (Live) and snap-trapping (Snap) in grassland, *Leucaena* forest, mixed, and native forest habitats on Guam, Rota, Saipan, and Tinian, Mariana Islands, 2005–2006.

	M. musculus				*R. diardii* spp.				*S. murinus*			
	Live		Snap		Live		Snap		Live		Snap	
Habitat	CAP	CPUE	CAP	CPUE	CAP	CPUE	CAP	CPUE	CAP	CPUE	CAP	CPUE
Guam												
Grassland	15	2.2	19	2.8	22	3.2	14	2.1	14	2.0	19	2.8
Leucaena forest 1					5	0.7	1	0.2				
Leucaena forest 2												
Leucaena forest 3					13	2.5	3	0.7				
Mixed					1	0.1	1	0.2			5	1.0
Native forest 1							1	0.2				
Native forest 2												
Rota												
Grassland	25	4.1	24	4.9	88	14.3	82	16.9				
Leucaena forest	19	3.6	9	2.2	42	7.9	20	5.0				
Mixed	32	6.1	15	3.8	106	20.3	79	19.9				
Native forest	1	0.2			11	1.9	4	1.0				
Saipan												
Grassland	51	8.1	52	8.4	41	6.5	32	5.2	19	3.0	12	1.9
Leucaena forest	2	0.3			50	7.9	63	14.7	43	6.8	80	18.7
Mixed 1					29	4.8	34	8.3	9	1.5	14	3.4
Mixed 2			1	0.2	8	1.1	15	2.6	47	6.6	20	3.4
Native forest					24	4.0	28	7.0	19	3.2	27	6.7
Tinian												
Grassland	9	1.4	2	0.5	106	16.5	145	35.4	11	1.7	6	1.5
Leucaena forest					55	9.0	41	9.1	93	15.2	62	13.7
Native forest					80	12.8	79	19.7	43	6.9	10	2.5

first sampling occasion for which rainamt included only the 12–16-hour period prior to trap monitoring. Before including rainamt in MARK models, we determined that rainfall averaged across sites did not differ appreciably between sampling occasions based on overlapping 95% confidence intervals. Following the addition of covariates, we generated model-averaged abundance estimates from all estimable models (Burnham and Anderson 2002).

Because we did not know true abundance, we compared mark–recapture and removal abundance estimates against each other on a site-specific basis. We evaluated abundance estimates based on the magnitude of coefficients of variation and the width of 95% confidence intervals. When necessary, we truncated 95% confidence interval lower limits to reflect the number of unique individuals captured. We considered estimates with small coefficients of variation ($\leq$0.30) and narrow 95% confidence intervals to be more precise and, therefore, more informative, than estimates with large coefficients of variation and wide 95% confidence intervals.

We then used the sampling method producing the greatest proportion of informative site-specific estimates to evaluate CPUE generated from both live-trapping and snap-trapping data using regression analyses (Proc REG; SAS Institute), with regressions constrained to pass through the origin. We present CPUE as captures/100 corrected trap-nights, where a trap-night is defined as one trap active for one night after correcting for sprung traps (Nelson and Clark 1973). We evaluated CPUE from the first day of sampling, 3 days of sampling, and 5 days of sampling to investigate the effect of sampling duration on index performance. We considered CPUE predictive utility to be directly related to 95% prediction interval width, where a prediction interval is a confidence interval for an individual predicted value.

Finally, we compared live-trapping and snap-trapping based on the effectiveness of each method for capturing target species as well as the cost of implementation. We evaluated trap effectiveness by comparing species-specific capture rates (captures/100 corrected trap-nights) during live-trapping and snap-trapping. Capture rate calculations included only sites where we captured a species. We investigated the cost of each sampling method by comparing the initial cost of supplies required to implement our sampling protocol, the mass and volume of those supplies, and the time required for site preparation and activities directly associated with sampling (i.e., trap baiting, trap monitoring, and processing of captured animals). We standardized time measurements to person-hours to avoid potential bias resulting from unequal participation in timed activities.

RESULTS

We captured 681 *R. diardii* spp., 298 *S. murinus*, 154 *M. musculus*, 15 *R. exulans*, and 5 *R. norvegicus* in 14,915 trap-nights (12,011.5 corrected trap-nights) during live-trapping and 642 *R. diardii* spp., 255 *S. murinus*, 122 *M. musculus*, 14 *R. exulans*, and 3 *R. norvegicus* in 14,915 trap-nights (8,952 corrected trap-nights) during snap-trapping (Table 2). Due to limited captures, we did not include *R. exulans* and *R. norvegicus* in our analyses. Live-trapping mortality was minor for *R. diardii* spp. (2 mortalities out of 681

individuals captured) and *M. musculus* (2 mortalities out of 154 individuals captured). For *S. murinus*, the rate was higher (16 mortalities out of 298 individuals captured).

The top *R. diardii* spp. mark–recapture model for live-trapping data (w_i = 0.871) allowed neophobia in capture probability (neo2) for each island (island[4]) as well as capture probability variation by the covariates sex, repstat, and rainamt, with recapture probability variation by island[4], sex, repstat, and rainamt. Covariate effects were strong and had 95% confidence intervals that did not overlap zero. Based on the top model, capture probability increased 3–5 times between occasion 1 to 3 and reproductively active females were on average more than twice as likely to be captured as nonreproductive males (Fig. 1). Capture probability increased with increasing rainfall; for a reproductively active female, the increase was from 0.15 to 0.22 for the lower and upper fifth percentiles of rainamt (0 mm and 22 mm). All other models with support contained a subset of these covariates and neither the top model without covariates (ΔAIC_c = 17.97) nor the p model (constant capture probability) had support (ΔAIC_c = 105.12).

The top *R. diardii* spp. removal model for snap-trapping data (w_i = 0.375) allowed capture probability to vary between Guam and the combination of Rota, Saipan, and Tinian (island[2]), sex, repstat, age, and body size. Covariate effects were strong and had 95% confidence intervals that did not overlap zero. Based on the top model, capture probability was approximately 2 times greater for reproductively active females than for nonreproductive males. Capture probability was also greater for adults than juveniles but lower for the largest individuals within each age class (Fig. 1). All other models with support contained a subset of these 4 covariates and neither the top model without covariates (ΔAIC_c = 12.08) nor the p model had support (ΔAIC_c = 15.09).

The top *S. murinus* mark–recapture model for live-trapping data (w_i = 0.994) allowed both temporal variation and heterogeneity (2 mixtures) in capture and recapture probability, with the temporal recapture probability variation differing by island[4]. No other models had support. Of the 2 effects on capture probability, unexplained capture heterogeneity was more important, with average capture probability across all occasions of 0.11 for the low probability class (65% of the population) and 0.67 for the high probability class (35% of the population). The top *S. murinus* removal model for snap-trapping data (w_i = 0.836) allowed neophobia in capture probability (neo1) for each habitat, where occasion 1 capture probability ranged from 0.01 in mixed habitat to 0.09 in grassland. The p model had no support (ΔAIC_c = 11.90).

The top *M. musculus* mark–recapture model for live-trapping data (w_i = 0.349) allowed both temporal variation and heterogeneity (2 mixtures) in capture and recapture probability, with the temporal variation in capture probability differing by island[2]. Of these effects, unexplained capture heterogeneity was more important, with average capture probability across all occasions ranging from 0.11 for

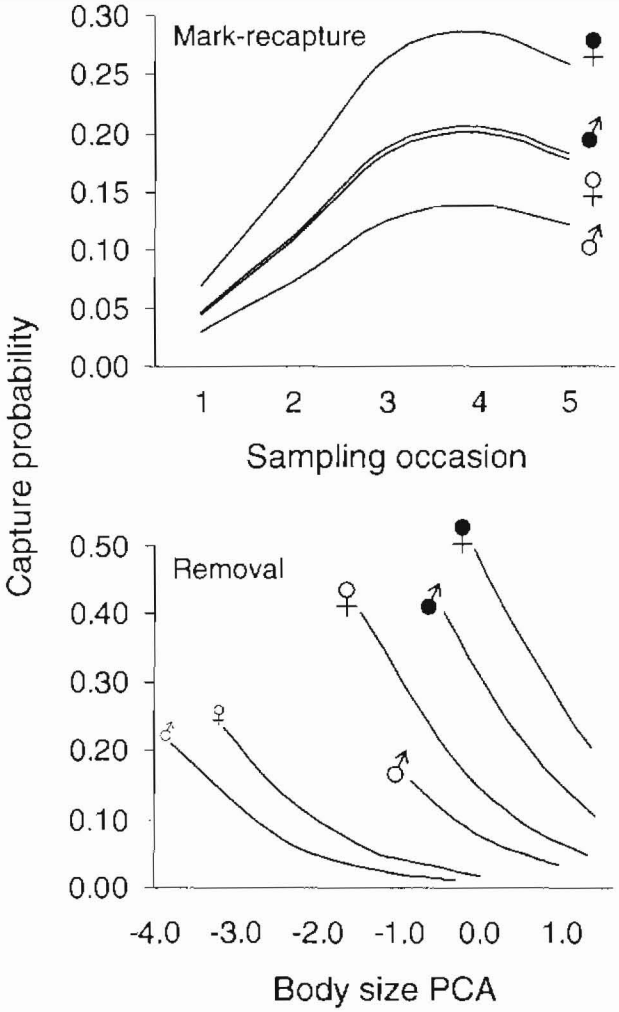

Figure 1. Effect of covariates on *Rattus diardii* spp. mark–recapture (upper panel) and removal (lower panel) capture probability using data from Saipan (Mariana Islands) collected 2005–2006. The top mark–recapture model included neophobia (reduced capture probability during occasions 1 and 2), sex, reproductive status (reproductively active = closed symbol, nonreproductive = open symbol), and rain amount. The top removal model included sex, reproductive status, age (ad = large symbol, juv = small symbol), and body size (created from a principal components analysis [PCA] of mass, head–body length, tail length, hind-foot length, and ear length), where body size increases from left to right on the x-axis.

the low probability class (67% of the population) to 0.56 for the high probability class (33% of the population). The p model had no support (ΔAIC_c = 35.91). The top *M. musculus* removal model for snap-trapping data (w_i = 0.745) allowed neophobia in capture probability (neo1) differing by island[2], where occasion 1 capture probability ranged from 0.12 on Rota, Saipan, and Tinian to 0.32 on Guam. There was minimal support for the p model (ΔAIC_c = 3.85).

Model-averaged mark–recapture abundance estimates from live-trapping ($\hat{N}_{M-R}$) and removal abundance estimates from snap-trapping ($\hat{N}_{REM}$) were often qualitatively similar, although there was an overall trend of $\hat{N}_{REM} > \hat{N}_{M-R}$ for *R. diardii* spp. (Table 3) and *S. murinus* (Table 4). For *M. musculus*, $\hat{N}_{M-R}$ and $\hat{N}_{REM}$ were generally similar

Table 3. *Rattus diardii* spp. model-averaged mark–recapture and removal abundance estimates, standard errors, coefficients of variation, and 95% confidence intervals generated from live-trapping ($\hat{N}_{M-R}$) and snap-trapping ($\hat{N}_{REM}$) data collected in grassland, *Leucaena* forest, mixed, and native forest habitats on Guam, Rota, Saipan, and Tinian, Mariana Islands, 2005–2006.

	$\hat{N}_{M-R}$				$\hat{N}_{REM}$			
Habitat	Abundance estimate	SE	CV	95% CI	Abundance estimate	SE	CV	95% CI
Guam[a]								
Grassland	41.1	9.4	0.23	22.8–59.5	17.5	5.2	0.30	14.0–27.7
Leucaena forest 1	6.6	1.7	0.26	5.0–9.9	1.1	0.5	0.45	1.0–2.1
Leucaena forest 3	22.9	5.8	0.25	13.0–34.3	3.7	1.4	0.38	3.0–6.4
Mixed	1.8	1.2	0.67	1.0–4.1	1.0	0.1	0.10	1.0–1.2
Native forest 1					1.1	0.2	0.18	1.0–1.5
Rota								
Grassland	142.4	22.8	0.16	97.6–187.1	210.0	107.0	0.51	82.0–419.6
Leucaena forest	70.0	12.9	0.18	44.7–95.2	34.9	9.2	0.26	20.0–52.9
Mixed	186.4	31.0	0.17	125.7–247.2	237.0	115.6	0.49	79.0–463.6
Native forest	17.8	4.3	0.24	11.0–26.3	9.1	5.2	0.57	4.0–19.3
Saipan								
Grassland	72.2	13.9	0.19	44.9–99.5	65.0	25.4	0.39	32.0–114.8
Leucaena forest	90.6	17.4	0.19	56.4–124.7	151.5	53.0	0.35	63.0–255.4
Mixed 1	54.8	11.7	0.21	31.9–77.7	82.5	38.6	0.47	34.0–158.1
Mixed 2	15.0	4.7	0.31	8.0–24.1	26.3	8.5	0.32	15.0–42.9
Native forest	47.1	11.1	0.24	25.4–68.8	55.4	16.6	0.30	28.0–87.9
Tinian								
Grassland	194.4	34.5	0.18	126.8–262.1	474.8	268.6	0.57	145.0–1001.2
Leucaena forest	85.6	14.1	0.16	58.0–113.2	122.8	79.3	0.65	41.0–278.2
Native forest	146.1	26.3	0.18	94.6–197.6	230.6	120.6	0.52	79.0–467.1

[a] We captured zero *R. diardii* spp. at 2 sites (1 *Leucaena* forest and 1 native forest).

(Table 5). For all species, $\hat{N}_{M-R}$ were more precise than $\hat{N}_{REM}$ based on coefficients of variation and 95% confidence interval width (Tables 3–5).

When evaluated against our most precise and information-rich abundance estimate, $\hat{N}_{M-R}$, the width of CPUE 95% prediction intervals decreased with increasing sampling duration for live-trapping but was relatively constant for snap-trapping. For example, a mid-range 1-day *R. diardii* spp. CPUE from live-trapping ($CPUE_{Live}$) predicts $\hat{N}_{M-R}$ of approximately 5–170 individuals, whereas a mid-range 5-day $CPUE_{Live}$ predicts $\hat{N}_{M-R}$ of approximately 75–125 individuals (Fig. 2). In contrast, there was no improvement between mid-range 1-day and 5-day CPUE from snap-trapping ($CPUE_{Snap}$), which predict $\hat{N}_{M-R}$ of approximately 50–150 and 85–190 individuals, respectively (Fig. 2). Similar patterns were evident for *S. murinus* and *M. musculus*, with the exception that *M. musculus* $CPUE_{Snap}$ 95% prediction interval width decreased slightly with increasing sampling duration.

We captured *R. diardii* spp., *S. murinus*, and *M. musculus* in all traps during live-trapping and snap-trapping, although effectiveness of each trap differed between species. *R. diardii*

Table 4. *Suncus murinus* model-averaged mark–recapture and removal abundance estimates, standard errors, coefficients of variation, and 95% confidence intervals generated from live-trapping ($\hat{N}_{M-R}$) and snap-trapping ($\hat{N}_{REM}$) data collected in grassland, *Leucaena* forest, mixed, and native forest habitats on Guam, Rota, Saipan, and Tinian, Mariana Islands, 2005–2006. We did not capture or observe *S. murinus* on Rota.

	$\hat{N}_{M-R}$				$\hat{N}_{REM}$			
Habitat	Abundance estimate	SE	CV	95% CI	Abundance estimate	SE	CV	95% CI
Guam[a]								
Grassland	20.3	5.8	0.29	14.0–31.7	80.9	97.0	1.20	19.0–271.0
Mixed					27.9	37.2	1.33	5.0–100.7
Saipan								
Grassland	28.8	8.5	0.30	19.0–45.5	53.1	65.7	1.24	12.0–181.8
Leucaena forest	67.8	20.1	0.30	43.0–107.2	436.8	550.0	1.26	80.0–1514.7
Mixed 1	13.6	4.5	0.33	9.0–22.4	80.3	103.8	1.29	14.0–283.8
Mixed 2	70.6	19.2	0.27	47.0–108.3	114.8	147.5	1.28	20.0–403.9
Native forest	30.0	9.4	0.31	19.0–48.4	135.4	168.8	1.25	27.0–466.2
Tinian								
Grassland	17.3	5.8	0.34	11.0–28.7	26.6	33.6	1.26	6.0–92.5
Leucaena forest	143.1	39.7	0.28	93.0–220.8	338.9	427.2	1.26	62.0–1176.3
Native forest	63.7	17.0	0.27	43.0–97.0	49.9	63.2	1.27	10.0–173.7

[a] We captured zero *S. murinus* at 5 sites (3 *Leucaena* forest and 2 native forest).

Table 5. *Mus musculus* model-averaged mark–recapture and removal abundance estimates, standard errors, coefficients of variation, and 95% confidence intervals generated from live-trapping ($\hat{N}_{M-R}$) and snap-trapping ($\hat{N}_{REM}$) data collected in grassland, *Leucaena* forest, mixed, and native forest habitats on Guam, Rota, Saipan, and Tinian, Mariana Islands, 2005–2006.

	$\hat{N}_{M-R}$				$\hat{N}_{REM}$			
Habitat	Abundance estimate	SE	CV	95% CI	Abundance estimate	SE	CV	95% CI
Guam[a]								
Grassland	17.5	4.0	0.23	15.0–25.3	35.2	20.7	0.59	19.0–75.7
Rota								
Grassland	41.5	10.1	0.24	25.0–61.3	54.4	37.8	0.69	24.0–128.4
Leucaena forest	32.0	8.3	0.26	19.0–48.3	20.5	14.8	0.72	9.0–49.5
Mixed	53.2	12.7	0.24	32.0–78.1	34.0	23.9	0.70	15.0–80.9
Native forest	1.7	1.2	0.71	1.0–4.0				
Saipan[b]								
Grassland	80.5	17.4	0.22	51.0–114.6	117.9	80.7	0.68	52.0–276.1
Leucaena forest	3.2	1.6	0.50	2.0–6.3				
Mixed					2.3	2.3	1.00	1.0–6.8
Tinian[c]								
Grassland	14.6	4.4	0.30	9.0–23.3	4.5	3.9	0.87	2.0–12.2

[a] We captured zero *M. musculus* at 6 sites (3 *Leucaena* forest, 1 mixed habitat, and 2 native forest).
[b] We captured zero *M. musculus* at 2 sites (1 mixed habitat and 1 native forest).
[c] We captured zero *M. musculus* at 2 sites (1 *Leucaena* forest and 1 native forest).

spp. captures were approximately 11 times greater in Haguruma live-traps and Victor snap-traps, whereas *S. murinus* and *M. musculus* captures were only slightly greater in Sherman live-traps and Museum Special snap-traps (Fig. 3).

Initial supply cost was much lower for snap-trapping (approx. US$700 for traps) than for live-trapping (approx. US$3,000 for traps, ear tags, and application pliers). Victor and Museum Special snap-traps were also smaller and lighter (approx. 11 kg) than Haguruma and Sherman live-traps (approx. 45 kg). On average, snap-trapping required less time (19.7 person-hr, SD = 3.8) over the 5-night sampling period than did live-trapping (31.8 person-hr, SD = 10.5). However, sampling time was generally less than site preparation time (48.6 person-hr, SD = 26.9), such that overall time requirements were not markedly different between live-trapping (81.0 person-hr, SD = 26.6) and snap-trapping (67.9 person-hr, SD = 27.2).

DISCUSSION

Mark–Recapture and Removal Abundance Estimates

Using data collected during consecutive live-trapping and snap-trapping events, we demonstrate that mark–recapture abundance estimates generated from live-trapping data ($\hat{N}_{M-R}$) were more precise than removal abundance estimates generated from snap-trapping data ($\hat{N}_{REM}$). Unfortunately, without knowledge of true abundance we cannot evaluate the accuracy of these estimates. In practice, truth is rarely known and researchers must rely on abundance estimates to answer research questions. In that framework, the generally poor precision of $\hat{N}_{REM}$, as demonstrated by large coefficients of variation (>0.30) and wide 95% confidence intervals, limits the utility of these estimates for conservation or management applications. In contrast, most of $\hat{N}_{M-R}$ had small coefficients of variation (≤0.30) and 95% confidence intervals. Typically, bias decreases and variance increases as the number of parameters in a model increases (Burnham and Anderson 2002); however, this was not the case for our mark–recapture models, which had higher mean parameter counts (*R. diardii* spp. = 16, *S. murinus* = 13, *M. musculus* = 12) than did removal models (4, 4, 3, respectively).

We suspect that the high $\hat{N}_{REM}$ variance is largely attributable to nondeclining captures over successive sampling occasions. Snap-trapping captures of new individuals declined at only 4 of 14 sites with >5 *R. diardii* spp. captures, 1 of 9 sites with >5 *S. murinus* captures, and 2 of 5 sites with >5 *M. musculus* captures. The obvious explanation for nondeclining captures is a failure of population closure (i.e., births, deaths, emigration, or immigration during sampling). Of these, neither deaths nor emigration can explain nondeclining captures. In contrast, both births and immigration would add animals to the sampling area over time. We suspect that births are unimportant for short-duration sampling events, although the maturation of juvenile animals could be important. In fact, *R. diardii* spp. juvenile captures increased from 17% of total captures during live-trapping to 35% of total captures during snap-trapping, and juvenile *M. musculus* showed a similar increase from 2% to 12.5% of total captures. Although these increases could indicate that maturation of juvenile animals made them increasingly available for capture, it seems unlikely that this phenomenon would occur across multiple sites, habitats, and islands.

A more plausible explanation is that removal of dominant adults during snap-trapping altered behavior of nondominant juveniles, thereby increasing their capture probability (Summerlin and Wolfe 1973). Removal of animals also increases immigration risk, because territorial vacancies may attract animals from outside the sampling area (Stickel 1946, Fitzgerald et al. 1981). If immigration were occurring, we would expect most new individuals to be captured on the

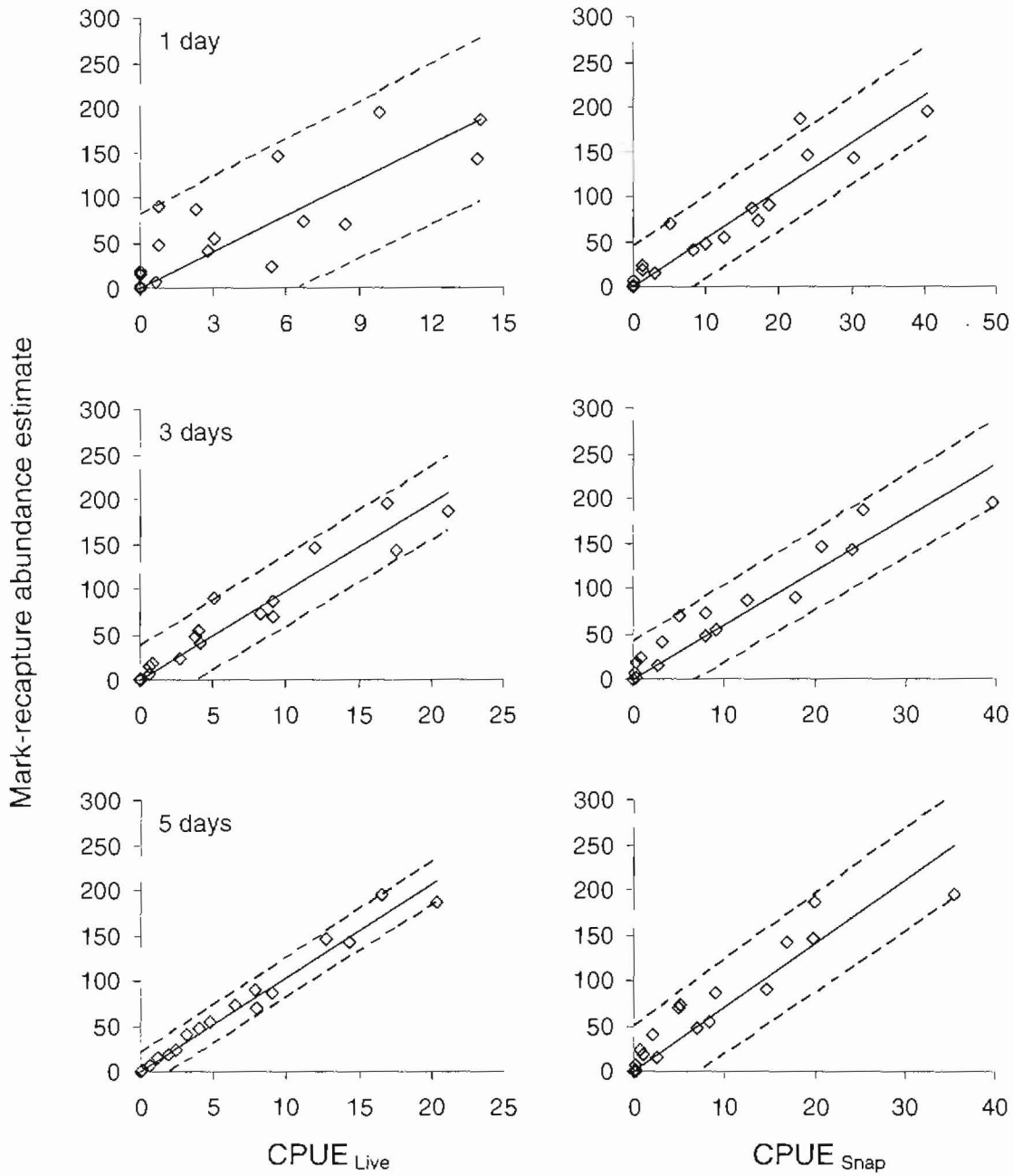

Figure 2. Relationship between *Rattus diardii* spp. mark–recapture abundance estimates generated from live-trapping data and captures per unit effort (CPUE, captures/100 corrected trap-nights) from 1 day, 3 days, and 5 days of live-trapping ($CPUE_{Live}$) and snap-trapping ($CPUE_{Snap}$) conducted at sites on Guam (n = 7), Rota (n = 4), Saipan (n = 5), and Tinian (n = 3), Mariana Islands, 2005–2006. Solid lines indicate the best-fit line, constrained to pass through the origin; dashed lines indicate 95% prediction intervals.

perimeter of the grid, especially during later sampling occasions. However, analysis of captures in perimeter (the 2 outer grid rows and columns) and interior traps revealed little evidence for immigration. Observed captures in perimeter and interior traps were generally within 5–10% of expected captures based on trap availability and never exceeded expected captures by >10% during sampling occasions 3–5.

In a post hoc attempt to further evaluate sources of $\hat{N}_{REM}$ variance, we compared $\hat{N}_{REM}$ with removal estimates generated from the live-trapping data set after excluding recaptures. Because these removals were figurative, we did not expect increased capture probability of nondominant individuals or immigration and, therefore, predicted improved precision in comparison to $\hat{N}_{REM}$. Contrary to expectations, *R. diardii* spp. removal estimates generated from live-trapping data generally had larger coefficients of variation and wider 95% confidence intervals than did $\hat{N}_{REM}$. In contrast, *S. murinus* removal estimates generated from live-trapping data had smaller coefficients of variation and

narrower 95% confidence intervals than did $\hat{N}_{REM}$. *M. musculus* coefficients of variation and 95% confidence intervals were generally similar between removal estimates generated from live-trapping data and $\hat{N}_{REM}$. These results suggest that factors other than increased capture probability of nondominant individuals or immigration influenced $\hat{N}_{REM}$ precision. We suspect that the reduced information content used to generate removal estimates (from either live-trapping or snap-trapping data) limits their precision in comparison to more information-rich mark–recapture estimates.

Count-Based Index

Using $\hat{N}_{M-B}$ as our best measure of small-mammal abundance, we found that $CPUE_{Live}$ generally had narrower 95% prediction intervals than $CPUE_{Snap}$. The predictive value of $CPUE_{Live}$ increased with increasing sampling duration for all species. In contrast, there was little apparent benefit to increased sampling duration on the predictive value of $CPUE_{Snap}$, except for *M. musculus*. We suspect that this improvement may relate to *M. musculus* snap-trapping capture suppression by *R. diardii* spp. or *S. murinus* during early sampling occasions (Brown et al. 1996), which could inflate 95% prediction intervals for $CPUE_{Snap}$ from 1 day or 3 days of sampling.

Indices such as CPUE are commonly used when relative, rather than absolute, measures of abundance are thought to be adequate to answer research questions, under the assumption that they require less costly data collection and analysis methods than those required for abundance estimation (Engeman 2003, 2005). When an index is used to monitor populations across space or time, however, the implicit assumption is that the relationship between the index and true abundance is monotonic and spatially and temporally constant (Nichols 1992; Anderson 2001, 2003); in classic population modeling terminology this is analogous to the constant capture probability (p) model. Without knowledge of true abundance, we cannot directly evaluate this relationship, but we can use information provided by our modeling of live-trapping and snap-trapping data to evaluate the assumption of constant capture probability. Our modeling indicated no support for the p model for *R. diardii* spp. and at best limited support for *S. murinus* and *M. musculus*. Instead, capture probability varied over time and between habitats or islands for each species. Modeling of *R. diardii* spp. data also identified several covariates (i.e., sex, age, reproductive status, body size, and rain amount) that influenced capture probability. Similarly, capture probability heterogeneity (in the form of mixture models) was important during mark–recapture modeling of *S. murinus* and *M. musculus* live trapping data. For these data, the assumption of constant capture probability intrinsic to the application of indices was not met.

In practice, spatial, temporal, or individual variation in capture probability seem likely during any population study. Nonetheless, many have argued that when data are sparse or capture probabilities are low, the known negative bias (unless capture probability = 1) of count-based indices may be preferred (McKelvey and Pearson 2001, Engeman 2005)

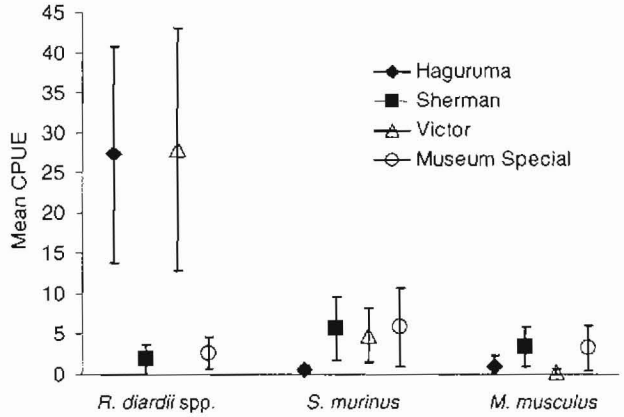

Figure 3. Mean *Rattus diardii* spp., *Suncus murinus*, and *Mus musculus* captures per unit effort (CPUE, captures/100 corrected trap-nights) in Haguruma (Standard Trading Co., Honolulu, HI) and Sherman (H. B. Sherman Traps, Inc., Tallahassee, FL) live-traps and Victor and Museum Special snap-traps (Woodstream Corporation, Lititz, PA) during small-mammal sampling on Guam, Rota, Saipan, and Tinian, Mariana Islands, 2005–2006. Sampling effort in CPUE calculations includes only sites where we captured a species. *R. diardii* spp., $n = 17$ sites, *S. murinus*, $n = 10$ sites, and *M. musculus*, $n = 9$ sites. Bars indicate 95% confidence intervals.

over the instability of model selection procedures, unknown bias, and large standard errors associated with estimates generated under these conditions (Otis et al. 1978, Menkens and Anderson 1988, Manning et al. 1995, Stanley and Burnham 1998). Although this may have been true in the past, advances in population modeling procedures address many of these concerns. For example, Program MARK allows sites to be grouped based on common characteristics, such as island or habitat, to increase sample size, thereby reducing negative impacts of sparse data or low capture probability at some sites (Bowden et al. 2003, White 2005). Information-theoretic model selection procedures offer improvements over earlier techniques such as those implemented in Program CAPTURE (Otis et al. 1978) and allow generation of model-averaged abundance and variance estimates (Burnham and Anderson 2002). The ability to incorporate covariates into population modeling has also improved flexibility and biological relevancy of modeling procedures and can result in improved parameter estimation accuracy and precision (White 2005).

Our evaluation of abundance estimates and index performance is somewhat limited because we did not know the true abundance of the small-mammal populations we sampled. We note, however, that few comparisons of estimator or index performance involving small-mammal populations of known abundance exist (e.g., Manning et al. 1995, Parmenter et al. 2003, Conn et al. 2006). These controlled studies may have reduced applicability towards wild small-mammal populations. For example, it is not clear that single-species populations in small enclosures (e.g., 0.02 ha, Conn et al. 2006; 0.2 ha, Manning et al. 1995) or provided with supplemental food (Conn et al. 2006) are analogous to wild populations. Further, the effort involved in studying enclosed populations necessarily limits sample size, such that

the range of observed densities (e.g., 2,700–14,700 *M. musculus*/ha, Conn et al. 2006) may not be comparable to more natural conditions. Similarly, simulation-based evaluation of sampling methods, estimator performance, or index performance (Otis et al. 1978, Menkens and Anderson 1988, McKelvey and Pearson 2001, Conn et al. 2004), although valuable for investigating robustness to violations of major assumptions, may not represent the full suite of conditions encountered during sampling of wild small-mammal populations.

Trap Capture Rates

We found variable capture rates between our live- and snap-traps, most likely due to species-specific behavioral and morphological traits. We suspect that high *R. diardii* spp. capture rates in Haguruma live-traps relate to the wire-mesh construction of this trap, which may reduce the neophobic response observed for many *Rattus* spp. (Temme and Jackson 1979, Inglis et al. 1996, Clapperton 2006) relative to the more enclosed Sherman trap. We suspect that low *S. murinus* and *M. musculus* Haguruma capture rates relate to reduced trap effectiveness due to the combination of feeding behavior (limited observations suggest that these species were less likely than *R. diardii* spp. to attempt to remove bait from the hanging trigger in Haguruma traps) and low body mass. Sherman traps, which require an animal to walk across the treadle upon entering the trap, seem more suitable for capturing low-mass species. Several studies comparing wire mesh traps (Haguruma or others) with box traps (Sherman or Elliot traps) have noted similar results (O'Farrell et al. 1994, Wilson et al. 2007).

We suspect that differential capture rates in snap-traps relate primarily to morphology. Low *R. diardii* spp. capture rates in Museum Special traps likely occurred because the trap does not consistently kill this species, with some injured animals likely escaping from the trap. Similarly, we suspect that the low body mass of *M. musculus* often prevents this species from activating Victor traps, which have considerable trigger tension. The equivalent *S. murinus* capture rate in both snap-traps suggests that this intermediate-sized species was not subject to the same trap-specific issues as *R. diardii* spp. and *M. musculus*. Other studies comparing snap-traps have noted similar species-specific results (Wiener and Smith 1972, Pendleton and Davison 1982, Perry et al. 1996), suggesting that snap-trap effectiveness should be assessed for target species prior to large-scale sampling activities.

Sampling Cost and Effort

We found that initial supply cost was approximately 4 times lower for snap-trapping than for live-trapping based on our protocol. Victor and Musuem Special snap-traps were also smaller and lighter (approx. 5 times lighter) than Haguruma and Sherman live-traps, which could prove advantageous for research conducted in remote areas, rugged terrain, or dense vegetation. Although average snap-trapping time was less than average live-trapping time, site-specific differences were only pronounced at sites with abundant small-mammal populations. More importantly, when we also considered site preparation time there was, on average, only a 16% time savings for snap-trapping. We note, however, that rugged terrain and dense vegetation increased our site preparation time considerably; preparation time would likely be much lower in other locations.

MANAGEMENT IMPLICATIONS

In our experience, snap-trapping and CPUE often produce unreliable information about small-mammal populations. However, continued use of these methods, especially CPUE and other indices of abundance, seems likely due to limited research budgets. We found that the predictive utility of CPUE improved with increasing sampling duration, largely negating perceived time savings associated with this index. Snap-trapping and count-based indices may have utility after validation against more rigorous sampling or estimation procedures. To be effective, however, validation should occur across the full breadth of conditions from which index data will be collected. The resources required for thorough and repeated validation efforts might be better invested in implementing rigorous and robust sampling methods and population abundance-estimation procedures.

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