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Food supplementation and abundance estimation in the white-footed mouse

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Abstract: Food availability often drives consumer population dynamics. However, food availability may also influence capture probability, which if not accounted for may create bias in estimating consumer abundance and confound the effects of food availability on consumer population dynamics. This study compared two commonly used abundance indices (minimum number alive (MNA) and number of animals captured per night per grid) with an abundance estimator based on robust design model as applied to the white-footed mouse (*Peromyscus leucopus* (Rafinesque, 1818)) in food supplementation experiments. MNA consistently generated abundance estimates similar to the robust design model, regardless of food supplementation. The number of animals captured per night per grid, however, consistently generated lower abundance estimates compared with MNA and the robust design model. Nevertheless, the correlations between abundance estimates from MNA, number of animals captured, and robust design model were not influenced by food supplementation. This study demonstrated that food supplementation is not likely to create bias among these different measures of abundance. Therefore, there is a great potential for conducting meta-analysis of food supplementation effect on consumer population dynamics (particularly in small mammals) across studies using different abundance indices and estimators.

Résumé : La disponibilité de la nourriture explique souvent la dynamique de population des consommateurs. Cependant, la disponibilité de la nourriture peut aussi affecter la probabilité de capture, ce qui, si on n'en tient pas compte, cause une erreur dans l'estimation de l'abondance des consommateurs et obscurcit les effets de la disponibilité de la nourriture sur la dynamique de population des consommateurs. Notre étude compare deux indices d'abondance couramment utilisés (nombre minimal d'individus vivants (MNA) et nombre d'animaux capturés par nuit par grille) avec un estimateur d'abondance basé sur un modèle de design robuste chez des souris à pieds blancs (*Peromyscus leucopus* (Rafinesque, 1818)) dans des expériences d'addition de nourriture. La méthode de MNA produit toujours des estimations comparables à celles du modèle de design robuste, quel que soit le supplément de nourriture fourni. La méthode du nombre d'animaux capturés par grille par nuit sous-estime systématiquement l'abondance par comparaison aux méthodes de MNA et du modèle de design robuste. Néanmoins, il n'y a pas d'influence de l'addition de nourriture sur les corrélations entre les estimations d'abondance par les méthodes de MNA, du nombre d'animaux capturés et du modèle de design robuste. Notre étude démontre que l'addition de nourriture ne risque pas de générer des erreurs dans ces diverses mesures de l'abondance. Il y a donc une excellente possibilité de mener à bien des méta-analyses des effets de l'addition de nourriture sur la dynamique de population des consommateurs (particulièrement chez les petits mammifères) à partir d'études qui utilisent différents indices et estimateurs d'abondance.

[Traduit par la Rédaction]

Introduction

Food availability often drives consumer population dynamics. For example, in eastern North America, population abundance of *Peromyscus leucopus* (Rafinesque, 1818) (white-footed mouse) and *Peromyscus maniculatus* (Wagner, 1845) fluctuates with acorn mast events (Wolff 1996; Elkinton et al. 1996; McCracken et al. 1999; McShea 2000; Elias et al. 2004). However, *Peromyscus* populations responded to food supplementation in some experiments but not in others (Bendell 1959; Hansen and Batzli 1978; Gilbert and Krebs 1981; Taitt 1981; Briggs 1986; Wolff 1986; Duquette and Millar 1995; Galindo-Leal and Krebs 1998; Terman 1999). A possible explanation for such discrepancies is that different abundance measures were used in different studies without considering the potential influences of food supplementation on measures of mouse abundance.

Although abundance estimators based on statistical mod-

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els should be used in preference to indices whenever possible (Nichols and Pollock 1983; Efford 1992; Hilborn and Krebs 1992; Tuyttens 2000; McKelvey and Pearson 2001; Pocock et al. 2004), there are times when indices are useful (e.g., sample size is small and data are too poor to correctly select appropriate statistical models; Pocock et al. 2004). Empirically, it was shown that capture probability in gray squirrel (*Sciurus carolinensis* Gmelin, 1788) negatively correlated with food availability (Gurnell 1996). Therefore, abundance indices that do not account for heterogeneous capture probability can create biased abundance estimates and confound the effects of food availability on consumer population dynamics. Previous studies testing the effects of supplemental food on small-mammal population abundance often relied on abundance indices such as the minimum number alive (MNA) and the number of animals captured per unit trapping effort (e.g., Hansen and Batzli 1978; Gilbert and Krebs 1981; Taitt 1981; Briggs 1986; Wolff 1986; Duquette and Millar 1995; Wolff 1996; Galindo-Leal and Krebs 1998; McCracken et al. 1999; Terman 1999; McShea 2000; Yunger 2002; Elias et al. 2004). However, if food supplementation has an effect on capture probability, indices such as MNA or the number of animals captured may generate biased results. In contrast, statistical models such as robust design models (Pollock 1982; Kendall and Nichols 1995) provide abundance estimates that are robust to heterogeneous capture probability and should generate unbiased results. At the very least, statistical models generate error estimates to help determine the reliability of the abundance estimation. The purpose of this study was to compare two commonly used abundance indices (MNA and the number of animals captured) with an abundance estimator based on robust design model as applied to the white-footed mouse in food supplementation experiments.

Methods

Study site and experimental design

The study site was located at the University of Virginia's Blandy Experimental Farm (Clarke County, Virginia; 78°00′W, 39°00′N), where two separate food supplementation experiments were conducted between 2002 and 2004.

Long-term experiment

Two sites approximately 2 km from each other were used, each with a woodlot adjacent to an old field. Each habitat had two trapping grids, with adjacent grids being 70–180 m apart. Each grid had 25 trapping stations in a 5 × 5 array with 10 m between stations. Two Sherman traps were placed at each trapping station, giving a total of 50 traps per grid. A total of eight grids were trapped for 3–4 days every 1–3 months from 2002 to 2004, except for one trapping session when the grids were trapped for 2 days (September 2003). Upon capture, mice were individually marked with ear tags, and their sex, age, and mass were recorded. After processing, mice were released at the trapping station where they were captured. All trapping procedures were approved by the University of Virginia's Animal Care and Use Committee. There were a total of nine trapping sessions conducted throughout the experimental period on a monthly to seasonal basis, which were divided into two annual cycles. The year 2002–2003 served as a control for the year 2003–2004 when an artificial seed mast event was created (five trapping sessions in 2002–2003 and four trapping sessions in 2003–2004). In September 2003, approximately 22.7 kg of blackseeded proso millet (*Panicum miliaceum* L.) seeds were added to half of the trapping grids (i.e., one of the two grids in each habitat at each site was selected as seed-supplemented grids, whereas the rest served as control) every 10 days for four times, resulting in a total millet seed density of 364 kg/ha.

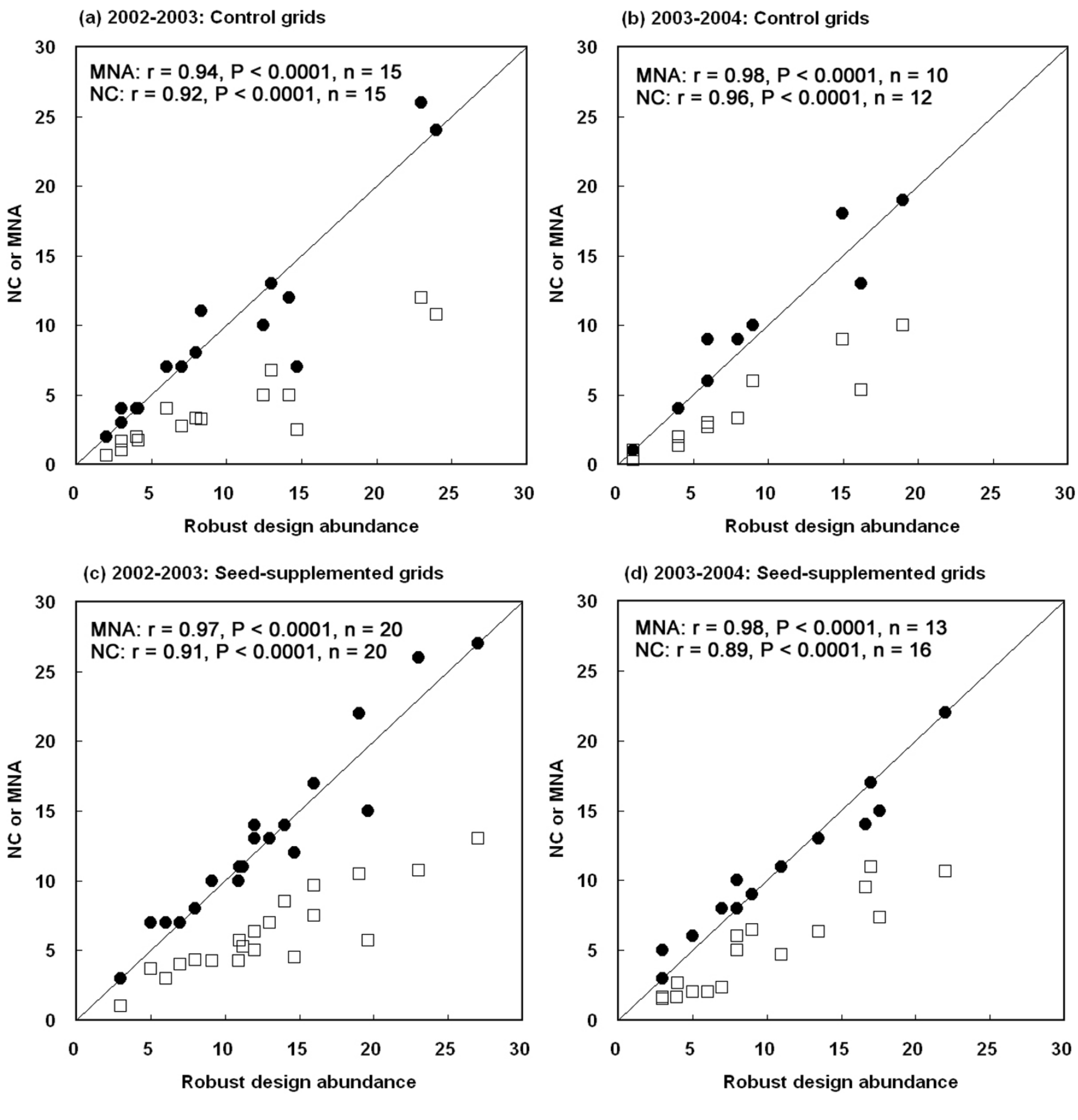
Short-term experiment

The short-term experiment was conducted on the same two sites as the long-term experiment, but focused on the forest habitats. Within each of the two forests, three trapping grids were located with adjacent grids 90 m apart. The trapping protocol was the same as the long-term experiment, except that each trapping session consisted of 4–6 consecutive nights both before and after a short-term food addition in July 2004. Each grid was supplemented with one of three food types: millet seeds, mealworms (beetle larvae belong to the family of Tenebrionidae), and a mixture of seeds and mealworms at equal proportion. Data before food addition were used as the control (i.e., no addition) for each of the grids. Seeds and beetle larvae are common food items for the white-footed mouse in natural environments, yet they represent food items with different nutritional quality: seeds have higher energy contents and lower protein contents than mealworms (Allen 1989; United States Department of Agriculture 2004). Therefore, the three food-addition types provided a range of food qualities to the white-footed mouse. An equal amount of food was added each day, resulting in a cumulative food density of 18 kg/ha over the 20 day period of the experiment. Both millet seeds and mealworms were confirmed to be acceptable food items to the mice through feeding trials, and millet seed consumption by the mice was further confirmed with stable carbon isotopic data (P.-J.L. Shaner, unpublished data).

Population abundance estimation

Population abundance of the white-footed mouse was estimated with MNA (Krebs 1966), the number of animals captured per night per grid, and the robust design model as implemented in the program MARK (White 2000). MNA is simply the actual number caught at time t plus the number of previously marked individuals caught after time t but not at that time. The number of animals captured per night per grid (i.e., per 50 traps) is the total number of captures over the trapping period divided by the number of trapping nights in that period. The robust design model allows for variable capture probabilities, as well as birth, death, immigration, and emigration rates. In the robust design model used for the long-term experiment, there were nine primary trapping sessions between 2002 and 2004, with two to four consecutive trapping nights within each primary trapping session (each of these trapping nights was a secondary trapping occasion). However, because of the small sample size, I was not able to estimate abundance for some of the grids. As a result, sample sizes were slightly different between years and type of grids. For the short-term experiment, there were two primary trapping sessions (before and after food addition),

Fig. 1. Spearman's correlations between the minimum number alive (MNA) and the robust design abundance, and between the number of white-footed mice (*Peromyscus leucopus*) captured and the robust design abundance for the long-term experiment. Solid circles denote MNA and open squares denote the number of white-footed mice captured (NC). Note that seed-supplemented grids in 2002–2003 (*c*) had not yet received seed addition. Among the four panels, only seed-supplemented grids in 2003–2004 (*d*) received seed addition. A 1:1 line is plotted for visual comparison.



each consisting of three to six secondary trapping occasions. Populations were assumed closed within each primary session, but were subject to birth, death, immigration, and emigration between primary sessions. Capture probability, the probability of first capture in any primary session, was assumed to vary between any two secondary trapping occasions. Recapture probability, the probability of a previously marked individual being captured at a successive occasion within any primary session, was assumed constant between trapping occasions but could vary among primary trapping sessions.

To compare the differences in abundance estimates between the two indices and the robust design model, Spearman's correlation was calculated between (*i*) MNA and the robust design abundance and (*ii*) the number of mice captured per night per grid and the robust design abundance.

Fig. 2. Spearman's correlations between the MNA and the robust design abundance, and between the number of white-footed mice captured and the robust design abundance for the short-term experiment. Solid circles denote MNA and open squares denote the number of white-footed mice captured (NC). A 1:1 line is plotted for visual comparison.

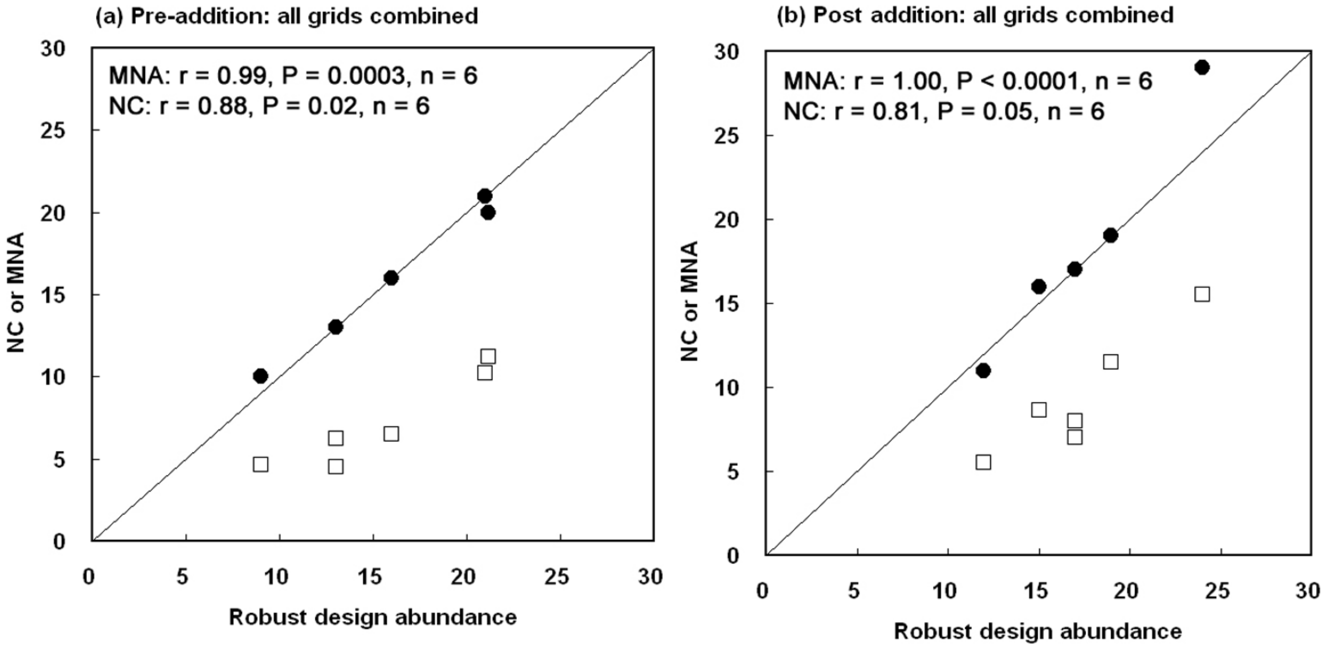


Table 1. Differences between the MNA and the robust design abundance, and between the number of white-footed mice (*Peromyscus leucopus*) captured and the robust design abundance.

Experiment	Group	df	*t*	*P*
MNA versus robust design abundance				
Long-term	2002–2003: control grids	14	0.41	0.69
	2002–2003: seed-supplementated grids	19	–0.73	0.47
	2003–2004: control grids	9	–0.92	0.38
	2003–2004: seed-supplemented grids	12	0.18	0.86
Short-term	Pre-addition: all grids combined	5	0.00	1.00
	Post-addition: all grids combined	5	–0.96	0.38
Number of animals captured versus robust design abundance				
Long-term	2002–2003: control grids	14	5.16	0.0001
	2002–2003: seed-supplemented grids	19	8.16	<0.0001
	2003–2004: control grids	11	4.09	0.002
	2003–2004: seed-supplemented grids	15	5.45	<0.0001
Short-term	Pre-addition: all grids combined	5	8.59	0.0004
	Post-addition: all grids combined	5	13.45	<0.0001

Results and discussion

The error estimates associated with robust design abundance were low. In the long-term experiment, the error estimates ranged from 0.0 to 5.5, except for one estimate where the error term was 11.1 (15 ± 11.1). In the short-term experiment, the error estimates ranged from 0.0 to 3.3. These low error estimates suggest that robust design model is relatively reliable in this study.

Different type of food used in the short-term experiment did affect mouse abundance estimated with the robust design model, MNA, or the number of animals captured (repeated-measures ANOVA — robust design model: food type, $F_{[2,3]}$ = 0.33, P = 0.74; trapping session, $F_{[1,3]}$ = 0.62, P = 0.49; food type × trapping session, $F_{[2,3]}$ = 1.01, P = 0.46; MNA: food type, $F_{[2,3]}$ = 0.61, P = 0.60, trapping session, $F_{[1,3]}$ = 1.22, P = 0.35, food type × trapping session, $F_{[2,3]}$ = 1.15, P = 0.43; number of animals captured: food type, $F_{[2,3]}$ = 0.72, P = 0.56, trapping session, $F_{[1,3]}$ = 1.61, P = 0.29, food type × trapping session, $F_{[2,3]}$ = 0.94, P = 0.48). Therefore, abundance data were pooled across all grids in testing correlations between the robust design model, MNA, and the number of animals captured per night per grid.

The robust design abundance correlated with both the MNA and the number of animals captured in both long-term and short-term experiments (Figs. 1, 2). Furthermore, MNA showed a consistent 1:1 relationship with the robust design abundance (Table 1). By contrast, the number of animals captured was consistently lower than mouse abundance estimated with the robust design model (Table 1). Nevertheless, the number of animals captured remained highly correlated with abundance estimates from the robust design model, regardless of food supplementation (Figs. 1, 2).

The results suggest that MNA is as reliable as the robust design model for measuring changes in mouse abundance in response to food supplementation. The number of animals captured, although possibly an underestimate of mouse abundance, is also reliable for detecting trends in abundance changes, which supports the findings from previous theoretical studies (McKelvey and Pearson 2001; Pocock et al. 2004). Interestingly, data from the long-term experiment showed that, as mouse abundance increased, the number of mice captured seemed to deviate more from MNA and the robust design model (Fig. 1). One explanation for this is trap saturation (Xia 1992). Specifically, once a mouse is caught in a trap, the trap becomes ineffective for the rest of the night. When the number of mice is much higher than the number of traps within a grid, the number of mice caught per night is likely to underestimate mouse abundance. By contrast, the robust design model takes into account capture probability when estimating population abundance, allowing it to be more robust to trap saturation.

The role of food limitation on consumer population dynamics has been a central theme in ecology. For example, Boutin (1990) reviewed 38 studies of food supplementation effect on population density of small mammals and reported that, while food supplementation frequently increases population density, it sometimes limits population density. Other factors, such as timing of food supplementation, may influence whether population density responds positively or negatively to food supplementation. This study demonstrated that food supplementation experiments are not likely to create bias in different abundance measures, especially MNA and robust design model. With the continuous use of food supplementation in field experiments since Bountin's (1990) review more than 15 years ago, there is now a great opportunity for a new meta-analysis of food supplementation effect on consumer population dynamics across studies using different abundance measures.

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