ORIGINAL ARTICLE

Running title: Rodent damage patterns in rice fields

The stadium effect: Rodent damage patterns in rice fields explored using giving-up densities

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Abstract

Rodents are globally important pre-harvest pests of rice. In South-East Asia, rodent damage to growing rice crops is commonly concentrated towards the center of rice fields, away from the field edge, resulting in a clear pattern known as the “stadium effect.” To further understand this behavior of rodent pests and to develop recommendations for future research and management, we examined the relation between giving-up densities (GUDs) and damage patterns. In Tanay, Luzon, Philippines, GUD trays containing pieces of coconut in a matrix of sand were placed at 4 different distances from the field edge to quantify the perceived risk of predation in a rice field pest, *Rattus tanezumi*. GUDs were recorded during a dry and wet season crop at the reproductive and ripening stages of rice. In addition, assessments of active burrows, tracking tile activity and rodent damage to the rice crop, were conducted in the dry season. GUDs were significantly lower in the center of the rice fields than on the field edges, suggesting that rodent damage to rice is greater in the middle of rice fields due to a lower perceived predation risk. Furthermore, this perception of predation risk (or fear) increases towards the field edge and was greatest on the rice bund, where there was no vegetation cover. We discuss the implications for rodent management and rodent damage assessments in rice fields. This is the first documented use of GUDs in a rice agro-ecosystem in Asia; thus we identify the challenges and lessons learned through this process.

Key words: habitat use, landscape of fear, pest management, *rattus tanezumi*, rodent behavior.

INTRODUCTION

Rodents are responsible for eating or spoiling enough food to feed approximately 280 million people for a year (Meerburg *et al*. 2009). In South-East Asia, rats are considered to be one of the most damaging pre-harvest pests of rice (Geddes 1992; John 2014). For example, in Luzon, Philippines, chronic pre-harvest losses to rodents are estimated to be between 5 and 10% per annum (Singleton *et al*. 2008). *Rattus tanezumi* (Temminck), the most common rodent pest in Luzon, is considered the most serious pest of rice in the

Philippines (Marquez *et al*. 2008). Large areas of rat damage can have a devastating impact on the local economy, particularly on the lives of subsistence rice farmers where many farmers typically own only 1.5 ha of land or less in lowland cropping areas (Singleton *et al*. 2010). Stuart *et al*. (2011) estimated that rice farmers lose approximately US$352 per year to rat damage alone. This is substantial given an annual average income for farmers of US$634 per year (or less than US$2 per day). To be able to manage rodent pests effectively and cost-efficiently, it is crucial to understand the ecology of *R. tanezumi* (Singleton *et al*. 2004).

Rodent damage, while often uneven within a rice field (Aplin *et al*. 2003), usually occurs in the middle of the paddy when damage is high, while the edges remain relatively intact (Buckle *et al.* 1985; Buckle 1994; Hoque & Sanchez 2008; Miller *et al*. 2008). Fall (1977) referred to this pattern in the Philippines as "eat-outs." Subsequent research in the Philippines described the pattern of rodent damage as "doughnut-shaped" (Duque *et al*. 2008). Aplin *et al*. (2003) and Miller *et al*. (2008) called it the "stadium effect." Buckle *et al*. (1985) observed the same phenomenon in central Java, Indonesia. The reason for the pattern is unknown (Miller *et al*. 2008), although Fall (1977) suggested that the low level of losses around the crop margins could reflect a high level of disturbance around crop edges. Farm size is typically less than 1.5 ha in the Philippines and the secondary bunds are important paths for human movement. In addition, rice farmers commonly clear vegetation from field edges and bunds as a method of rodent pest management (Stuart *et al*. 2011). Rodent pests of rice tend to nest on field edges, on rice bunds and in adjacent habitats rather than within the rice field itself, especially during flooded conditions (Lam 1982; Marquez *et al*. 2008; Stuart *et al*. 2012); thus, there is likely to be an increased energetic cost associated with travelling further from their nest sites to reach food (Ylonen *et al*. 2002). Therefore, there must be a perceived fitness or survival advantage with feeding in the center of the rice field.

To further understand this behavior, we examined the giving-up densities (GUDs) of *R. tanezumi* at the edge and at different distances into rice fields. The GUD is the density of resources remaining in a patch when an individual ceases foraging (Brown 1988). Where resources can be depleted, the individual will leave the patch when the benefits of harvesting that patch no longer outweigh the cost. These costs include predation risk, food handling time, and the cost of missed opportunities where the individual could have been using energy to perform other tasks such as reproduction (Bedoya-Perez *et al*. 2013). Balancing the risk of predation with the benefit of energetic rewards is important for maintaining fitness (Brown 1988). The benefit of a food patch is determined by its density and nutritional value, because higher density food sources may encourage animals to take greater risks (Stephens *et al*. 2007). Predator avoidance, however, has a significant impact on behavior such as foraging tactics, activity time and habitat selection of small mammals (Jacob & Brown 2000). Harvest rates at a patch have been reported to reduce as predation pressure increases (Bowers & Breland 1996).

Behavioral responses to the risk of predation are often linked to the amount of vegetation cover (Wheeler & Hik 2014). In response to direct and indirect predation risk, foragers react similarly with a reduction in foraging time and a shift to a denser habitat with more cover (Brown *et al*. 1988). Multimammate mice show lower GUDs in patches with cover and quit foraging earlier in open riskier patches (Mohr *et al*. 2003). When experimenting with GUDs, food resources are placed within a substrate, rather than being freely available; therefore, the harvest rate is a decreasing function of patch resource density (Brown 1988). By comparing food patches that simultaneously provide equal opportunities, GUDs provide an unbiased and controlled measure of the foraging cost of predation (Baker & Brown 2010).

In the case of rats in rice fields, we surmise that the edges of rice fields, which are generally bunds or levees, often have less vegetation cover than within a rice crop, and, thus, present a higher risk of predation. We hypothesize that rodents seek protection by moving into rice fields where there is cover from both avian and terrestrial predators. In the Philippines, the Eastern Grass Owl (*Tyto longimembris*), the brown rat snake (*Coelagnathus erythrurus*) and other species of snake, domestic cats and dogs, as well as humans, prey on rats in and around rice fields. We hypothesize that the perceived risk of predation is higher towards the edge of the rice field, and lowest towards the center, which generates the “stadium” pattern of damage. By using GUDs to test this hypothesis, we expect a lower GUD in the middle of the rice field than the edge. A better understanding of the edge effect on rodent behavior in rice fields will assist in developing recommendations for future research and management of rodent pests in rice crops.

MATERIALS AND METHODS

Study site

The study site, approximately 1 ha in area, was located at Rizal Agricultural Station in Tanay, Rizal, in Central Luzon (14°34 N, 121°20S, 360-m a.s.l.). The study was conducted during the dry and wet seasons of 2014. The dry season in this region of the Philippines occurs from November to April and the wet season is from May until October. In the dry season, the mean temperature is 28°C, with a mean monthly rainfall of 3 mm. In the wet season the mean temperature is 26°C, with a mean monthly rainfall of 300 mm. During both the sampling periods in the dry season, less than 22% of the moon was illuminated, with scattered cloud conditions and no rainfall. In the wet season, less than 30% of the moon was illuminated during the first sampling period, with light rain showers, and 73–81% of the moon was illuminated in the second sampling period, with no rainfall. Both sampling periods in the wet season had cloudy conditions.

Experimental design

Four replicate field plots (16–49 m) were established and separated by bunds (earthen levees). Each rice plot was managed under the same crop management practices. GUDs were measured over 2 consecutive nights at 2 crop stages: reproductive (60–75 days after transplanting (DAT) and ripening (75–90 DAT), when the fields were dry. A total of 20 coconut pieces (each measuring approximately 10 × 13 × 3 mm) were placed in each tray, 18 were buried randomly and 2 were placed on top of the sand. GUDs were measured by counting the remaining coconut pieces in trays filled with sand to a depth of 70 mm. In the dry season, wooden trays (200 × 200 × 80 mm) were used. In the wet season, plastic trays (180 × 120 × 70 mm) were used due to the increased likelihood of wet conditions. The trays were placed in one half of each plot at 4 locations: on the bund, 0.5 m from the bund, 3 m from the bund and in the middle of the plot (see Fig. 1). Vegetation cover (>10 cm above ground level) during the reproductive to ripening stage was typically 0–25% on the bund and 50–100% in the field. Preliminary trials, with a range of baits that included peanuts and pumpkin seeds, identified coconut to be the most attractive and less likely to deteriorate from humid conditions. Trays were placed on top of the soil surface within the plots and positioned between rice hills to prevent damage to the crop. Trays were checked daily within 1.5 h of sunrise to record the number of remaining coconut pieces. During preliminary trials, trays also were checked in the late afternoon. No coconut was consumed during diurnal periods; thus, we assumed that coconut was only consumed by rodents between dusk and dawn. After each check, the number of coconut pieces was replenished to 20 pieces per tray.

Rat damage assessments were conducted at the reproductive and ripening crop stages during the dry season to monitor the damage in the experimental plots. Transects were established at 0.5 and 3 m from the bund, and in the middle of the plot (see Fig. 1). Each transect had 5 sampling points that were perpendicular to the bund, and each sampling point was 1 m apart. The numbers of cut, mature and re-growing tillers were counted in a rice hill at each sampling point. If the rice hill contained fewer than 20 tillers, adjacent rice hills were assessed until a minimum of 20 tillers was reached.

During the dry season, an index of relative rat abundance was recorded using tracking tiles. For each field, 24 tiles were covered with a mixture of grease and motor oil and placed within the field against the side of bunds every 10 m. The tiles were operational over 3 consecutive nights. Each morning, the percentage of the tile that was marked by rodent footprints or tail swipes was recorded. Tracking tiles were used at the same time as GUD monitoring activity for each crop stage.

To estimate the relative abundance of nesting rats within the fields, the number of active rat burrows in the bunds surrounding each rice field plot was counted. Burrow counts were conducted over 2 days at each crop stage during the dry season. On the first day, burrow entrances were covered with mud and checked the following morning. A burrow entrance cleared of mud was considered active. This was repeated for a second consecutive night. Due to logistical difficulties, we were not able to conduct tracking tile, burrow or damage assessments during the wet season crop.

Data analysis

Statistical analyses were carried out using SPSS v.18. We used linear mixed models with a maximum likelihood estimation to analyze the effect of distance to the rice bund on GUDs and rank-transformed damage scores. Fixed effects entered into the model, along with their interactions, included distance to rice bund, crop stage and season. Crop stage and season were entered as repeated variables with diagonal repeated covariance. Plot number was included as a random effect. Post-hoc pairwise comparisons were performed using the Bonferroni test.

RESULTS

The distance to the rice field edge significantly influenced GUDs in rice fields (Table 1 and Fig. 2). Post-hoc analysis revealed that GUDs were significantly lower ($P < 0.05$) in the field than on the bund. GUDs were on average 13, 21 and 27% lower at 0.5, 3 and 6 m from the bund than on the bund, respectively. Within the field, GUDs were 16% lower in the center than 0.5 m from the edge ($P = 0.002$). There was a significant difference in GUDs between seasons and crop stages (Table 1). However, the distance × crop stage × season interaction was also significant. In the dry season, GUDs were on average 34% lower in the reproductive stage than in the ripening stage, whereas the reverse pattern (13% difference) was evident in the wet season. During the crop stages when GUDs were lower (i.e. reproductive stage in the dry season and ripening stage in the wet season), there was an inverse linear relationship between the GUD score and distance to the bund. During other crop stages with higher GUDs, there was no statistically significant difference in GUDs with distance to the bund.

During the dry season, the level of rodent damage per transect ranged from 0 to 10%, with significantly higher damage towards the center of the rice field ($F_{2,23.2}$ = 3.873, P = 0.035; Fig. 3). There was no statistically significant difference in damage between crop stages ($F_{1,23.2}$ = 1.552, P = 0.225) and the distance x crop stage interaction was not significant ($F_{2,23.2}$ = 0.982, P = 0.389). In line with the GUD results, rodent activity during the dry season as determined by tracking tiles was higher in the reproductive phase (19.8% ± 3.4; mean ± SE) compared to the ripening stage (8.3% ± 1.8). The mean number of active burrows was similar between the reproductive stage (7.0 ± 3.0 active burrows/100 m^2) and the ripening stage (9.0 ± 3.4 active burrows/100 m^2).

DISCUSSION

During both wet and dry seasons, a trend of decreasing GUDs towards the center of the rice field was evident during sampling periods when there was sufficient food intake. These results support our hypothesis that rodent damage to rice is greater in the middle of rice fields due to lower perceived risk of predation. The perception of predation risk (or fear) increased towards the field edge and was greatest on the rice bund, where there was no vegetation cover. This provides a preliminary insight into the rodent "landscape of fear" (sensu Laundre *et al*. 2010) within rice field habitats. These findings support the suggestion by Fall (1977) that the low level of damage by *R. tanezumi* to rice near to the margins of the crop may reflect high (human) disturbance. The finding of high GUDs in an "open habitat" on the bund is also similar to previous studies in which GUDs for small mammals were higher in open habitat patches due to a higher perceived risk of predation (Brown *et al*.

1998; Jacob & Brown 2000; Jacob *et al*. 2003; Baker & Brown 2010). For example, Jacob and Brown (2000) found that common voles (*Microtus arvalis*) showed lower GUDs in areas of high cover with unmown grass when compared to areas of mown grass.

Baker and Brown (2010) reported evidence of an edge effect using GUDs in the four-striped grass mouse (*Rhabdomys pumilio*); with high-risk habitat within wooded patches, moderate risk habitat within 3 m of a wooded patch, and core, safe habitat in remaining grassland areas. Based on our results, a similar spatial distribution map of perceived predation risk by *R. tanezumi* could be applied to rice fields; with high risk habitat on rice bunds with no vegetation cover, moderate risk habitat within 0.5 m from the field edge and core, safe habitat in the remainder of the rice field.

Our findings have important implications for rodent management. Recommendations for rodent control in rice fields often include placing rodenticide bait or traps on or alongside rice bunds and field edges (Buckle *et al*. 1999; Hoque & Sanchez 2008), presumably due to assumed movements of rats along bunds, greater ease of access for the operator and to avoid flooding. However, our GUD findings indicate that baits and traps placed in the center of the field, away from the field edge, are likely to have greater success. To avoid submergence, these should be applied when the field is dry, for example during the mid-season drainage of rice crops; otherwise raised or floating platforms could be used. Further research is needed to investigate the effectiveness of rodenticide baits and trap placement at varying distances from the field edge. An alternative option worth investigating is to create "safe spots" on rice bunds or field margins where bait is provided within small vegetation patches with cover.

We observed no trend in GUD scores during periods of low food intake. This is likely due to the low sensitivity of GUDs when food intake is low. Bedoya-Perez *et al*. (2013) suggest that in order for GUD studies to be successful it is important to identify a suitable bait and substrate that results in a fine balance between high visitation rates and above zero GUD values. They further suggest that if the quality of the food provided in the artificial patch is too high and the substrate is easily searchable, then this can mask the effects of predation risk due to high food intake across all microhabitat patches. Whereas, if the food is of low quality and the substrate is too challenging, then the missed opportunity costs and predation risk outweigh the benefits, resulting in low rates of patch visitation and, thus, low numbers of replicates for researchers to analyze. In addition, if too much food is provided, the animal may become satiated. In our study, 2 sampling periods provided sufficient food intake for meaningful results. We acknowledge that rodent density, weather, lunar phase, and/or availability of alternative food (e.g. ripening rice grain) may influence the success of research using GUDs in tropical rice-based ecosystems. Further testing using alternative baits, substrate or different bait to substrate ratios is needed. In addition, Kotler *et al*. (2001) suggest matching the correct substrate to the species. We originally tried using sand mixed with gravel, but during preliminary testing, the use of gravel resulted in reduced visitation rates. Perhaps food intake could be increased by simply increasing the size of coconut pieces or by reducing the burial depth, thus decreasing the costs of foraging

(Bedoya-Perez *et al*. 2013). In larger fields, wider spacing between GUD trays may yield more pronounced results.

Even though rodent damage was relatively low during the dry season (mean of 1.5% damage), where damage was present, there was a noticeable trend of increasing damage towards the center of the field. This is in contrast to previous suggestions that rodent damage in rice is patchy when damage is low (Buckle 1994; Singleton 2003). Our findings support recommendations for rodent damage assessments in rice to be conducted using a stratified sampling approach that includes sampling sites near the edge of the rice field as well as near the middle (Aplin *et al*. 2003; Stuart *et al*. 2014). In addition, considering the edge effect of rice bunds on rodent foraging behavior, rice bunds should be considered as the boundaries of the field plot to be assessed using this stratified approach. In some previous studies, the field edge during damage assessments was considered to be a non-rice habitat (Stuart *et al*. 2014).

Recommendations for future research

This is the first documented use of GUDs for assessing rodent behavior in a rice environment in Asia. The lessons learned can, thus, be applied to future research on rodent behavior in rice-based agro-ecosystems. For example, GUDS could be used to investigate the influence of growing flowering plants on rice bunds, an ecological engineering approach to promote beneficial arthropods (Horgan *et al*. 2016), on rodent foraging behavior within a rice field, or to understand the effects of other crop management methods, such as intermittent drying of rice fields (Lampayan *et al*. 2015), on how rodents use a landscape. Through manipulative studies, it also would be interesting to use GUDs to explore the effects of vegetation cover, human activity and other predator activity on the rodent's perceived risk of predation in a rice field habitat.

Although the theory of GUDs is based on simple principles, careful and considerable planning is required for accurate measurements (Bedoya-Perez *et al*. 2013). Certain species require an initial time period to get used to the novel food patch (Wheeler & Hik 2014). This requires the GUD experiment to be conducted over a greater number of days. The accuracy of a single day or night of data collection is questionable, depending on the target species. We recommend that each session is carried out over at least 2 nights, unless "habituation days" are used that allow rodents to get used to the bait stations (see Ylonen *et al*. 2002). Preliminary trials should also be conducted so that any issues encountered may be addressed prior to conducting the full experiment (Bedoya-Perez *et al*. 2013).

CONCLUSION

We demonstrated that GUDs can be a useful tool for investigating rodent behavior in tropical rice-based ecosystems in Asia. The distribution of rodent damage in rice fields is related to the rodent's perceived risk of predation, which is, in turn, affected by the distance to the field edge. This has important implications for both rodent management and rodent damage assessments in rice fields. Using GUDs as one tool, further research is needed to understand how rice field management can be optimized to increase the landscape of fear for rodent pests and, hence, reduce damage.

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REFERENCES

Aplin KP, Brown PR, Jacob J, Krebs CJ, Singleton GR (2003). *Field Methods for Rodent Studies in Asia and the Indo-Pacific.* ACIAR Monograph no. 100. Australian Center for International Agricultural Research, Canberra.

Baker MAA, Brown JS (2010). Islands of fear: Effects of wooded patches on habitat suitability of the striped mouse in a South African grassland. *Functional Ecology* **24**, 1313–22.

Bedoya-Perez MA, Carthey AJR, Mella VSA, McArthur C, Banks PB (2013). A practical guide to avoid giving up on giving-up densities. *Behavioral Ecology and Sociobiology* **67**, 1541–53.

Bowers MA, Breland B (1996). Foraging of gray squirrels on an urban-rural gradient: Use of the GUD to assess anthropogenic impact. *Ecological Applications* **6**, 1135–42.

Brown JS (1988). Patch use as an indicator of habitat preference, predation risk, and competition. *Behavioral Ecology and Sociobiology* **22**, 37–47.

Brown JS, Kotler BP, Smith RJ, Wirtz II WO (1988). The effects of owl predation on the foraging behavior of heteromyid rodents. *Oecologia* **76**, 408–15.

Brown JS, Kotler BP, Knight MH (1998). Patch use in the pygmy rock mouse (*Peromyscus collins*). *Mammalia* **62**, 108–12.

Buckle AP (1994). Damage assessment and damage surveys. In: Buckle AP, Smith RH, eds. *Rodent Pests and their Control*. CAB International, Wallingford, pp. 219–48.

Buckle AP (1999). Rodenticides – Their role in rodent pest management in tropical agriculture. In: Singleton GR, Hinds LA, Leirs H, Zhang Z, eds. *Ecologically-based Management of Rodent Pests*. Australian Centre for International Agricultural Research, Canberra, pp. 163–77.

Buckle AP, Yong YC, Abdul Rahman H (1985). Damage by rats to rice in Southeast Asia with special reference to an integrated management scheme proposed for Peninsular Malaysia. *Acta Zoologica Fennica* **173**, 139–44.

Duque UG, Joshi RC, Singleton GR, Marquez LV, Florage MA, Sebastian LS (2008). Biology and management of rodent communities in intensive lowland irrigated rice cropping systems in Luzon Island. In: Singleton GR, Joshi RC, Sebastian LS, eds. *Philippine Rats: Ecology and Management*. Philippine Rice Research Institute, Science City of Muñoz, Nueva Ecija, pp. 57–65.

Fall MW (1977). Rodents in tropical rice. *University of the Philippines Technical Bulletin* **36**, 37.

Geddes A (1992). The relative importance of pre-harvest crop pests in Indonesia. *Bulletin* **47**. Natural Resources Institute, UK.

Hoque MM, Sanchez FF (2008). Development of rodent management in the Philippines from 1968–1988. In: Singleton GR, Joshi RC, Sebastian LS, eds. *Philippine Rats: Ecology and Management*. Philippine Rice Research Institute, Science City of Muñoz, Nueva Ecija, pp. 9–24.

Horgan FG, Ramal AF, Bernal CC, Villegas JM, Stuart AM, Almazan MLP (2016). Applying ecological engineering for sustainable and resilient rice production systems. *Procedia Food Science* **6**, 7–15.

Jacob J, Brown J (2000). Microhabitat use, giving-up densities and temporal activity as short- and long-term anti-predator behaviors in common voles. *Oikos* **91**, 131–8.

Jacob J, Nolte D, Hartono R (2003). Pre-and post-harvest movements of female rice-field rats in West Javanese rice fields. In: Singleton GR, Hinds L, Krebs CJ, Spratt DM, eds. *Rats, Mice and People: Rodent Biology and Management*. Australian Centre for International Agricultural Research, Canberra, pp. 277–80.

John A (2014). Rodent outbreaks and rice pre-harvest losses in Southeast Asia. *Food Security* **6**, 249–60.

Kotler BP, Brown JS, Oldfield A, Thorson J, Cohen D (2001). Foraging substrate and escape substrate: Patch use by three Species of Gerbils. *Ecology* **82**, 1781–90.

Lam YM (1982). Rats as rice field pests – Their importance and control. In: Khoo KC, Lam YM, Teoh CH, Lim WH, Mohamad BM, eds. *Rodent Pests of Agricultural Crops in Malaysia*. Malaysian Plant Protection Society, Kuala Lumpur, pp. 9–17.

Lampayan RM, Rejesus RM, Singleton GR, Bouman BAM (2015). Adoption and economics of alternate wetting and drying water management for irrigated lowland rice. *Field Crops Research* **170**, 95–108.

Laundre JW, Hernandez L, Ripple WJ (2010). The landscape of fear: Ecological implications of being afraid. *The Open Access Journal* **3**, 1–7.

Marquez LV, Joshi RC, Duque UG, Florague MA Sebastian LS (2008). Development of ecology-based management system at the Philippine Rice Research Institute farm: researchers' experience. In: Singleton GR, Joshi RC, Sebastian LS, eds. *Philippine Rats: Ecology and Management*. Philippine Rice Research Institute, Science City of Muñoz, Nueva Ecija, pp. 67–84.

Meerburg BG, Singleton GR, Leirs H (2009). The year of the rat ends—Time to fight hunger! *Pest Management Science* **65**, 351–52.

Miller R, Stuart AM, Joshi RC, Banks P, Singleton GR (2008). Biology and management of rodent communities in complex agroecosystems–rice terraces. In: Singleton GR, Joshi RC, Sebastian LS, eds. *Philippine Rats: Ecology and Management.* Philippine Rice Research Institute, Science City of Muñoz, Nueva Ecija, pp. 25–36.

Mohr K, Vibe-Petersen S, Jeppesen LL, Bildsoe M, Leirs H (2003). Foraging of multimammate mice, *Mastomys natalensis*, under different predation pressure: Cover, patch-dependent decisions and density-dependent GUDs. *Oikos* **100**, 459–68.

Singleton GR (2003). Impacts of rodents on rice production in Asia. *IRRI Discussion Paper Series No. 4*5, International Rice Research Institute, Los Baños.

Singleton GR, Brown PR, Jacob J (2004). Ecologically based rodent management: Its effectiveness in cropping systems in South-East Asia. *NJAS: Wageningen Journal of Life Sciences* **52**, 163–71.

Singleton GR, Joshi RC, Sebastian LS (2008). Ecological management of rodents: The good, the bad, and hindi naman masyadong pangit! In: Singleton GR, Joshi RC, Sebastian LS, eds. *Philippine Rats: Ecology and Management*. Philippine Rice Research Institute, Muñoz, Nueva Ecija, pp. 1–7.

Singleton GR, Belmain S, Brown PR, Aplin K, Htwe NM (2010). Impacts of rodent outbreaks on food security in Asia. *Wildlife Research* **37**, 355–9.

Stephens DW, Brown JS, Ydenberg RC (2007). *Foraging: Behavior and Ecology*. University of Chicago Press, USA.

Stuart AM, Prescott CV, Singleton GR, Joshi RC (2011). Knowledge, attitudes and practices of farmers on rodent pests and their management in the lowlands of the Sierra Madre Biodiversity Corridor, Philippines. *Crop Protection* **30**, 147–54.

Stuart AM, Prescott CV, Singleton GR (2012). Natal nest locations of the Asian house rat (*Rattus tanezumi*) in lowland rice–coconut cropping systems: A coconut penthouse or rice bunds with water frontage? *Wildlife Research* **39**, 496–502.

Stuart AM, Prescott CV, Singleton GR (2014). Habitat manipulation in lowland rice-coconut cropping systems of the Philippines – An effective rodent pest management strategy? *Pest Management Science* **70**, 939–45.

Wheeler HC, Hik DS (2014). Giving-up densities and foraging behaviour indicate possible effects of shrub encroachment on arctic ground squirrels. *Animal Behaviour* **95**, 1–8.

Ylonen H, Jacob J, Davies MJ, Singleton GR (2002). Predation risk and habitat selection of Australian house mice *Mus domesticus* during an incipient plague: Desperate behaviour due to food depletion. *Oikos* **99**, 284–9.

Table 1. Results from a linear mixed model of the effect of distance, crop stage and season on the giving-up density

Source	d.f.	*F*-ratio	*P*
Intercept	1	5027.479	<0.001
Distance	3	24.651	<0.001
CropStage	1	13.977	0.001
Season	1	68.972	<0.001
Distance * *CropStage*	3	1.158	0.346
Distance * *Season*	3	6.265	0.003
CropStage * *Season*	1	81.564	<0.001
Distance * *CropStage* * *Season*	3	12.927	<0.001

FIGURES

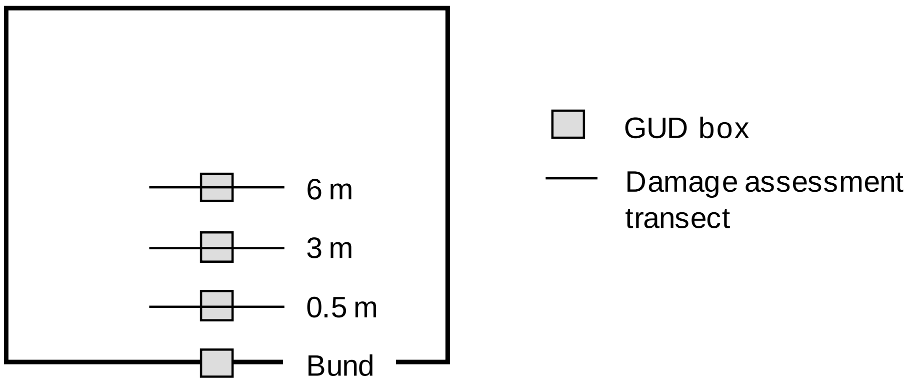

Figure 1 Lay-out of the giving-up density (GUD) boxes and the damage assessment transects within a plot

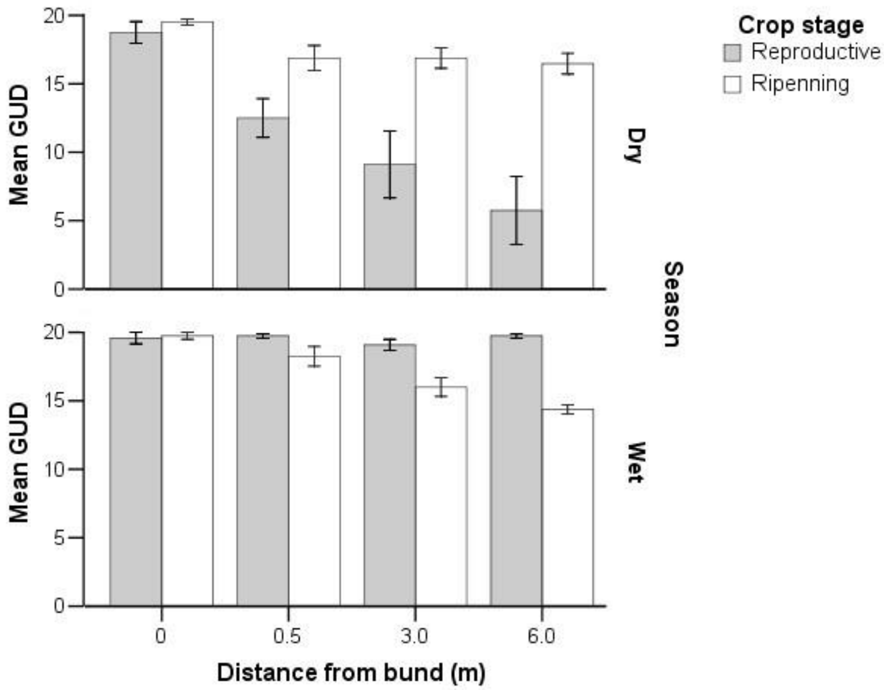

Figure 2 The mean and SE for giving-up density (GUD; number of coconut pieces remaining) in rice field plots at different distances from the rice bund for the dry and wet seasons during the reproductive and ripening rice crop stages.

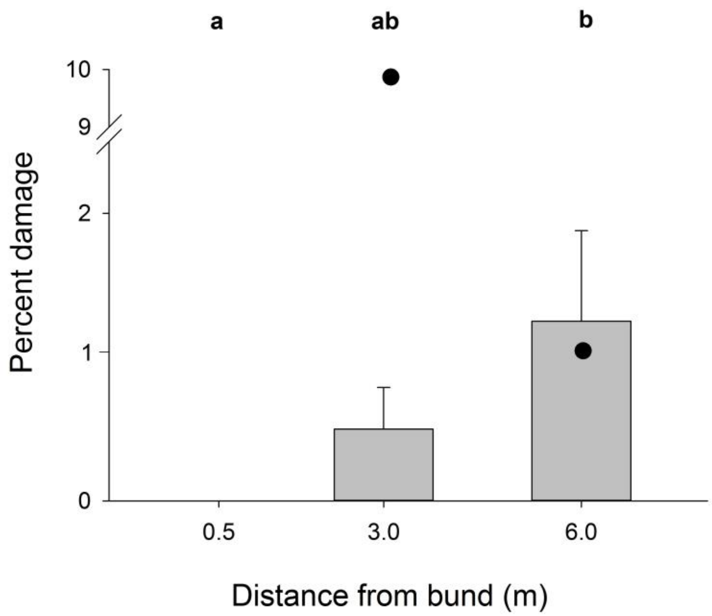

Figure 3 Rodent damage levels (% of rice tillers cut) in each plot (*n* = 4) at varying distances from the rice bund during the reproductive (dots) and ripening (bars) stages of the dry season rice crop. During the reproductive stage, damage was only recorded in 1 plot; thus, only the values for that plot are presented for this crop stage. Distances that share the same letter are not statistically different at 0.05 probability level.