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ASSISTED DISPERSAL OF TROPICAL DUNG BEETLES

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ABSTRACT. — As habitat fragmentation and climate change degrade the suitability of natural habitats, many species are likely to become threatened with local or global extinction. In the future, conservation of species and management of degraded areas may need to employ radical solutions, such as assisted dispersal and colonisation. Here, we report the findings of a small scale, two-fold investigation into potential management actions for reintroducing functionally important species (dung beetles) in a fragmented system. We tested two a priori hypotheses: 1) dung supplementation will increase dung beetle population sizes in the short term; and 2) introducing dung beetles into a previously uninhabited area (assisted dispersal) will establish viable populations. Although we expected population sizes to increase following dung supplementation, there was no significant effect on beetle population sizes on eight small islands when compared to eight control islands. However, introducing 827 individuals of the common species *Paragymnopleurus maurus* to two previously uninhabited islands had mixed results. On one island, the newly founded population persisted beyond 51 days but rapidly declined on the other. Follow-up investigations suggested that invasive, predatory yellow crazy ants (*Anoplolepis gracilipes*) may have prevented population establishment on the island where this failed. Assisted dispersal, and colonisation, may provide mechanisms to combat some effects of fragmentation and climate change if isolation is the primary cause of the population decline, but success depends on extensive prior suitability assessment. Although suggestive, our results should be interpreted with caution because of experimental limitations.

KEY WORDS. — assisted dispersal, biodiversity, conservation, fragmentation, land-bridge islands, land use management

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INTRODUCTION

The synergistic effects of anthropogenic ecosystem alterations, including habitat fragmentation and climate change, are resulting in the loss of species at an unprecedented rate (Millennium Ecosystem Assessment, 2005; Brook et al., 2008). Habitat protection is the most urgent task faced by conservation biologists, but the increasing pace of environmental change dictates more proactive approaches (Hobbs & Cramer, 2008). One proposed conservation tool is assisted colonisation, defined by Ricciardi & Simberloff (2009a) as "translocation of a species to favourable habitat beyond their native range to protect them from human-induced threats". While this encapsulates the practice of moving species outside their distribution range, we note that the concept should be expanded to include "assisted dispersal" (Vitt et al., 2009), that is, introducing species to suitable but unoccupied habitat fragments within their distribution range.

Assisted colonisation is not a new practice. Success has been achieved in moving threatened species to New Zealand's offshore islands (Saunders & Norton, 2001) and in the assisted colonisation of UK butterflies (Carroll et al., 2009; Willis et al., 2009). The practice has, however, stimulated considerable debate in recent years (McLachlan et al., 2007; Ricciardi & Simberloff, 2009a; Schlaepfer et al., 2009; Minteer & Collins, 2010), the main contention being the potential negative impacts of introduced species if they become invasive outside their native range (Ricciardi & Simberloff, 2009a, 2009b). Previous cases of species translocation have created myriad unintended consequences, e.g., the cane toad (*Bufo marinus*) introduction to Australia (Crossland et al., 2008). Theoretically, any species moved beyond its native range has the potential to become invasive (Ricciardi & Simberloff, 2009a). The increased attention on assisted colonisation reflects the urgency of an impending biodiversity crisis, where conventional in situ conservation approaches can no longer keep pace with climate change and habitat degradation (McLachlan et al., 2007; Seddon, 2010; Thomas, 2011).

Habitat fragmentation is one of the major causes of local species extinction resulting not only from reduced habitat area, but also from increased isolation (Fahrig, 2003; Bennett & Saunders, 2010). Dispersal limitation has been shown, even for volant taxa (Moore et al., 2008), to play a role in community structuring between fragments (Zalewski & Ulrich, 2006). Assisted dispersal, in the form of short distance jump re-colonisation, has been proposed to compensate for isolation and helps to maintain a species' metapopulation dynamics in fragmented habitats (Armstrong & Seddon, 2008; Vitt et al., 2009), while minimising the risk of target species becoming invasive (Price, 2010; Thomas, 2011). Assisted dispersal experiments can provide important insights into the effectiveness and pitfalls of larger scale assisted colonisation, in a more manageable context.

Food limitation in habitat fragments is potentially another important factor causing population decline in biological communities given their isolated nature (Zanette et al., 2000). There have been a considerable number of food supplementation experiments under field conditions on terrestrial vertebrates (Boutin, 1990), and collectively these suggested that food addition did not prevent major declines in fluctuating populations. However, there has been a lack of well-replicated food supplementation experiments in tropical environments (Boutin, 1990), and a general lack of studies that target invertebrates.

Here, we report the first study on food supplementation and assisted dispersal of dung beetles (Coleoptera: Scarabaeidae: Scarabaeinae) on the land-bridge islands of Lake Kenyir, Malaysia. We test the effectiveness of food supplementation in augmenting dung beetle abundance, and the feasibility of assisted dispersal by translocating a common species to previously unoccupied islands, where we quantified persistence of these populations.

MATERIAL AND METHODS

Study site and subjects. — The study was conducted at Lake Kenyir (5°00'N, 102°48'E; 145 m a.s.l.), Malaysia, a reservoir with 340+ land-bridge islands formed in 1986 by the construction of a hydroelectric dam. The forests on all the islands as well as the surrounding mainland were similarly selectively logged and disturbed prior to the flooding, but the lowland dipterocarp forest structure remains relatively intact. We focused our study on dung beetles as they have unique roles in nutrient recycling and other important ecosystem functions (Nichols et al., 2008), while being sensitive to forest modifications (Nichols et al., 2007; New, 2010).

Dung supplementation experiment. — We selected 16 islands smaller than 5 ha (Fig. 1) with species richness and community compositions that are influenced by a small island effect (SIE) (Qie et al., 2011). Hence, environmental factors other than island size (such as food availability) are expected to play major roles in community structure and survival. Asian elephant (*Elephus maximus*) and Malayan tapir (*Tapirus indicus*) were observed to visit these islands and dung beetles were found within fresh elephant dung pads (L. Qie, pers. obs.), however, the availability of natural dung sources was difficult to assess due to the opportunistic nature of large mammal visits. Experimental dung supplementation provides an unbiased means to test whether dung beetle communities on these islands are limited by food availability. Cattle dung, a readily harvested dung supply, has been successfully used in dung removal experiments at this site before (Kudavidanage et al., 2012). Between 16 Jun.2008 and 12 Apr.2009, 4–7 repeated dung beetle surveys were conducted prior to supplementation to assess baseline diversity and abundance.

During each survey, between 3–5 pitfall traps (200 ml plastic cups buried in the ground) were set up on each island, dependant on island area and logistical capability. Approximately 15–20 g human dung was suspended above each trap, in plastic mesh, with a rain cover above. Each trap was covered by an inverted funnel to prevent beetles from escaping. Traps were not filled with any solution, to prevent mortality, and small draining holes were made in the bottom of the cup with a piece of tissue paper placed in the cup to drain or absorb excess rain water, also providing cover for the captured dung beetles captured. Traps were checked after 48 h, and dung beetles were identified, counted, and released at the same location.

Our previous study revealed minimal spatial autocorrelation in community structure (Qie et al., 2011), although we paired islands with close neighbours where possible. For relatively isolated islands, those with similar community compositions were paired (Qie et al., 2011). We randomly assigned islands to be in the treatment or control groups. Between 12 Apr.2009 and 1 Sep.2009, we placed 10 kg of freeze-sterilised cattle dung in 0.5–1 kg piles onto each of the eight treatment islands every 10–15 days. Supplementation in this manner was conducted to mimic island visitation by a large herbivore, presumed to be the staple food supply of local dung beetle populations (Hanski, 1991). All 16 islands were surveyed every month during the period of supplementation to monitor dung beetle communities over time. All surveys used human dung as bait because this has been shown to attract species attracted to cattle dung and additional species (Doube & Wardhaugh, 1991).

***Assisted dispersal of* Paragymnopleurus maurus.** — *Paragymnopleurus maurus* was the most common dung beetle species in the study area (Qie et al., 2011), but was not found on two relatively isolated islands, named Island 22 (I22; 0.9 ha) and I24 (0.5 ha; Fig. 1), which were included in the dung supplementation study. Between 14–15 May 2010, 534 live individuals of *P. maurus* were collected with human dung baited pitfall traps in the mainland forest (Fig. 1) and marked with Sharpie® waterproof silver ink markers before being released onto I22. Beetles were stored in a cage for no more than 6 h before release. Beetles were released at 10–15 different locations on each island along trails and between them to minimise aggregation. Between 18–20 May 2010, 293 individuals were collected and released onto I24 in a similar manner. We allowed approximately 24 h after release before conducting the first round of post-translocation surveys on both islands (termed Day 1). The second and third rounds of post-translocation surveys were conducted on Day 25 and 51 respectively. For each post-translocation survey, 15 human dung baited live pitfall traps were set up on each island. We used a high trap density to maximise detection probability. To minimise the mortality of dung beetles captured, traps

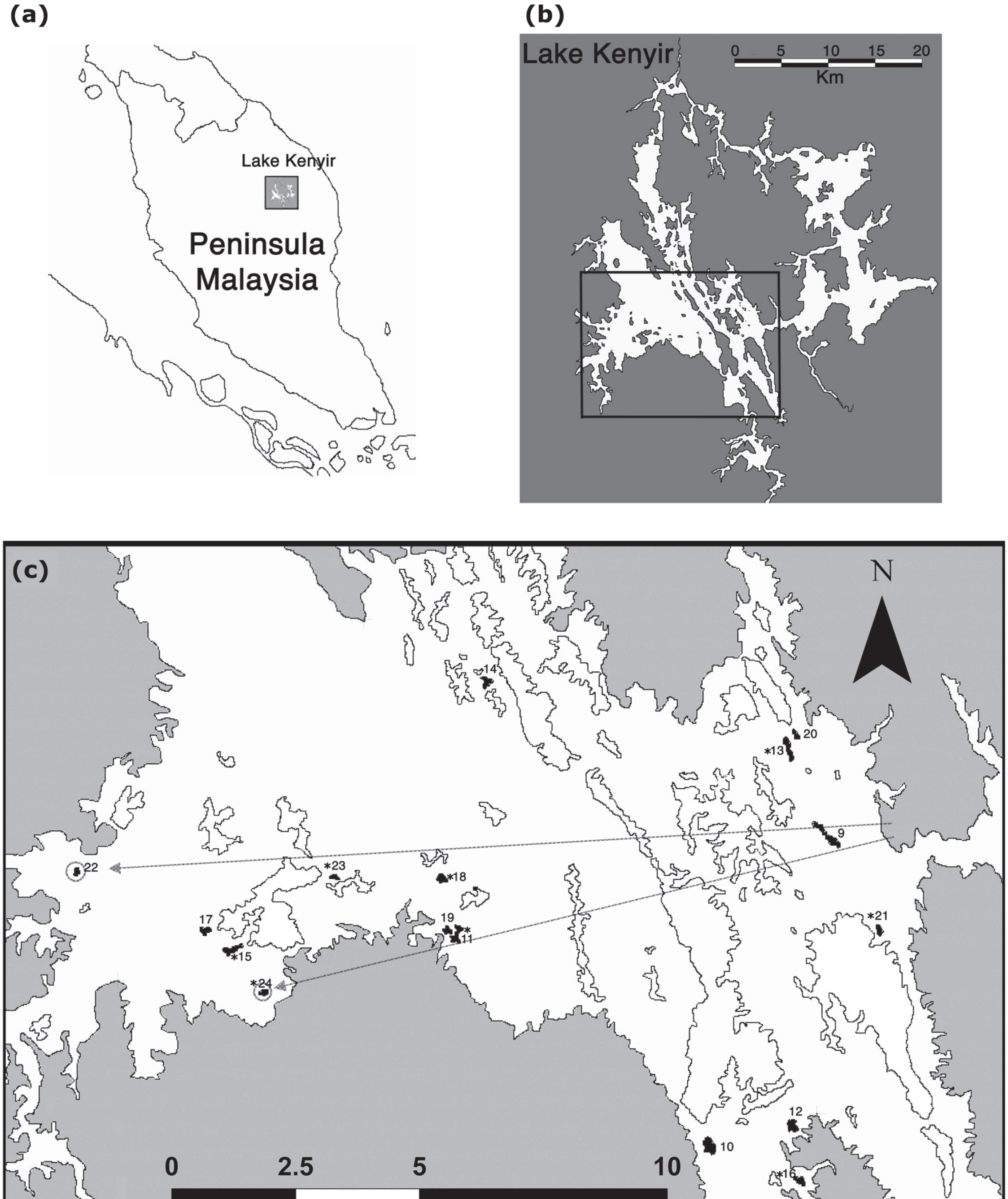

Fig. 1. Map of Lake Kenyir indicating its location within Peninsular Malaysia (a & b). 16 islands used for the supplementation experiment are highlighted in black (c). Islands selected for supplementation treatment are further denoted by an asterisk (*). I22 and I24 (circled) were also recipient islands for the *Paragymnopleurus maurus* translocation experiment, indicated by the arrows.

were left open for only 24 h with captured individuals being released after identification.

***Sampling of the invasive ant* Anoplolepis gracilipes.** — During our assisted dispersal experiment, the impact of the invasive yellow crazy ant (*Anoplolepis gracilipes*) on dung beetle persistence was noted. To take into consideration *A. gracilipes* abundance as a covariate to our assisted dispersal outcome, we compared the species density of ground-dwelling ants on I22, I24, along with three other islands (0.8, 45.8, and 146.1 ha) and a mainland site with an objective to determine the status of the invasive species *A. gracilipes.* Two locations 50 m apart were chosen at each site where the leaf litter on the forest floor was cleared. At each location, we placed two baits of tuna (from canned tuna flakes in water, drained of excess fluid before use) and two cotton wool balls saturated with 70% sucrose solution on the forest floor, at the four corners of a 15 × 15 cm square. All baits were approximately 2 cm^3, and baits of the same type were placed diagonally across from each other. All baiting locations were monitored for 1 h at 15-min intervals by the same observer. The maximum abundance (worker recruitment) of each ant species occurring at the baits was recorded separately for each bait type. For abundant ant species, the number of worker ants per species was estimated to the nearest 50. Voucher specimens of each species were collected for identification.

Statistical analyses. — All statistical analyses were conducted in R Version 2.10.1 (R Development Core Team, 2009). We first tested for temporal autocorrelation within time series data using an autocorrelation function, and compared the correlations with the 95% confidence intervals calculated from uncorrelated series. We found no evidence of significant temporal autocorrelation in dung beetle abundance on any of the 16 islands. To analyse the effect of dung supplementation on dung beetle abundance, we employed Generalised Linear Mixed Models (GLMMs). Because the dung beetle communities on the small islands were depauperate with extremely low population density and high spatial variability (Qie et al., 2011), there were a large number of zero's as well as over-dispersion in the count data. We employed zero-inflated GLMMs with negative binomial error distribution to account for these issues in the data (Zuur et al., 2009), implemented in the glmmADMB package (Skaug et al., 2011). The response variable was the mean number of individuals per trap on each island during each sampling period. The predictor variables in the maximum model were *time*, measured in days since start of the experiment, *supplementation*, and the interaction between *time* and *supplementation*. *Island* was fitted as a random intercept to account for the number of dung beetles over time on the same islands. If dung supplementation had a positive effect on dung beetle abundance, it would result in a significant interaction effect between *time* and *supplementation*. This was tested by comparing two models using the likelihood ratio test (LRT) (Burnham & Anderson, 2002; Zuur et al., 2009): (a) *time* + *supplementation*, and (b) *time* + *supplementation* + *time* × *supplementation*, where *time* × *supplementation* denotes the interaction term of interest.

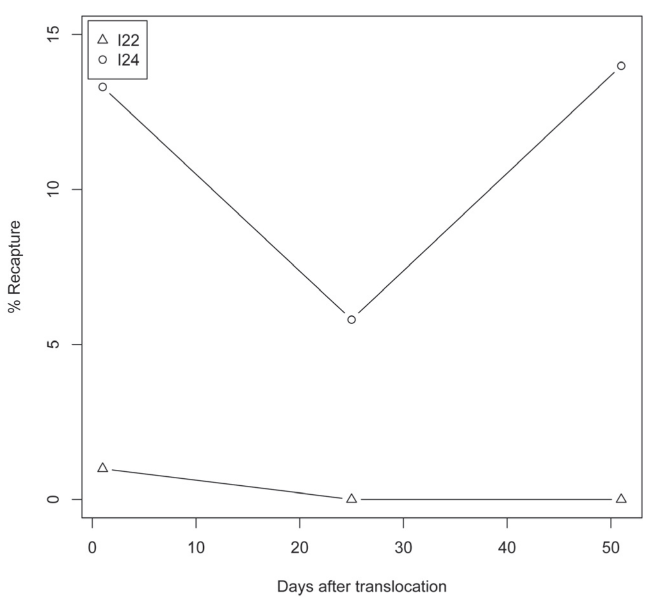

Fig. 2. Percentage recapture of *Paragymnopleurus maurus* following translocation to I22 and I24.

RESULTS

We tested the effect of supplementation over time by comparing zero-inflated GLMM models with and without the *supplementation* × *time* interaction and found little support for the effect of supplementation on dung beetle abundance (likelihood ratio χ^2 = 2.86, d.f. = 1, *P* = 0.09).

We recaptured five marked individuals of *P. maurus* (0.9% of 534 individuals) on Day 1 after translocation to I22. All five individuals were found dead with the ant species *A. gracilipes* present in and around the traps. No *P. maurus* were captured on I22 on Day 25 and 51 (Fig. 2). On I24, however, 39 individuals (13.3% of 293 individuals) were recaptured on Day 1. This number dropped to 17 (5.8%) on Day 25 and returned to 41 (14.0%) on Day 51 (Fig. 2). As no new marked individuals could have entered the population this rise is likely due to differences in detection probability. All recaptured individuals on I24 were alive, and were released.

Anoplolepis gracilipes was not found during the assessment on the mainland nor on the two larger islands (45.8 and 146.1 ha), but was found on small islands. On I22 (where dung beetles did not establish), *A. gracilipes* was the only species of ground-dwelling ant found, and was in considerably higher density than other islands (maximum worker recruitment on I22 was 500 workers/hour, compared to 220 workers/hour on I24 and 255 workers/hour on another small island). *Anoplolepis gracilipes* was observed attacking newly released beetles and foraging on the forest floor in all parts of the island. On I24 however, *A. gracilipes* was apparently not as abundant as other ant species (38.6% of ants at baits were *A. gracilipes*). The foraging activities of *A. gracilipes* were less conspicuous during the translocation experiment on I24 than on I22.

DISCUSSION

Our dung supplementation experiment does not support the hypothesis that supplementing dung resources will increase dung beetle population sizes over a 6-month period. The normal development time of a dung beetle from egg to adult is 30–50 days with no diapause between generations in the tropics (Halffter & Matthews, 1966). Thus, any increase in breeding success, immigration, or reduction in adult mortality due to supplementation effects should have been detectable.

The translocated *P. maurus* population on I24 remained relatively stable during the 51 days we monitored it after release. Although the monitoring period was not sufficient to conclude establishment, it partially supports a dispersal limitation hypothesis. The rapid decline of the population translocated to I22 is correlated with the hyper-abundance of aggressive *A. gracilipes* ants. The contrasting outcomes on I22 and I24 strongly suggest that environmental factors in the recipient habitat, such as predators, are critical for the survival of translocated dung beetles. Overall, assisted dispersal of dung beetles at Lake Kenyir may be feasible if recipient islands are free of invasive predatory species.

Our study sheds light on the potential use of assisted dispersal for facilitating metapopulation dynamics in biological communities suffering from habitat fragmentation. By identifying proximal populations with naturally impaired connectivity and by moving individuals between fragments, we can enhance the effective metapopulation size and gene pool, thus improving resilience to local extinction. Furthermore, if we identify habitat fragments where local extinction has already taken place due to lack of immigration, we may attempt to restore the population using assisted dispersal. Before such steps are taken, however, it is important to identify the processes causing population decline in the first place. We note that assisted dispersal may be useful only if isolation is the primary cause of the population decline, while the habitat remains suitable for the species.

Dung beetles are an indispensable insect group with important ecosystem functions (Nichols et al., 2008; New, 2010) and we suggest that it may be possible to functionally rehabilitate forest fragments. Admittedly this study is non-representative at a large scale due to the limitation of time and sample size. Nonetheless, we propose that similar experiments should be conducted on other functionally important groups such as pollinators and seed dispersers. In sum, our study demonstrates that colonisation of degraded areas by artificially translocated populations is possible, but comprehensive habitat evaluation may be needed prior to animal release to ensure success.

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