Contents lists available at ScienceDirect

# **Biological Conservation**

journal homepage: www.elsevier.com/locate/biocon

## Nest site restoration increases the breeding density of blue-tailed bee-eaters

Yi-Ping Wang<sup>a</sup>, Lynn Siefferman<sup>b</sup>, Yuan-Jyun Wang<sup>c</sup>, Tzung-Su Ding<sup>c</sup>, Chyi-Rong Chiou<sup>c</sup>, Bao-Sen Shieh<sup>d</sup>, Fu-Shung Hsu<sup>e,\*</sup>, Hsiao-Wei Yuan<sup>c,\*</sup>

<sup>a</sup> Chiayi Forest District Office, Council of Agriculture, Forestry Bureau, Executive Yuan. No.1, Linsen W. Rd., East District, Chiayi City 600, Taiwan

<sup>b</sup> Department of Biology, Appalachian State University, 572 Rivers St., Boone, NC 28608, USA

<sup>c</sup> School of Forestry and Resource Conservation, National Taiwan University, No.1, Sec. 4, Roosevelt Road, Taipei 106, Taiwan

<sup>d</sup> Department of Biomedical Science and Environmental Biology, Kaohsiung Medical University. 100 Shi-chuan 1st Road, Kaohsiung, Taiwan

<sup>e</sup> Department of Biological Resources, National Chiayi University, 300 University Road, Chiayi, Taiwan

#### ARTICLE INFO

Article history: Received 17 July 2008 Received in revised form 11 March 2009 Accepted 15 March 2009 Available online 21 April 2009

Keywords: Burrow-nesting bird Habitat restoration Kinmen Island Merops philippinus Nest site availability

## ABSTRACT

For birds that excavate their own nest burrows, the availability of suitable nest sites and substrates may influence the number and density of breeding birds. However, few studies of burrow-nesting birds have experimentally manipulated nest site or substrate availability. The blue-tailed bee-eater (*Merops philippinus*) is a colony breeding, summer migrant that excavates nest burrows in sandy banks on Kinmen Island, 5 km east of mainland China. To test whether substrate availability influenced the density or reproductive success of breeding pairs of bee-eaters, we removed all vegetation and old nest holes on treated slopes and left control slopes unmanipulated in 2003 and 2004. Plant cover on control slopes was 37.7% (11.9–67.7%). Slope gradient, soil penetration resistance and vegetation height in front of slopes did not differ between treated and control slopes in either year. Combining data from both years, the density of active nests was significantly higher (3.1-fold) on treated and control slopes did not differ beformance of bee-eaters nesting on treated and control slopes did not differ between the performance of bee-eaters nesting on treated and control slopes did not differ between the performance of bee-eaters nesting on treated and control slopes did not differ between the performance of bee-eaters nesting on treated and control slopes did not differ between the performance of bee-eaters nesting on treated and control slopes did not differ between the performance of bee-eaters nesting on treated and control slopes did not differ between the number of breeding blue-tailed bee-eaters. This technique could be used to support and manage populations of this species and other burrow-nestling species with similar habitat requirements.

© 2009 Elsevier Ltd. All rights reserved.

## 1. Introduction

In birds, breeding success depends, in part, on environmental resources, including habitat for nesting and for foraging, food availability, and microclimate (White et al., 1978; Cody, 1981; Steele, 1993; reviewed in Jones, 2001). Additionally, the number and distribution of predators and competitors can affect nest site selection (Cody, 1981; Norment, 1993; reviewed in Jones, 2001). These ecological factors can influence individual performance, the density and overall output of a breeding population, and the community structure (Steele, 1993; Newton, 1994; Pöysä and Pöysä, 2002).

Nest site and substrate availability are some of the most important determinants of the size and distribution of breeding populations, particularly for birds that nest in tree cavities or on cliffs (Newton, 1994). For many cavity-nesting species, the major ecological determinant of suitable breeding habitat is hardness of trees (Schepps et al., 1999) which can be influenced by fungal breakdown (reviewed in Bednarz et al., 2004). Experimental manipulation of nest site availability of cavity-nesting species (e.g. nest boxes) influences both the number and density of breeding pairs (Copeyon et al., 1991; reviewed in Newton, 1994; Pöysä and Pöysä, 2002; Taylor, 2003), demonstrating that suitable nesting habitat is a limiting resource.

Many species that excavate burrows in soil often nest colonially and the availability of suitable nest sites influences the density of breeding birds. Some ecological correlates of nest site suitability for burrowing birds include particle size or composition of soil, penetrability of soil, and vegetation cover near the nest sites. In general, many burrow nesters appear to prefer sandy to clay loam soils (White et al., 1978; Kossenko and Fry, 1998; Boland, 2004; Yuan et al., 2006a). For example, particle size of soil influences the distribution of breeding European bee-eaters (*Merops apiaster*; Heneberg and Šimeček, 2004), Eurasian kingfishers (*Alcedo atthis*; Heneberg, 2004), and sand martins (*Riparia riparia*; Heneberg, 2001; Heneberg and Šimeček, 2004), however, species differ in the type of soil they prefer and their tolerance to variability in soil composition. Moreover, soil penetrability influences nesting sites





<sup>\*</sup> Corresponding authors. Tel.: +886 5 2717828 (F.-S. Hsu), tel.: +886 2 33664634; fax: +886 2 23654520 (H.-W. Yuan).

*E-mail addresses*: b87605409@ntu.edu.tw (Y.-P. Wang), sieffermanlm@appstate.edu (L. Siefferman), r91625049@ntu.edu.tw (Y.-J. Wang), ding@ntu.edu.tw (T.-S. Ding), esclove@ntu.edu.tw (C.-R. Chiou), bsshieh@kmu.edu.tw (B.-S. Shieh), richbear@mail.ncyu.edu.tw (F.-S. Hsu), hwyuan@ntu.edu.tw (H.-W. Yuan).

<sup>0006-3207/\$ -</sup> see front matter  $\odot$  2009 Elsevier Ltd. All rights reserved. doi:10.1016/j.biocon.2009.03.013

of European bee-eaters, Eurasian kingfishers, sand martins (Heneberg, 2008), and blue-tailed bee-eaters (M. philippinus; Yuan et al., 2006b); birds appear to avoid banks composed of too compact or too lose soils. Thus, for many burrowing species, breeding appears to be limited by the availability of sandy cliffs that are soft enough to be excavated, but strong enough to avoid collapse. Sandy soils should also allow faster and easier excavation of nest cavities, and better drainage (Brooks and Davis, 1987). Moreover, sandy soils also exhibit high porosity, and may allow burrows better ventilation and appropriate levels of O<sub>2</sub> and CO<sub>2</sub> (White et al., 1978). Finally, vegetation on slopes can be another important determinant of nesting site; white-fronted bee-eaters (M. bullockoides) and blue-tailed bee-eaters prefer slopes with the least vegetation near burrows (White et al., 1978; Kossenko and Fry, 1998; Boland, 2004; Yuan et al., 2006a). Slopes with vegetation may be avoided as roots could impede successful excavation of the nest tunnel (Brooks and Davis, 1987) or because predators are more difficult to detect (Norment, 1993; Yuan et al., 2006a).

The blue-tailed bee-eater is a migratory species that ranges from New Guinea north to Southeast Asia and China and west to India and Pakistan (Fry and Fry, 1992). Blue-tailed bee-eaters nest throughout southern Asia. Like other bee-eater species, they excavate nest burrows in sparsely vegetated, sandy soils including the banks of rivers and ponds, piles of sand, and natural and artificial cliffs (White et al., 1978; Emlen, 1990; Kossenko and Fry, 1998; Fry, 2001; Burt, 2002; Boland, 2004; Yuan et al., 2006a). This species arrives on the Kinmen Island breeding grounds in March and April and breeds from late May to early August. The three main soil types of Kinmen Island are clay loam (20%), sandy clay loam (<2%) and sandy loam (78%) (Kuo and Chen, 2002). However, no bee-eater colonies have been found in clay loam and most of the colonies (89%) are found in sandy loam (74% of all individuals) (Yuan et al., 2006b). Because of the increased rate of tourism and infrastructure development on Kinmen Island in the past few years, researchers have become concerned that the availability of nesting habitat for bee-eaters is in decline (Wang and Yuan 2005). Although colonies of blue-tailed bee-eaters sometimes return to the same nesting area in subsequent years, they rarely return to sites that have become heavily vegetated or saturated with old burrow entrances (Yuan et al., 2006a).

Despite the extensive literature on cavity-nesting species, few studies have experimentally manipulated nest site or substrate availability for species of wild birds that excavate their own nest burrows (Newton, 1994). To our knowledge, the only test employed artificial nesting tubes and boxes for carmine bee-eaters (M. nubicus) propagated in captivity (Elston et al., 2007). The purpose of our study was to assess the effect of nest slope restoration of previously-used, sandy loam soil slopes on the density of breeding pairs and breeding performance of blue-tailed bee-eaters. We manipulated nesting substrates in an attempt to increase nest site availability on Kinmen Island. We removed vegetation and previously-used nesting burrows on treatment slopes, but did not alter vegetation or nesting substrate on control slopes. Finally, we assessed the effectiveness of this treatment as a potential management tool for conserving blue-tailed bee-eaters and other burrow-nesting species.

## 2. Methods

## 2.1. Study area

Kinmen Island (24°27′N, 118°24–28′E), is located in the Taiwan Strait less than 5 km east of China. Kinmen has a subtropical, oceanic monsoon climate (mean winter temperature = 12.7 °C, mean summer temperature = 28.2 °C). Precipitation is not evenly

distributed throughout the year and winter is dry. The primary soil type is sand and laterite clay (Kuo and Chen, 2002).

We conducted the study at two study sites, Youth Farm (YF) and Tianpu (TP), where blue-tailed bee-eater nests have been monitored since 2002. Both sites are in eastern Kinmen where the slopes consist of sandy soils (Yuan et al., 2006a). TP is close to the sea and YF is approximately 2 km inland. Bee-eaters dig burrows into the banks of ponds, and piles of sand. Most slopes were separated by level terrain. However, there were two pairs of slopes in which the two slopes were on the same bank, but separated by shrubby vegetation. Each slope was at least 30 m from every other slope. The boundary of each slope was defined by the distinct edge of the slope and the surrounding vegetation, which included Casuarina equisetfolia, Lantana camara, Sageretia thea and Rubus parvifolius. The area of each slope was measured according to this boundary. The average height of each slope was 1.5 m (range: 0.7-3 m) and the width ranged from 1.5 to 22.8 m. Slope area ranged from 1.2 to 115.2 m<sup>2</sup>. Most vegetation on slopes was herbaceous and included Ageratina adenophora, Bidens chinensis, and Richardia scabra.

### 2.2. Treatment

During February and March of 2003 and 2004, before the beeeaters arrived, we randomly assigned previously-used nest slopes at TP and YF to vegetation removal or control treatments. To remove all vegetation, we scraped soil, to a depth of 50–100 cm, from the face of each slope with a shovel or, where necessary, with a bulldozer. This process also removed all old nest entrances and part of the old nest tunnels. We filled nest tunnel remnants with sand so that the entire slope had a uniform, freshly scraped appearance. For control slopes we left the vegetation and old nests untouched. In 2003, there were five scraped and five control slopes. In 2004, we had six scraped and four control slopes (Table 1).

Some slopes were used in both years, however, no slope was used as treatment in 2003 and then control in 2004. Therefore we consider all slopes to be independent data both within and between years. YF-4 and YF-5 were randomly assigned as control slopes in both 2003 and 2004, and YF-3 was randomly assigned as control slope in 2003 but a treated slope in 2004. The area of YF-3 increased from 22.6 to 64.0 m<sup>2</sup>, because we removed vegetation from the original YF-3 slope and the adjacent, heavily vegetated slopes at each end of YF-3 in 2004. To assess the effective time span of habitat restoration on treated slopes from the previous year, we monitored the breeding outcome of slopes YF-1, YF-2, TP-1 and TP-3 which were treatment slopes in 2003 (we removed vegetation and old nest holes), but were untouched in 2004.

#### 2.3. Monitoring breeding success

To monitor nests, we used a video camera  $(4 \times 4 \text{ cm})$  mounted on a 2 m pole and inserted the pole into each nest to view contents. We viewed entire burrows by manipulating pulleys that allowed us to move the camera lens. When burrows were near completion, we inspected them every 2 days. The number of eggs, nestlings, and fledged young were recorded. Nests were considered active when they contained at least one egg. Nestlings present at the time of the final visit to the nest (20 days post hatch or later) were considered fledged. We calculated hatching rate as the number of nestlings divided by the number of eggs, and fledging rate as the number of fledglings divided by the number of hatchlings. This research was conducted in accordance with a banding permit from the Kinmen County government.

Nesting slope area and the n	umber of active blue	-tailed bee-eater nests in tr	reated and control slopes on	Kinmen Island, 2003–	2004.		
Year	Treated			Control			
	Site	Area (m <sup>2</sup> )	No. of nests	Site	Area (m <sup>2</sup> )	No. of n	
2003	YF-1	23.4	11	YF-3	22.6	0	
	YF-2	8.0	1	YF-4	7.4	0	
	TP-1	8.2	6	YF-5	6.1	2	
	TP-2	4.0	2	TP-4	13.1	1	
	TP-3	2.8	3	TP-5	10.7	1	
Density (mean ± SD)	$0.54 \pm 0.33 \text{ nests/m}^2$			$0.10 \pm 0.13 \text{ nests/m}^2$			
2004	YF-3	64.0	32	YF-4	7.4	0	
	YF-6	19.2	2	YF-5	6.1	1	
	YF-7	8.0	1	YF-8	1.2	1	
	TP-6	115.2	32	TP-9	8.9	0	
	TP-7	76.5	20				
	TP-8	45.5	72				
Density (mean ± SD)	0.47 ± 0.56 r	nests/m <sup>2</sup>		0.25 ± 0.40 m	ests/m <sup>2</sup>		

#### 2.4. Nest site characteristics

At the beginning of the breeding season, we took digital photographs of each slope, and then calculated vegetation cover of each slope using ADOBE PHOTOSHOP (version 7.0). Using the "Magic Wand Tool", we transferred the vegetation portions on the slope in the photos to black color. We then calculated the percentage of vegetation cover by using the histogram (color level) of this photo which measured the percentage of pixels of black color in the photo. After the offspring had fledged, we measured slope area and the density of active nests (August 4–6, 2003 and August 9–12, 2004). At this time, we also measured the physical characteristics of the slopes including gradient, penetration resistance, and vegetation structure (height) directly in front of the slope. We measured the gradient using an inclinometer. We used different penetrometers and different sampling methods to measure penetration resistance in 2003 and 2004. In 2003, we divided each nest slope into upper, middle and lower sections and measured the slope gradient and penetration resistance at three randomly chosen locations in each section. The penetrometer was pressed 5 cm into the bank, perpendicular to the slope. In 2004, we measured slope gradient and penetration resistance at 10, randomly selected locations on each nesting slope. Penetration resistance was measured on the surface of the bank. For each year, we averaged measurements to calculate slope gradient and penetration resistance for each nest slope.

The height of vegetation in front of a slope could impair the ability of bee-eaters to detect predators (Norment, 1993; Yuan et al., 2006a), which might influence nest site selection. Therefore, we measured vegetation height in front of each slope. We established three, 50 m transects on the ground, directly in front of each nest slope. One transect started at the middle of the slope and ran perpendicular to it. The other two transects began at the same point but angled away at 60° to the left and right of the perpendicular transect. We measured vegetation height at 5 m intervals on each transect. We calculated the average vegetation height and SD for each slope. Five treated slopes and four control slopes were facing ponds (the three ponds were about  $30 \text{ m} \times 15 \text{ m}$ ,  $15 \text{ m} \times 5 \text{ m}$ , and  $20 \text{ m} \times 20 \text{ m}$ ). When a measurement point fell in the pond, vegetation height was recorded as 0 cm.

## 2.5. Statistical analyses

In all analyses, each slope was considered an independent data point. Because we used different soil penetration methods in 2003 and 2004, we analysed the data separately by year.

We used two-way ANOVA to compare the slope gradient, penetration resistance and vegetation height in front of slopes of treated and control slopes to know whether year or treat influenced nest site characteristics. We used Mann-Whitney U tests to determine the effect of treatment on breeding performance, including clutch size, hatching and fledging rate. A General Linear Model (GLM) was used to further examine the effect of treatment while considering the effects of slope area and year difference on active nest density. Data are means ± SD unless stated otherwise; the significance level was p < 0.05. Statistical calculations were done using SPSS Version 10.0 and SAS Version 9.1.

ests

#### 3. Results

Bee-eaters bred in all treated slopes (five in 2003 and six in 2004), but in only five of nine control slopes. Site YF-3 was control slope with no nests  $(0 \text{ nest/m}^2)$  in 2003, but was a treatment slope in 2004 with 32 nests  $(0.5 \text{ nest/m}^2)$  showing a noticeable positive effect. Sites YF-1, TP-1 and TP-3 were scraped in 2003 and had 11, 6, and 3 nests, respectively. In 2004, these three sites were untouched and none had active nests. Only YF-2, which was scraped in 2003 and untouched in 2004, had the same number of nests- one active nest in each year. Nest density on treated slopes was 5.2 and 1.9-fold higher than control slopes in 2003 and 2004, respectively. Combining the data for both years, nest density on scraped slopes  $(0.52 \pm 0.46 \text{ nest/m}^2)$  was 3.1-fold greater compared to control slopes  $(0.17 \pm 0.27 \text{ nest/m}^2; \text{ Table 1}).$ 

Before treatment, the plant cover of the treated slopes  $(40.2 \pm 19.8\%, \text{ median} = 35.6\%, n = 11)$  were very similar to the control slopes (37.7  $\pm$  19.1%, median = 32.5%, *n* = 9). Immediately after the treatment, the plant cover of the treated slopes was 0%. Within control slopes, bee-eaters bred on the slopes with plant cover between 11.9% and 32.5%. We found no significant differences in slope gradient, penetration resistance or vegetation height in front of each slope between 2003 and 2004 (two-way ANOVA, p = 0.317, 0.576, 0.354, respectively), and treated and control slopes (two-way ANOVA, p = 0.987, 0.855, 0.261, respectively, Table 2). Pairs breeding in treatment versus control slopes did not significantly differ in clutch size, hatching and fledging rate between treated and control slopes (Mann-Whitney U test, p > 0.05; Table 3).

Although we found significant effects of vegetation removal, slope area, and year on active nest density (GLM type three test, df = 1, p < 0.001 for all variables), vegetation removal explained most of the variation in active nest density (Table 4). The propensity for birds to build nests in treated slopes was 14.3 times higher than in control slopes. For every one m<sup>2</sup> increase in slope area, there was 1.01 times higher tendency for birds to build nests. The propensity for birds to build nests was 3.09 times higher in 2004 than in 2003.

#### Table 2

Physical characteristics of treated and control nesting slopes of blue-tailed bee-eaters on Kinmen Island in 2003 and 2004. "Vegetation height" refers to vegetation in front of, not on, the slope. See text for details. Data were analysed with two-way ANOVA (*n* = number of slopes).

Variable	Year	Treate	Treated			Control			Р
		n	Mean	SD	n	Mean	SD		
Gradient (°)	2003 2004	5 6	74.7 66.8	3.4 11.2	5 4	71.7 69.7	10.8 17.5	0.00	0.987
Penetration resistance (kg/m <sup>2</sup> )	2003	5	4.8 4.0 <sup>a</sup>	3.8	5	4.9 4.5ª	2.3		
	2004	6	7.3 8.3ª	12.2	4	5.9 7.4 <sup>a</sup>	4.7	0.03	0.855
Vegetation height (cm)	2003 2004	5 6	75.5 149.5	35.9 121.7	5 4	162.4 172.1	121.9 112.8	1.36	0.261

<sup>a</sup> Median of penetration resistance.

#### Table 3

Breeding performance of blue-tailed bee-eaters nesting in treated and control slopes on Kinmen Island, 2003–2004. Data were analysed with Mann–Whitney *U* tests (*n* = number of nests).

Variable	Year	Treatmen	Treatment			Control			Р
		n	Mean	SD	n	Mean	SD		
Clutch size	2003 2004	23 159	4.52 4.55	1.31 1.33	4	5.50 5.50	1.29 0.71	28.5 77.5	0.215 0.198
Hatching rate (%)	2003	23	64	47	4	90	12	41.0	0.705
Fledging rate (%)	2004	159 16	75	34 26	2	92 91	12 11	124.0 18.0	0.571
riciging face (,s)	2004	136	84	25	2	100	0	81.0	0.268

#### Table 4

Relative risk on nest building explained by treatment, slope area, and yearly difference using GLM.

Explanatory variable	df	Chi-square	р	Estimate (reference)	Relative risk	Wald 95% confidence limits
Treatment	1	38.96	<0.0001	2.662 (control)	14.331	1.8264/3.4984
Area (m <sup>2</sup> )	1	21.55	< 0.0001	0.010 (scale)	1.010	0.0058/0.0142
Year	1	22.23	<0.0001	1.129 (2003)	3.093	0.6598/1.5984

## 4. Discussion

The number and density of blue-tailed bee-eaters nesting in sandy slopes scraped free of vegetation was greater than that of control slopes. This treatment increased the number of birds nesting in these slopes. Overall, the number of bee-eaters fledged from scraped slopes was greater than from control slopes because more birds nested in scraped slopes. Treating previously-used nest slopes increased the likelihood they would be used again the following breeding season. By increasing available nesting space, we increased the number of breeding pairs. When the most limiting resource is removed, a breeding population will experience its greatest increase in population size (Newton, 1994). However, because we did not measure the population size of blue-tailed bee-eaters on Kinmen Island before or after our study, we do not know whether the increased number of fledglings emerging from treated slopes increased the overall population of blue-tailed bee-eaters on the island.

Because we only conducted this experiment on sandy loam soil, this restoration method might not be applicable to slopes with sandy clay loam soil. We have two reasons to believe that this practice is applicable primarily to sandy loam slopes. First, at Kinmen, slopes with sandy clay loam have much less vegetation growing on them compared to sandy loam slopes (Yuan, pers. obs.). Second, we have observed that some bee-eaters used old nest holes on sandy clay loam slopes left from previous years (Yuan, unpub. data).

Our results indicate that vegetation cover is an important factor in nest site selection by blue-tailed bee-eaters and suggest that removal of vegetation can be an effective management tool for restoring bee-eater nesting habitat. Because our experimental design simultaneously scraped slopes free of vegetation and removed old nest burrows, we can not separate the effects of the removal of vegetation from the removal of old nest burrows on breeding density. Reusing old nest sites can lead to nest site instability (e.g. Shields and Crook, 1987) or greater likelihood of adults and nestlings being exposed to parasites or disease (e.g. Barclay, 1988). Thus, bee-eaters, like other cavity nesters may have to choose between reusing successful nesting locations and risking increased parasite load (Stanback and Dervan, 2001).

Our results demonstrating that vegetation removal increases the nest density are consistent with previous correlational research on blue-tailed bee-eaters and other Coraciiform species. Yuan et al. (2006a) noted that blue-tailed bee-eaters on Kinmen Island place burrow entrances away from vegetation, suggesting that the amount of vegetation on slopes may influence nest site availability and the placement of individual bee-eater burrows. European beeeaters, rainbow bee-eaters (M. ornatus), and white-fronted beeeaters also tend to nest on portions of the nesting slope with the least vegetation (White et al., 1978; Kossenko and Fry, 1998; Boland, 2004). Belted kingfishers (Ceryle alcyon), another Coraciiformes species, excavates nest burrows on bare river banks, far from rocks and vegetation, purportedly to avoid obstructions to digging (Brooks and Davis, 1987). The Eurasian kingfisher is one exception; this species prefers to nest in areas with greater vegetation (Straka and Grim, 2007).

We also found that the larger the area of the nest slope scraped free of vegetation exhibited a greater density of active nests. This was especially true in 2004. These findings are consistent with observations of rainbow bee-eaters (Boland, 2004), belted kingfishers (Shields and Kelly, 1997) and choughs (*Pyrrhocorax pyrrhocorax*; Blanco et al., 1998). Our study, however, is the first experimental test of the relationship between nest area and the number of nests of a self-excavating, burrow-nesting bird species.

We found no evidence, however, that the experiment influenced the individual reproductive success of bee-eaters. Pairs nesting in scraped slopes did not fledge more or fewer offspring compared to pairs nesting in control slopes. In other colonial species, including the European bee-eater (Hoi et al., 2002), breeding success is often negatively related to colony size and this is thought to be due to increased competition of resources, numbers of predators, and infection by parasites or disease (e.g. Hunt et al., 1986; Stokes and Boersma, 2000; Pöysä and Pöysä, 2002). Other studies, however, have found either no relationship (e.g. Davis and Brown, 1999; Václav and Hoi, 2002) or a positive relationships between colony size and reproductive success (e.g. Barbose et al., 1997). Predation by snakes is reason we could have expected a positive relationship between colony size or treatment and individual reproductive success. Predation by snakes is a threat to successful reproduction in this species. Reduced vegetation at the colony likely facilitates detection of predators and increases the effectiveness of mobbing behavior.

Our habitat restoration experiment was successful in attracting breeding pairs of bee-eaters. Our experimental area, however, was relatively small. It is possible that birds that were displaced from other slopes, which were destroyed by human activity, moved onto our treated slopes. Currently, the blue-tailed bee-eater is not listed as endangered or threatened in Taiwan. However, Kinmen Island is the largest known breeding population of this species in the southeast China area, Rapid development on Kinmen Island and in many other areas of southeast China is likely decreasing nesting habitat for the blue-tailed bee-eater (Wang and Yuan, 2005). We found that suitable nesting habitat can be maintained by removing vegetation and old nest holes from previously-used nesting slopes. On some of the scraped slopes in this study, the vegetation re-grew quickly. In August, toward the end of the breeding season, the vegetation cover on scraped slopes was up to 30% of the pre-treatment level. Sites YF-1, YF-2, TP-1 and TP-3 were treatment slopes in 2003 with active bee-eater nests, but in 2004 all were left untouched and only YF-2 had one nest. Therefore, treated slopes need to be scraped each year. However, this work could be completed in only 2 days. Thus, we suggest this technique can be used to support and manage populations of this species and other species with similar habitat requirements.

#### Acknowledgements

We thank Mr. Wu for allowing us access to his land, and Dr. Alan Warneke for English editing. We thank Kinmen National Park and the Council of Agriculture, Taiwan for financial support, and we thank students in the School of Forestry and Resource Conservation, National Taiwan University, for field assistance. Finally we thank the Consulting Center for Statistics and Bioinformatics of National Taiwan University.

#### References

- Barbose, A., Moreno, J., Poot, J., Merino, S., 1997. Breeding group size, nest position and breeding success in the chinstrap penguin. Polar Biology 18, 410–414.
- Barclay, R.M.R., 1988. Variation in the costs, benefits, and frequency of nest reuse by barn swallows (*Hirundo rustica*). Auk 105, 53–60.

- Bednarz, J.C., Ripper, D., Radley, P.M., 2004. Emerging concepts and research directions in the study of cavity-nesting birds: keystone ecological processes. Condor 106, 1–4.
- Blanco, G., Fargallo, J.A., Cuevas, J.A., Tella, J.L., 1998. Effects of nest-site availability and distribution on density-dependent clutch size and laying dater in the chough *Pyrrhocorax pyrrhocorax*. Ibis 140, 252–256.
- Boland, C.R.J., 2004. Introduced cane toads *Bufo marinus* are active nest predators and competitors of rainbow bee-eaters *Merops ornatus*: observational and experimental evidence. Biological Conservation 120, 53–62.
- Brooks, R.P., Davis, W.J., 1987. Habitat selection by breeding belted Kingfishers *Ceryle alcyon*. American Midland Naturalist 117, 63–70.
- Burt, D.B., 2002. Social and breeding biology of bee-eaters in Thailand. Wilson Bulletin 114, 275–279.
- Cody, M.L., 1981. Habitat selection in birds: the roles of vegetation structure, competition, and productivity. BioScience 31, 107–113.
- Copeyon, C.K., Walters, J.R., Carter III, J.H., 1991. Induction of red-cockaded woodpecker group formation by artificial cavity construction. Journal of Wildlife Management 55, 549–556.
- Davis, J.A., Brown, C.R., 1999. Costs of coloniality and the effect of colony size on reproductive success in purple martins. Condor 101, 735–737.
- Emlen, S.T., 1990. White-fronted bee-eaters: helping in a colonially nesting species. In: Stacey, P.B., Koening, W.D. (Eds.), Cooperative Breeding in Birds: Long-term Studies of Ecology and Behavior. Cambridge University Press, New York, pp. 256–489.
- Elston, J.J., Carney, J., Quinones, G., Sky, C., Plasse, C., Bettinger, T., 2007. Use of novel nest boxes by carmine bee-eaters (*Merops nubicus*) in captivity. Zoo Biology 26, 27–39.
- Fry, C.H., Fry, K., 1992. Madagascar Bee-eater and Blue-tailed Bee-eater. In: Kingfishers, Bee-eaters and Rollers: A Handbook. Princeton University Press, New Jersey. pp. 273–75.
- Fry, C.H., 2001. Meropidae (Bee-eaters). In: Hoyo, J.D., Elliot, A., Sargatal, J. (Eds.), Handbook of the Birds of the World, vol. 6. Lynx Edicions, Barcelona, pp. 286– 325.
- Heneberg, P., 2001. Size of sand grains as a significant favor affecting the nesting of bank swallows (*Riparia riparia*). Biologia 56, 205–210.
- Heneberg, P., 2004. Soil particle composition of Eurasisan kingfisher's (Alcedo atthis) nest sites. Acta Zoologica Academiae Scientiarum Hungaricae 50, 185– 194.
- Heneberg, P., 2008. Soil penetrability as a key factor affecting the nesting of burrowing birds. Ecological Research. doi: 10.1007/s11284-008-0520-2.
- Heneberg, P., Šimeček, K., 2004. Nesting of European bee-eaters (*Merops apiaster*) in central Europe depends on the soil characteristics of nest sites. Biologia 59, 205–211.
- Hoi, H., Hoi, C., Krištofík, J., Darolová, A., 2002. Reproductive success decreases with colony size in the European bee-eater. Ethology Ecology & Evolution 14, 99– 110.
- Hunt Jr., G.I., Eppley, S.A., Schneider, D.C., 1986. Reproductive performance of seabirds: The importance of population and colony size. Auk 103, 306–317.
- Jones, J., 2001. Habitat selection studies in avian ecology: a critical review. Auk 118, 557–562.
- Kossenko, S.M., Fry, C.H., 1998. Competition and coexistence of the European Beeeater *Merops apiaster* and the Blue-cheeked Bee-eater *Merops persicus* in Asia. Ibis 140, 2–13.
- Kuo, C.M., Chen, Z.S., 2002. Soil analyses and vegetation adaptations in Kinmen National Park. Technical Report. Kinmen National Park, Taiwan.
- Newton, I., 1994. Experiments on the limitation of bird breeding densities: a review. Ibis 136, 397-411.
- Norment, C.J., 1993. Nest-site characteristics and nest predation in Harris' Sparrows and White-crowned Sparrows in the Northwest Territories, Canada. Auk 110, 769–777.
- Pöysä, H., Pöysä, S., 2002. Nest-site limitation and density dependence of reproductive output in the common goldeneye *Bucephala clangula*: implications for the management of cavity-nesting birds. Journal of Applied Ecology 39, 502–510.
- Schepps, J., Lohr, S., Martin, T.E., 1999. Does tree hardness influence nest-site selection by primary cavity nesters? Auk 116, 658–665.
- Shields, W.M., Crook, J.R., 1987. Barn swallow coloniality: a net cost for group breeding in the Adirondacks? Ecology 68, 1373–1386.
- Shields, S.J., Kelly, J.F., 1997. Nest-site selection by belted Kingfishers Ceryle alcyon in Colorado. American Midland Naturalist 137, 401–403.
- Steele, B.B., 1993. Selection of foraging and nesting sites by black-throated blue warblers: their relative influence on habitat choice. Condor 95, 568–579.
- Stanback, M.T., Dervan, A.A., 2001. Within-season nest-site fidelity in eastern bluebirds: disentangling effects of nest success and parasite avoidance. Auk 118, 743–745.
- Straka, O., Grim, T., 2007. Nest site selection in the Kingfisher (*Alcedo athis*). Sylvia 43, 109–122.
- Stokes, D.L., Boersma, D.P., 2000. Nesting density and reproductive success in a colonial seabird, the magellanic penguin. Ecology 81, 2878–2891.
- Taylor, R.V., 2003. Factors influencing expansion of the breeding distribution of Bewick's Wren into riparian forests of the Rio Grande in Central New Mexico. Southwestern Naturalist 48, 371–382.
- Václav, R., Hoi, H., 2002. Importance of colony size and breeding synchrony on behaviour, reproductive success and paternity in house sparrows *Passer domesticus*. Folia Zoologica 51, 35–48.

- Wang, Y.-P., Yuan, H.-W., 2005. Monitoring the changes of nesting sites and breeding population size of blue-tailed bee-eater (*Merops philippinus*) on Kinmen Island. Journal of National Park 15, 31–41.
- White, F.N., Bartholomew, G.A., Kinney, J.L., 1978. Physiological and ecological correlates of tunnel nesting in European bee-eater, *Merops-Apiaster*. Physiological Zoology 51, 140–154.
- Yuan, H.W., Burt, D.B., Wang, L.P., Chang, W.L., Wang, M.K., Ding, T.S., 2006a. Colony site choice of blue-tailed bee-eaters: influences of soil, vegetation and water quality. Journal of Natural History 40, 485–493.
  Yuan, H.-W., Wang, M.-K., Chang, W.-L., Wang, L.-P., Chen, Y.-M., Chiou, C.-R., 2006b.
- Yuan, H.-W., Wang, M.-K., Chang, W.-L., Wang, L.-P., Chen, Y.-M., Chiou, C.-R., 2006b. Soil composition affects the nesting behavior of blue-tailed bee-eaters *Merops philippinus* on Kinmen Island. Ecological Research 21, 510–512.