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Malaysian populations of 'edible-nest' swiftlets (Aves: Apodidae) have declined markedly over the last century. These declines are attributed principally to deleterious effects of nest-harvesting on swiftlet reproduction. The aim of this study was to quantify the impact of nest-harvesting on the reproductive success of the black-nest swiftlet *Aerodramus maximus* at Gomantong Caves (Sabah), and predict whether sufficient nestlings are allowed to fledge to maintain the population. Experimental nests were harvested at both the beginning and the end of one breeding season. The manipulation had a significant effect; although all harvested nests were subsequently rebuilt they fledged 17% less nestlings than unharvested controls during the breeding season. Also, the time period between eggs and nestlings appearing in nests, and the time period which nestlings spent in the nest, were both significantly longer at experimental nests than at unharvested controls. This implies that nest-harvesting increases the energetic stress of breeding adult swiftlets. Theoretically, however, enough nestlings do fledge from harvested nests at Gomantong Caves to maintain the population of black-nest swiftlets.

Key words: Apodidae, edible-nest, harvesting, reproduction

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Certain species of cave swiftlet (Aves: Apodidae) which occur in Malaysia produce the 'edible birds' nests' prized in Chinese medicine (Daly 1888, Medway 1969). These are the white-nest swiftlet *Aerodramus fuciphagus* and the black-nest swiftlet *Aerodramus maximus* whose nests, which occur in clusters on cave walls and ceilings, are formed from hardened salival secretions (Marshall & Folley 1956, Medway 1962). Swiftlet nests are reputed to enhance vigour and recuperate sufferers of chronic diseases such as TB, dysentery and malaria (Mainka & Mills 1995), forming the basis of a multi-billion dollar industry (Lau & Melville 1994).

During this century marked declines in the Malaysian populations of edible-nest swiftlets have occurred (Francis 1987a, Good 1993). This is a common pattern across the Southeast Asian range of these birds (Er, Vardon, Tanton, Tidemann & Webb 1995), and is attributed principally to deleterious effects of nest-harvesting on swiftlet reproduction (Kang, Hails & Sigurdsson 1991, Tompkins 1997). Concern over these effects has led to a recent proposal to list the swiftlet under Appendix II of CITES (Convention on the Trade in Endangered Species of Wild Flora and Fauna) (TRAFFIC 1995).

The primary site for the birds' nest industry in Malaysia is Gomantong Caves (5°31'N, 118°04'E), a cave complex in the state of Sabah, home to approximately 1.5 million swiftlets. Here, in an attempt to maintain swiftlet population sizes, the harvesting of nests is limited by the Sabah Wildlife Department; only two harvests are allowed during the birds' breeding season (February - September), with a few nests also being taken outside the breeding season (Francis 1987a). The first harvest occurs during April; nests are taken immediately after being built and before more than 10% contain eggs. The second harvest occurs during August after nestlings have fledged from 90% of nests. This regime is designed to allow the birds to breed successfully once each year - one complete cycle of nest-building, egg-laying and incubation, and nestling growth to fledging takes approximately four months (Francis 1987a).

The goal of this study was to quantify the impact of nest-harvesting on the reproductive success of the black-nest swiftlet at Gomantong Caves, and to determine whether or not the current level of control is theoretically sufficient to maintain its population. Previous work has shown that nest-harvesting at the beginning of the breeding season reduces the reproductive success of both white- and black-nest swiftlets through an influence on egg-laying (Kang et al. 1991). Furthermore, an impact of nest-harvesting on the survival rate of white-nest swiftlet nestlings has also been documented (Phach & Voisin 1998). No study, however, has as yet quantified the impact which nest-harvesting has on the total number of nestlings fledged by black-nest swiftlets during each breeding season.

Methods

The reproductive success of black-nest swiftlets at two nest clusters within the same region of the caves was observed during March - August 1995. Both clusters contained approximately 200 nests each, at similar densities. The first cluster was harvested under the current regime (on 7 April and 13 August in 1995) whilst the second cluster was left unharvested for the entire breeding season. Adult swiftlets are nest-site specific, rebuilding nests on the same exact sites both within and between seasons (Kang et al. 1991, Phach & Voisin 1998).

Black-nest swiftlets at Gomantong Caves nest high (≥15 m) on the cave walls and ceiling. Also, ropes and ladders cannot be left in place whilst studying the birds at the caves since the edible-nests are inevitably stolen (regardless of their contents). Thus, it was only possible to observe the breeding activity in nests using 10 × 40 binoculars. Fifty nests chosen at random from each cluster were monitored over the breeding season, their positions being noted in sketch maps. Nests were first observed on 24 March and subsequently monitored every two weeks thereafter. Nest contents were noted as either egg (the black-nest swiftlet has a single egg clutch), or nestling. If a nestling was observed in a nest on at least three consecutive visits it was assumed to have fledged when it disappeared from the nest. This is a realistic measure, since at least 93% of four-week-old black-nest swiftlet nestlings at Gomantong Caves fledge successfully (D. Tompkins, unpubl. data).

Results

On 7 April, prior to the first harvest, similar numbers of nests in both clusters contained eggs (24% of the harvested nests and 28% of the unharvested controls; $\chi^2 = 0.21$, df = 1, P = 0.65). All of the harvested nests were rebuilt on the exact same sites. The reappear-

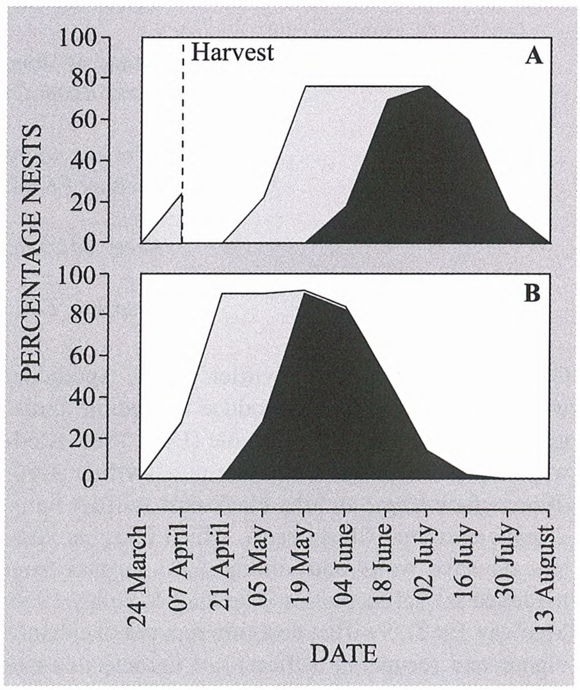

Figure 1. Percentage of nests containing either eggs ( ) or nestlings ( ) over the course of the study for: A) nests harvested on 7 April (N = 50), and B) nests left unharvested (N = 50).

ance of eggs in the harvested nests, however, was delayed by approximately four weeks relative to the unharvested controls (Fig. 1). Furthermore, eggs and nestlings were subsequently observed in only 76% of the harvested nests, compared to 92% of the unharvested controls ($\chi^2 = 4.76$, df = 1, P = 0.03).

The time period between eggs and nestlings appearing in nests was longer at the harvested nests than at the unharvested controls. At all of the 46 active unharvested nests, eggs were only ever observed at two consecutive monitoring visits (at 2-week intervals) before nestlings appeared, whereas at four of the 38 active harvested nests (11%) eggs were observed at three consecutive monitoring visits before nestlings appeared (Fisher's exact P = 0.04).

The time period which nestlings spent in the nest was also longer at the harvested nests than at the unharvested controls ($\chi^2 = 10.94$, df = 2, P = 0.002). At the 46 active unharvested nests, 24% of nestlings were observed at two consecutive monitoring visits before disappearing from the nest, 63% were observed at three consecutive monitoring visits, and 13% were observed at four consecutive monitoring visits. At the 38 active harvested nests, 76% of nestlings were observed at three consecutive monitoring visits before disappearing from the nest, and 24% were observed at four consecutive monitoring visits.

In all nests where eggs were laid (after 7 April for the harvested nests), nestlings were subsequently observed. Furthermore, all nestlings appeared to survive to fledging. However, due to the greater number of inactive nests, the proportion of harvested nests from which nestlings subsequently fledged was significantly lower than the proportion of unharvested nests from which nestlings subsequently fledged (0.76 and 0.92, respectively; $\chi^2 = 4.76$, df = 1, P = 0.03). All nests were empty prior to the second harvest on 13 August (see Fig. 1), and no pair of adults attempted to fledge more than one young over the breeding season.

Discussion

This study shows that nest-harvesting at Gomantong Caves significantly decreases the number of nestlings fledged by black-nest swiftlets each year. Although all nests harvested at the beginning of the breeding season were subsequently rebuilt, three times more harvested than unharvested nests showed no further sign of breeding activity (no egg laid). This resulted in harvested nests fledging 17% less nestlings than unharvested controls.

Previous studies have indicated two ways in which nest-harvesting may depress black-nest swiftlet reproduction. First, by forcing swiftlets to build multiple nests at the beginning of the breeding season, harvesting places an energetic strain on the breeding adults. This strain is greater if, as in this study, eggs are also lost at harvesting. As a consequence, subsequent egg production declines and nestling growth is inhibited (with an associated increase in mortality) due to poorer provisioning (Kang et al. 1991, Phach & Voisin 1998). Second, since harvesting effectively reduces the length of the breeding season, birds at harvested nests cannot have as many attempts each year to breed successfully as birds at unharvested nests. Since brood failure is common in swiftlets (Francis 1987b), harvesting may thus increase the proportion of breeding pairs each year which produce no young (Tompkins 1997).

An energetic cost of nest-harvesting explains the results seen in this study. As well as there being decreased egg production at harvested nests (see above), both the time period between eggs and nestlings appearing in nests and the time period which nestlings spent in the nest were longer at harvested nests than at unharvested controls. Since, in the common swift *Apus apus*, longer incubation periods reflect less faithful incubation (Lack & Lack 1951, Lack 1956), and longer nestling periods reflect lower rates of provisioning by adults (Martins 1997), these results are most likely due to breeding adult swiftlets at harvested nests being placed under greater energetic stress.

Nest-harvesting effectively reduces the black-nest swiftlet breeding season at Gomantong Caves from eight months (February - September) to four months (mid-April - mid-August). However, according to my study, four months per year is sufficient time for black-nest swiftlet reproduction at Gomantong Caves since no brood failure appeared to occur, no pair of adults attempted to fledge more than one young (even at unharvested nests), and all nestlings at both harvested and unharvested nests had fledged prior to mid-August (see Fig. 1).

The results presented show that, although the limited nest-harvesting allowed at Gomantong Caves still significantly affects the reproductive success of black-nest swiftlets, one young does fledge from over two thirds of the harvested nests each year. Since, according to the calculations of Francis

(1987a), only 40% of swiftlet nests must fledge at least one young per year if a population is to be maintained, the control measures imposed by the Sabah Wildlife Department thus appear to be sufficient to maintain the population of black-nest swiftlets at Gomantong Caves.

Although the main impact of nest harvesting is clearly documented in this study, two additional factors also need to be taken into account. First, in addition to less black-nest swiftlet nestlings fledging from harvested nests, those that do fledge may be at a fitness disadvantage due to being of poorer quality and fledging at a later date (e.g. Magrath 1991, Verboven & Visser 1998). This appears to be the case for other swiftlet species (Phach & Voisin 1998), and would represent an additional impact of nest harvesting. Second, the decrease in reproductive investment by adult swiftlets at harvested nests may actually increase the adult survival rate, countering some of the observed impact on the black-nest swiftlet population (e.g. Wernham & Bryant 1998).

Further research is also required to assess the impact of nest-harvesting on the other species of edible-nest swiftlet at Gomantong Caves, the white-nest swiftlet. Reducing the time available each breeding season for successful reproduction is more likely to affect this species since the white-nest swiftlet normally has multiple breeding attempts per season (Phach & Voisin 1998). Thus, a lower-impact nest-harvesting regime may be required to maintain its population at Gomantong Caves.

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