

Habitat refuges as alternatives to predator control for the conservation of endangered Mauritian birds

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Abstract Mammalian predators introduced to the island of Mauritius threaten the survival of several species of endemic birds. Long-term lethal predator control is achieving limited success against some predators but cannot be used against crab-eating macaques (*Macaca fascicularis*). Macaques are major nest predators on Mauritius, as confirmed by camera traps. Previous research suggested that plantations of non-invasive Japanese red cedar (*Cryptomeria japonica*) provide a refuge from nest predation. Using surrogate nests we show that nest predation by macaques is significantly lower in cedar than in native forest, including cedar plantations not currently occupied by rare native birds but which might be used for reintroductions. We present a simple habitat model showing how the careful planting and management of this non-invasive exotic, in conjunction with existing conservation efforts, could provide a sustainable solution to high predation rates by macaques.

Keywords nest predation; introduced predators; island ecosystems; predator control; refuges; invasive species; spatially explicit model.

INTRODUCTION

It is well known that animals that evolved in isolation on oceanic islands are hugely vulnerable to introduced, non-native, predators (King 1980; Atkinson 1985; Johnson and Stattersfield 1990; Moors *et al.* 1992). This is particularly evident on Mauritius, where predation by introduced mammals, in synergy with habitat destruction, has led to the extinction of at least nine endemic species of birds and reptiles (Cheke 1987). Predation of eggs, chicks and incubating adult birds (nest predation) is thought to be the greatest threat, posed chiefly by black rats (*Rattus rattus*) and crab-eating macaques (Safford and Jones 1998). In addition, feral cats (*Felis catus*) and lesser Indian mongooses (*Herpestes javanicus*) prey on adult birds (Roy 2001; C. G. Jones, pers. comm.). Consequently, black rats, feral cats and mongooses have for the last decade been controlled in areas where threatened endemic birds nest (Swinnerton *et al.* 1993). However, it is not clear whether control effort increases in direct proportion with the impact of a predatory species, and thus whether it is effective (cf. Côté and Sutherland 1997). Furthermore, eradication of most predators from Mauritius is not currently feasible due to its size, steep mountainous terrain and limited resources. Lethal control of macaques is anyway considered unacceptable, due to the socio-religious sensitivity of killing primates on Mauritius.

Predator control is now concentrated in conservation management areas (CMAs): fenced forest plots (1-23 ha; 2 m high galvanised steel fence) from which non-native rusa deer (*Cervus timorensis*) and wild boar (*Sus scrofa*) have been excluded and invasive non-native arborescent flora removed, permitting the regeneration of native forest trees (Strahm 1993). The latter are likely to provide more food for native birds (Safford and Jones 1998). On-going reintroductions of two endangered bird species, the pink pigeon (*Columba mayeri*) and echo parakeet (*Psittacula*

eques) are centred around CMAs, where released birds are also provided with supplementary food. Despite all these measures nest predation continues to limit growth of native bird populations (C. G. Jones, pers. comm).

There is little quantified information on the impacts of different nest predators on Mauritius. Impacts of introduced rats have been well documented in temperate forests in New Zealand (Innes 1990; Moors *et al.* 1992), but little is known about them in insular tropical forests like those on Mauritius where rat density may be very high. Macaques are also numerous on Mauritius, with an estimated population of 40,000 (Bertram and Ginsberg 1994). They have long been suspected as important nest predators (Grant 1801), a suspicion reinforced by more recent authors (McKelvey 1976; Jones 1987; Safford 1991), although some have questioned their importance (Sussman and Tattersall 1986). Thus it is not clear which predators have most impact on native birds.

In a recent study of nesting success of the critically endangered Mauritius fody (*Foudia rubra*), black rats and macaques were suspected as the main predators from indirect evidence such as nest damage and eggshell fragments, although their relative impact remains unresolved (Safford 1997a). Importantly, Safford's study revealed that nesting success in introduced, but non-invasive, Japanese red cedar was significantly higher (46%) than in other trees (6%). Furthermore, the last remaining wild pink pigeons nested only in a cedar plantation ("Pigeon Wood"), one of the four mainland sites used for their reintroduction. This raises a paradoxical opportunity for conservation management: if introduced cedar provides a refuge, should it be more widely planted to reduce predation pressure even though it is non-native? Cedar plantations could provide a sustainable, strategic, alternative to lethal predator control and a means of reducing the impact of macaques, which cannot be controlled.

In this paper we report on the value of automatic cameras and surrogate bird nests in identifying nest predators on Mauritius. We examine the *relative* impacts of different predators in potential refuge (cedar plantation) and other habitat types. We seek to extend Safford's (1997a) study by identifying the mechanism (e.g. relative predator density, habitat structure) that leads to some habitats experiencing lower rates of predation. We then develop a simple spatial model to suggest where new habitat refuges (cedar plantations) could be established to maximise benefits to endangered birds, without adversely affecting native vegetation. Our findings show that natural refuges from predation merit much more attention from conservationists attempting to combat the vast global impact of introduced predators.

METHODS

Study areas

We conducted fieldwork in the Black River Gorges National Park, Mauritius (Fig. 1). The National Park, established in 1995, covers 6574 ha and encompasses the largest tract of native forest on Mauritius (Page and D'Argent 1997). Work was concentrated in four areas: (i) Pigeon Wood and other nearby cedar plantations; (ii) Brise Fer; (iii) Bel Ombre; (iv) Combo (Fig. 1). The vegetation in the park ranges from heath and scrub to super humid upland cloud forest. Pigeon Wood (altitude 650-700 m) is in the latter zone and is the largest (6 ha) plantation of cedar that is surrounded by native forest. Brise Fer (300-650 m) is lower montane wet forest, dominated by *Diospyros* and contains a number of exceptionally rare endemic trees (Strahm 1993). Bel Ombre and Combo (200-400 m) are also lower montane wet forest. Bel Ombre is dominated by native trees such as *Labourdonnaisia glauca* (Page and D'Argent 1997), but has extensive plantations of exotic

pine (*Pinus* spp.). Combo consists of lower-canopied native forest, heavily invaded by the exotic *Syzygium jambos*, and plantations of exotics including cedar. Brise Fer and Bel Ombre contain several CMAs.

Surrogate nests

We used disused nests of the introduced village weaver *Ploceus cucullatus*, secured with wire in trees with sufficient vegetation to conceal them. We fixed nests at 1.5-4.0m above ground (mean 2.23, SE 0.05), and baited each with a single domestic quail (*Coturnix coturnix*) egg and a similar sized model egg made of clay. Clay eggs registered the imprints of predators' teeth and so enabled the identification of predators that removed quail eggs without leaving other field signs. They also enable identification of smaller nest predators such as house mice (*Mus domesticus*) that are unable to open quail eggs (Roper 1992; Haskell 1995; Bayne *et al.* 1997) which average 30 x 25 mm (S. P. Carter, pers. obs.), but are probably capable of opening the slightly smaller eggs of some Mauritian passerines (e.g. Mauritius fody 18.4-19.9 x 13.0-14.6 mm) (Cheke and Jones 1987).

We minimised human scent left on nests and eggs by wearing rubber gloves during nest collection and preparation, and by rubbing our hands with mud and leaf litter during nest placement and checking (Reitsma *et al.* 1990). We prepared the clay eggs several weeks before use, thereby reducing any odour they might give off. Nests were classified as predated when one or both eggs were missing, broken, or tooth marked. We collected all nests at the end of the trial and opened remaining quail eggs to determine if they were still fresh.

Predator identification

We placed cameras fitted with a remote trigger mechanism modified from Major (1991) around 20 surrogate nests at the Fixon plot, a CMA at Bel Ombre. Photographic evidence thus obtained was used to confirm predator identity inferred from field signs (Fig. 2). Rats frequently consume eggs in or at nests, leaving characteristic 'boat shaped' eggshell halves with tooth marks around the shell edge (Fig. 3), and relatively large fragments embedded in the nest lining (Moors 1978; Safford 1994). They may also make small holes in the side of domed nests (Frith 1976). Macaques consume eggs whole, scattering a few small shell fragments in the vicinity of the nest (Safford 1994), and often tear domed fody nests apart (Jones 1987; Safford 1994). There are no published descriptions of mongoose nest predation, although they may occasionally climb trees and rob nests (S. Roy, pers. comm.). To take account of this we carried out feeding trials on captive mongooses.

Experimental design

A preliminary experiment conducted in 1997 outside the bird breeding season enabled us to assess how many nests would be needed and how long eggs should be left ex-

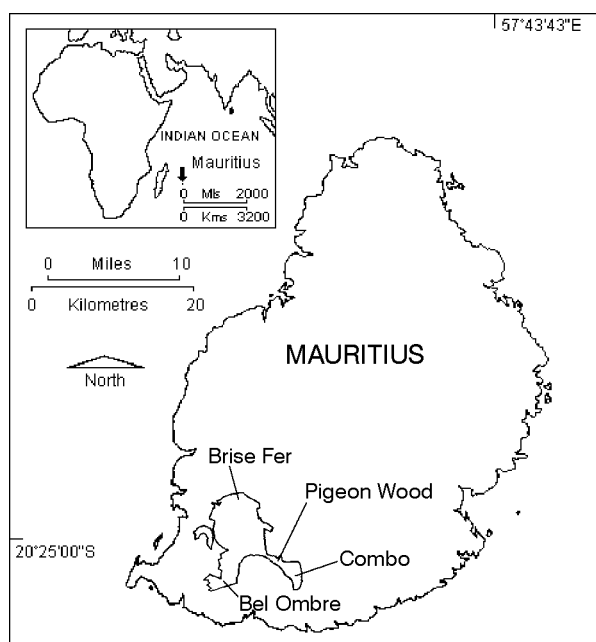


Fig. 1 Mauritius showing Black River Gorges National Park and the location of study areas.

posed in order to reliably measure predation rates. This experiment also provided a useful seasonal comparison of predation rates, although several of the CMAs were subject to varying intensities of rat control at this time. We placed up to 10 nests (mean 9.08, SE 0.53) at 25 m intervals, and at least 50 m from a vegetation type boundary, in three-seven replicate plots of three different vegetation types: (i) cedar; (ii) weeded native forest (CMAs); and (iii) unweeded native forest. Nests were left exposed for nine days and checked at intervals of three days.

We repeated the experiment during the 1998 breeding season (November-February) placing 10 nests in four replicate plots of the three vegetation types. During both experiments we ensured that no nest was visible to us from any of its neighbouring nests, and nest density (9/ha) was well below the recommended maximum for artificial nests (100/ha; Reitsma 1992).



Fig. 2 Photographs of nest predators taken with a nearby remote camera. Upper, crab-eating macaque; Lower, black rat. For trip cameras to function nests were placed in exposed positions and results from these nests were not included in the analysis.

Data analysis

Generalised linear models with binomial errors and logit link (GENSTAT®; Payne *et al.* 1997) were used to compare the proportion of nests predated in different vegetation types during the breeding season (S. P. Carter and P. W. Bright, pers. obs.). Statistical analysis was restricted to data collected during the breeding season at which time rat control was not being carried out in any of the native plots under study and only at low levels of intensity in one of the cedar groves. Separate models were derived for nests predated by rats and macaques. Minimum adequate models (Crawley 1993) were selected by first fitting all explanatory variables and first order interactions, and then testing the significance of each (using a χ^2 -test statistic) by successive deletion.

Modelling the impact of habitat manipulation

A map of vegetation types in the National Park (Page and D'Argent 1997) was digitised into a geographical information system. We followed Page and D'Argent's vegetation classification, viz. grade 1: high quality forest, >70% indigenous vegetation; grade 2: moderate quality forest, 50-70% indigenous vegetation; grade 3: degraded forest, 20-50% indigenous vegetation; grade 4: highly degraded forest, <20% indigenous vegetation; non-native: monospecific or mixed species plantations of non-native trees. We then modelled the number of new fody territories that new cedar plantations could support, subject to the following constraints: (i) new cedar plantations could only replace non-native vegetation; (ii) new planting would only take place within the National Park and within the most recently documented range of the Mauritius fody (Safford 1998). We assumed that cedar plantations would support 100 pairs per km², as in and around Pigeon Wood, and that nesting success (i.e. the percentage of nests fledging at least one chick) was 46% in cedar and 6% in all other vegetation grades (Safford 1997a, 1998).



Fig. 3 Nest contents from a rat-depredated nest. Eggshell fragment shown reveals that the quail egg was bitten along the longitudinal axis highly typical of rodent predation (Moors 1978). Rat incisor marks are clearly visible on the surface of the clay egg.

Mauritius fodies feed in native vegetation and nest in non-native trees only when there is native forest nearby (Safford 1998). Consequently cedar plantations remote from native forest might not be used due to the energetic costs of commuting flights between the two vegetation types, which we estimated as follows. We calculated total daily energy expenditure (DEE) for a passerine with the body weight of a fody (17.5 g; Cheke and Jones 1987), using the equation given by Walsberg (1983). Approximately half of DEE is required for general maintenance and at least 20% is directly expended in finding food (Walsberg 1983). We conservatively assumed that up to 25% of DEE was available to meet the costs of commuting flights during the nestling provisioning period. Flight costs per unit distance (kCal/km) were calculated using the equation for passerines derived by Kendeigh *et al.* (1977). We were thus able to determine the maximum total distance that could be flown by fodies expending 25% of DEE on commuting flights. Mauritius fodies have a relatively low provisioning rate of 2.8 feeds per nest per hour (Safford 1997b) as compared to other passerines of a similar size which make approximately eight feeds per hour (Williams 1987; Gill 1989). Allowing for twelve hours of daylight this amounts to 33.6 return nest visits per bird per day. Dividing total flight distance by the number of nest visits yielded the maximum distance between cedar plantations and native forest over which fodies could commute to forage.

Predation rates are likely to be higher where predators are more abundant, irrespective of potential habitat refuges. Macaque density is estimated to range from 0.33/ha in grade 1-2 forest to 1.3/ha in grade 4 forest and the mean troop home range size is 0.8 km² (Sussman and Tattersall 1986). We therefore incorporated a fourth constraint in our model: new cedar plantations must be >0.5 km from grade 4 forest, this distance being the radius of a macaque troops range in such forest. Black rat density appears to be high throughout the National Park, except where rats are controlled, and was thus not incorporated in the model.

RESULTS

Predator identification

The camera traps confirmed the validity of using previously-documented field signs to distinguish between different predators. In addition, rodent and macaque tooth marks in clay eggs enabled us to unambiguously identify the predatory species involved in 110 out of 122 cases of nest predation. Feeding trials confirmed that mongooses tended to carry eggs away from nests and broke eggshells into several large fragments and distinctive puncture marks from their canine teeth were often visible, however no nests were found to have been predated by mongooses in this study.

Black rats and crab-eating macaques were the only nest predators identified from photographs and field signs. At the end of the preliminary experiment 46 nests (34%) had been predated. Of these rats were responsible for 25 (54%),

macaques for 17 (37%), and four (9%) could not be attributed to either predator. During the breeding season 76 nests (63%) were predated; rats were responsible for 37 (49%), macaques for 31 (41%) and eight (10%) could not be attributed to particular predators.

Predation rate and vegetation type

In a generalised linear model of the proportion of nests predated by rats during the breeding season, vegetation type was not included; predation rate did not differ between vegetation types (Fig. 4A). In a model of macaque predation, vegetation type explained 43% of the deviance; macaque predation was significantly higher in weeded (35%) and unweeded native forest (35%) than in cedar plantations (7.5%; GENSTAT, binomial errors $P < 0.001$).

Outside the breeding season, vegetation type again affected predation by macaques. Predation by macaques was highest in unweeded native vegetation (37%), low in native weeded vegetation (9.2%), and absent from cedar plantations (Fig. 4B). Predation by rats was highest in cedar plantations (42%; similar to the rate during the breeding season) and low in both weeded and unweeded native vegetation (9.2% and 14.8% respectively). Figures 4A-B are not strictly comparable as several of the weeded plots and one

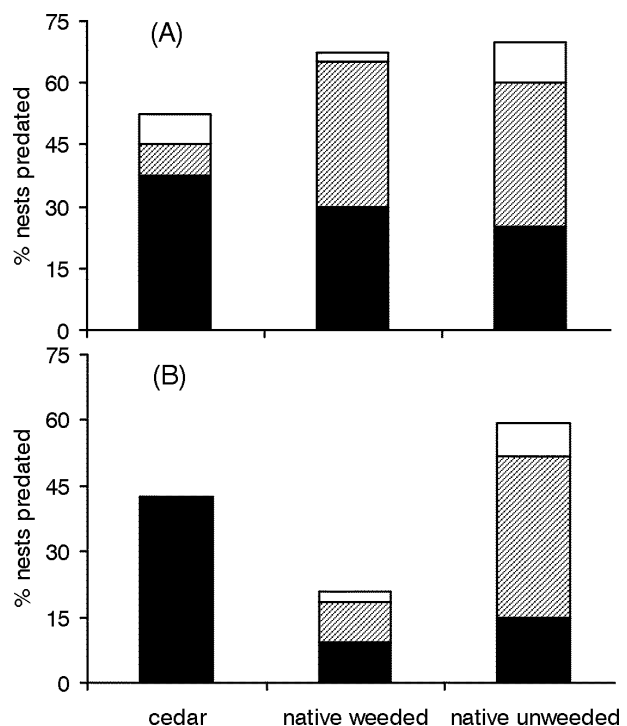


Fig. 4 Levels of predation in different vegetation types and during different seasons (A = breeding season; B = non-breeding season) on Mauritius from data collected using surrogate nests. Predators were black rats (solid bars) or macaques (striped bars) or unconfirmed (open bars). Sample sizes during the breeding season were 40 nests per vegetation type and outside the breeding season: 33 (cedar); 37 (native weeded); 27 (native unweeded).

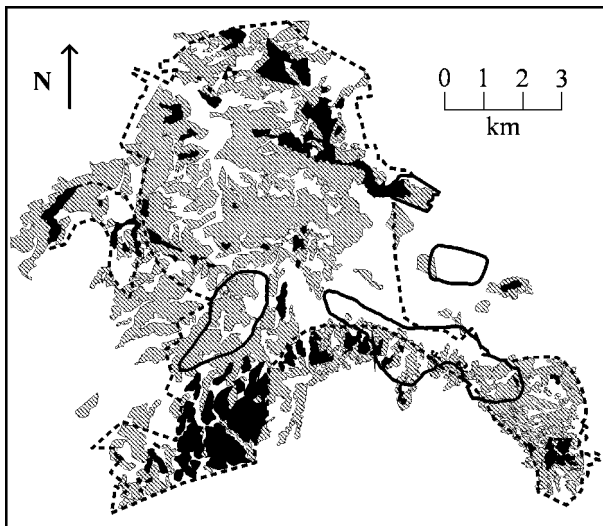


Fig. 5 Black River Gorges National Park (broken lines) showing extent of grade 1 and 2 forest (solid areas) and grade 3 forest (striped; see text for definitions), and last reported range of the Mauritius fody (solid lines; Safford 1998).

of the cedar groves were subject to varying intensities of rat control outside the breeding season; rat predation may have been higher in the absence of this control.

Siting of new cedar plantations

We estimated DEE of fodies to be 73.59 kJ/day and flight costs to be 0.57 kJ/km. Based on our model of 33.6 nestling provisioning flights per bird per day, this suggests a maximum distance of 1.02 km between new habitat refuges and native forest. However, fody territory size is seldom greater than 8 ha (Safford 1997b), therefore territory size is itself a constraint and, assuming a circular territory, new refuges would need to be within 320 m of native forest, this being the diameter of a circular territory 8 ha in area. There is approximately 5500 ha of native (grades 1-

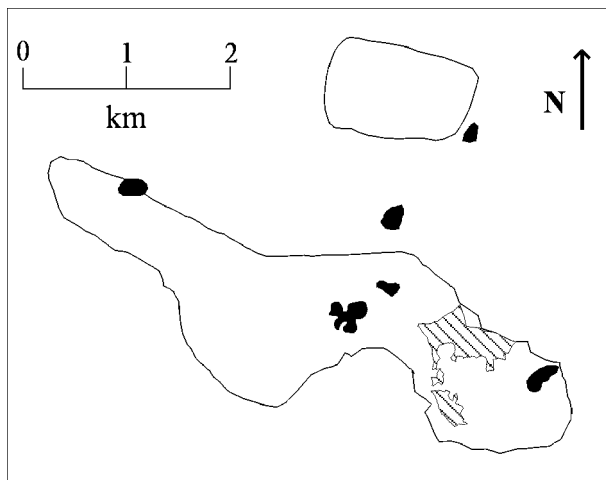


Fig. 6 Existing cedar groves (solid) within the vicinity of the Black River Gorges National Park and proposed areas for new cedar plantations (striped), in relation to part of the last reported range of the Mauritian fody (lines).

3) forest in and around the National Park (Fig. 5), and we calculated that there is 236 ha of exotic plantation (excluding cedar) within the National Park and present fody range. All of this is within 1 km of native forest, but if we assume that fodies cannot increase their territory size from 8 ha (see above) then the total amount of exotic plantation suitable for conversion is 192 ha. By imposing the additional constraint of increased macaque predation risk (i.e. new plantations should not be within 0.5 km of grade 4 forest), there are still 32 ha of exotic pine plantation that could be converted to cedar nest refuges (Fig. 6). The creation of each additional 5 ha of cedar could theoretically support five pairs of fodies, each of which may produce up to three broods per year (Safford 1997b). Based on Safford's (1997a) figures for fody breeding success, this could result in six new successful nests per year or one new successful fody nest for every hectare of cedar planted.

DISCUSSION

Surrogate nests and the measurement of nest predation

Deploying surrogate nests to estimate predation rates has three major advantages over observing predation rates on natural nests of rare wild birds: sample sizes can be much greater; nests can be positioned in habitats where relict populations may no longer nest, or perhaps have never nested; and no disturbance to nesting birds is caused. Surrogate nests provide a way to collect data of at least quasi-experimental rigour, which will often be of much more use in developing conservation management solutions than a few observations on individuals in a relict population. Such techniques have been criticised for lack of realism, but have usually involved the deployment of artificial nests which may not replicate real ones (e.g. Martin 1987; Picman 1988; Langen *et al.* 1991; Yahner 1991). In a recent review Major and Kendal (1996) showed that only 15 of 67 studies used nests constructed by the species under study or a similar species. In our study we used domed nests made by the village weaver, which closely mimicked those of the Mauritius fody (for nest descriptions see Crook 1963; Safford 1997c). We also very carefully concealed nests in live vegetation. There is thus every reason to expect that predators located and responded to our nests as they would to those of the Mauritius fody. The eggs we used were not intended to mimic those of the fody, since they would not have been visible to predators within the dark, domed weaver nests. With birds that construct cup nests, replicating the colour of eggs might obviously be important.

Despite the structural similarity between surrogate and fody nests, the former's paler colour may have made them more conspicuous to vision-oriented nest predators such as macaques. However, nest concealment was carefully quantified and analyses detected no association between macaque predation and nest visibility (S. P. Carter and P. W. Bright, pers. obs.). Furthermore, nest visibility did not differ between study plots or vegetation types. Olfactory

cues might have rendered surrogate nests, constructed of unfamiliar grasses not necessarily found locally, containing quail and clay eggs and perhaps carrying human scent, more readily detectable by predators like rats with high olfactory sensitivity. Human visits to nests are known to result in heightened predation (Major 1990; Whelan *et al.* 1994). However, we visited nests infrequently and took considerable precautions to reduce human scent being left on nests or eggs. Furthermore, only two out of 134 non-predated quail eggs were putrid when cracked open at the end of experiments. Clay eggs have a distinct odour but Bayne and Hobson (1999) found that this neither attracted nor repelled mammal nest predators.

The lack of activity or odour from adult and fledgling birds might have made surrogate nests less conspicuous than real ones, balancing their possible heightened detectability from other cues. However whilst differences in detectability may exist between real and surrogate bird nests, there is no reason to expect the behaviour of predators foraging on surrogate nests to differ between different plots or vegetation types. Consequently, surrogate nests should provide a highly-reliable comparative measure of *relative* predation rates (cf. Martin 1987; Roper 1992; Yahner 1996; Penloup *et al.* 1997). They are also the only way to obtain estimates of predation in areas not currently used for nesting, but which might be important refuges or possible sites for future reintroductions.

Are cedar plantations a refuge from nest predators?

On average 7% of surrogate nests were predated per day during the bird breeding season. This is over 20 times higher than reported for a comparable study in Hawaii, where black rats were the only identified predators (0.33% per day; Amarasekare 1993). We found that both black rats and crab-eating macaques were important predators in Mauritius. These predators are abundant in the forests, which support virtually all remaining endemic bird populations (S. P. Carter and P. W. Bright, pers. obs.; D. Hall, pers. comm.). However, predation by macaques in cedar plantations was low, suggesting that cedar does provide a partial refuge from predation. This accords with Safford's (1997a) direct observations of lower (41%) predation of fody nests in cedar trees, compared to other tree species (82%). However it is important to note that we measured relative predation rates that cannot be compared directly to Safford's (1997a) measurements.

Safford and Jones (1998) suggested that predatory mammals may avoid cedar plantations due to lower food availability or because they are repelled by the resinous sap of cedar. The former seems the most likely of these explanations, since macaques were less abundant in cedar plantations (S. P. Carter and P. W. Bright, pers. obs.), yet climb individual cedar trees with apparent impunity (S. P. Carter, pers. obs.). We found no evidence that rats avoided cedar. Safford (1997a) also suggested that lower predation in cedar was the result of nests being more effectively con-

cealed. However, concealment of surrogate nests did not influence predation by either rats or macaques. Lower predation by macaques is most simply explained by their lower abundance in cedar plantations.

Unsurprisingly, patterns of predation differed seasonally (cf. Safford 1997a). During the bird breeding season total predation was highest in unweeded and weeded native forest, and lowest in cedar plantations. Outside the breeding season, total predation was highest in unweeded forest and lowest in weeded forest plots (see below). Significantly, predation by macaques was lower in cedar than native forest both during and outside the breeding season. There is, however, a clear need for more information on the spatio-temporal dynamics of predator populations, which should greatly aid conservation management to reduce their impact on native ecosystems generally.

Predation in weeded native forest

Outside the bird breeding season total predation was much lower in weeded native forest. This might have been due to a behavioural 'fence effect' on the part of predators – the plots being surrounded by 2 m wire fencing – but neither rats nor macaques were physically excluded by the fence. Lower predation by rats at this time was almost certainly due in part to rat control being carried out at half of the weeded native plots. Perhaps as important was the lower cover of fruit-bearing shrub food sources, such as non-native guava (*Psidium* spp.), which had been removed from weeded plots and which fruits mainly outside the breeding season. In particular this may explain why predation by macaques was lower in the weeded plots at this time. As native canopy-forming trees mature in weeded forest plots, fruit-producing understorey shrubs may become less productive of fruits. Thus the restoration and maturation of native forest may at least partially help reduce predation – irrespective of seasonal effects – through reducing forest suitability for predators.

New cedar plantations as refuges from predation

Safford (1997a) showed that cedar plantations provide a refuge from predation for the Mauritius fody and anecdotal evidence suggests they are also a refuge for the pink pigeon. Using manipulative methods we have quantified the importance of different nest predators and have identified the probable mechanism leading to cedar being a refuge as lower macaque abundance in cedar plantations (S. P. Carter and P. W. Bright, pers. obs.). Cedar might thus be planted as a refuge for nesting birds from predation, and our model identified areas where this could be done without impinging on native forest which is under great threat (Lorence and Sussman 1986). The suitable areas are plantations of non-native pine and eucalyptus (*Eucalyptus robusta*) in and around the National Park.

A key requirement of new cedar plantations is that they are surrounded by or close to native forest where fodies

and other native passerines feed. Our spatial model suggested that new cedar plantations would need to be very close (<320 m) to native forest. If plantations are to be away from highly-degraded forest where macaques are likely to be most abundant, there are 32 ha of exotic pine and eucalyptus plantations that could be converted to cedar. Relaxing this constraint, since we showed that cedar provides a refuge even when macaques are abundant, increases the amount of exotic forest available for conversion to 192 ha. Cedar nesting refuges could also be created outside of the present, highly-restricted, fody range, provided they were near to fragments of native forest. These could be used for reintroductions, following the approaches that have proven so successful with the pink pigeon and other endangered endemics (Jones and Swinnerton 1997).

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