



Discovery of a novel predator reveals extreme but highly variable mortality for an endangered migratory bird

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ABSTRACT

Aim Introduced predators are a global driver of species decline, but their impact on highly mobile species is poorly understood. We report the severe impact of a previously undocumented introduced predator on the endangered, migratory swift parrot (*Lathamus discolor*). Sugar gliders (*Petaurus breviceps*), a supposedly benign introduced species, were detected acting as a major opportunistic predator of cavity-nesting birds. We assessed the intensity and geographical extent of sugar glider predation and investigated whether habitat loss exacerbated predation risk to swift parrots.

Location Tasmania, Australia.

Methods We monitored nests of swift parrots for 3 years with motion-activated cameras. We used bioclimatic modelling to predict the potential distribution of introduced sugar gliders across the study area and assessed the predation risk to swift parrots and other threatened birds in the region using nest-survival analysis.

Results Daily survival of nests in areas where sugar gliders occurred was mean 0.97, which equated to a true likelihood of 0.17 for a nest to survive the 60-day nesting period. No nests failed on an offshore island where sugar gliders were shown to be absent. Most cases (83.3%) of glider predation resulted in the death of the adult female parrot. On the Tasmanian mainland, there was a positive relationship between nest survival and increasing mature forest cover at the landscape scale.

Main conclusions Predation risk varied dramatically across the breeding range of swift parrots, depending on the presence of sugar gliders. Offshore islands are an important refuge for swift parrots because sugar gliders are absent. However, islands are vulnerable, and our bioclimatic model shows that they are bioclimatically suitable for sugar gliders. Synergistic interactions between predation and habitat loss combine with low breeding-site philopatry to expose swift parrots to dramatic variation in predation risk depending on nesting location.

Keywords

Endangered parrot, forest, habitat loss, introduced predator, *Lathamus discolor*, migratory bird, *Petaurus breviceps*, sex-biased mortality, sugar glider, tree cavity.

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INTRODUCTION

Migratory birds comprise a large proportion of bird diversity (Rappole, 1995), and their conservation is a major international priority (Martin *et al.*, 2007). Management of migratory birds is complicated by the diversity of threats they encounter over space and time (Faaborg *et al.*, 2010). Anthropogenic environmental change is the principal driver of a new wave of extinctions around the world (Barnosky *et al.*, 2011), and migratory birds may be especially vulnerable because of their specialized life histories and use of multiple habitats (Newton, 2004).

Migratory birds are vulnerable to predators while nesting, but the fitness consequences of predation are especially damaging to small or endangered populations (Serra *et al.*, 2009). The consequences of predation are worst when prey are confined to areas of high predation (e.g. on oceanic islands, Duncan & Blackburn, 2007) or for species strongly philopatric to habitats with high predation (Ekroos *et al.*, 2012). Introduced predators are particularly devastating (Salo *et al.*, 2007) and have driven biodiversity decline and extinctions globally (Clavero & Garcia-Berthou, 2005). The impacts of predation pressure do not occur in isolation, and bird populations are often subject to the cumulative impacts of several threatening processes acting simultaneously. For instance, habitat loss across North America has reduced many migratory passerines to remnant populations that cannot sustain additional pressure from predation, resulting in their dramatic, continental-scale decline (Wilcove, 1985).

Here, we report an unusual interaction between an introduced arboreal marsupial predator, *Petaurus breviceps* (sugar glider) and an endangered migratory, tree cavity-nesting bird, *Lathamus discolor* (swift parrot). Our study system is interesting for several reasons. First, ours is the only study to report sugar gliders, a predominantly insectivorous/nectarivorous species in its native range (Lindenmayer, 2002), preying on birds to the extent that they constitute a severe threatening process. Sugar gliders are native to continental Australia, but there is strong evidence to indicate that they were introduced to Tasmania, a large island to the south of the continent (Gunn, 1851; Rounsevell *et al.*, 1991; Lindenmayer, 2002). Swift parrots are breeding endemics to Tasmania and its smaller offshore islands.

Second, swift parrots are Austral migrants (i.e. species whose annual migration is undertaken entirely within the Southern Hemisphere), which are a major, but poorly studied component of global migratory bird diversity (Dingle, 2008). Swift parrots are threatened by broad-scale habitat loss (Mac Nally & Horrocks, 2000), which is likely to interact with other threatening processes such as heightened predation. Further, the Tasmanian breeding range of swift parrots is under ongoing pressure from habitat loss (Saunders & Tzaros, 2011).

Finally, swift parrots are extremely mobile and follow food resources (mostly nectar from flowering trees) across a large

area of potential habitat (Saunders *et al.*, 2007). Mobility in response to resource availability has been reported in other species (Gangoso *et al.*, 2013), but swift parrots change the location of their breeding sites every year (Webb *et al.*, 2012). Mobile birds with low breeding-site philopatry comprise a major proportion of migratory species, but their life history characteristics make them challenging to research and as a consequence, their population processes are poorly understood (Newton, 2012).

Here, we show that using a different breeding location each year exposes swift parrots to dramatic variation in predation risk depending on the occurrence of sugar gliders and the extent of habitat loss. By investigating these interactions, we demonstrate that swift parrots are vulnerable to unexpected trophic cascades from habitat loss. Our results highlight that mobile species, and especially those with low breeding-site fidelity, may suffer threatening processes that vary greatly across spatial and temporal scales. These species offer further insights into species decline, but also present additional conservation challenges.

METHODS

Study area and nest identification

The study was conducted across seven regions in the breeding range of the swift parrot in Tasmania, Australia (Fig. 1). Swift parrots usually nest in entirely different regions between years in breeding habitat characterized by mature *Eucalyptus*-dominated forest (Webb *et al.*, 2012). As part of an annual monitoring programme conducted since 2009, Webb *et al.* (2014) located the regions used by swift parrots each year across the large study area by repeatedly surveying c. 1000 sites across south-eastern mainland Tasmania and nearby offshore islands. In these surveys, when swift parrot breeding activity was detected, an intensive search was undertaken to locate the tree cavities used by breeding parrots (see Stojanovic *et al.*, 2012 for details). Although individual swift parrot's nests can be scattered across large areas, we selected our study sites where birds nested in aggregations.

Breeding success

We monitored swift parrot nests identified in the above survey for three consecutive breeding seasons between 2010 and 2012. We monitored nests every third day from the point of discovery until the nest either succeeded (i.e. produced at least one fledgling) or failed. We examined all cavities visually using a combination of tree climbing (2010–2012) and camera traps (2011 and 2012). During climbing, we used a small camera mounted on a flexible extension when visibility inside nests was poor (Stojanovic *et al.*, 2012). We used a combination of PixController™ (PixController Inc., Pittsburgh, PA, USA) and Reconyx HC500™ (Reconyx Inc., Holmen, WI, USA) camera traps. We deployed cameras at

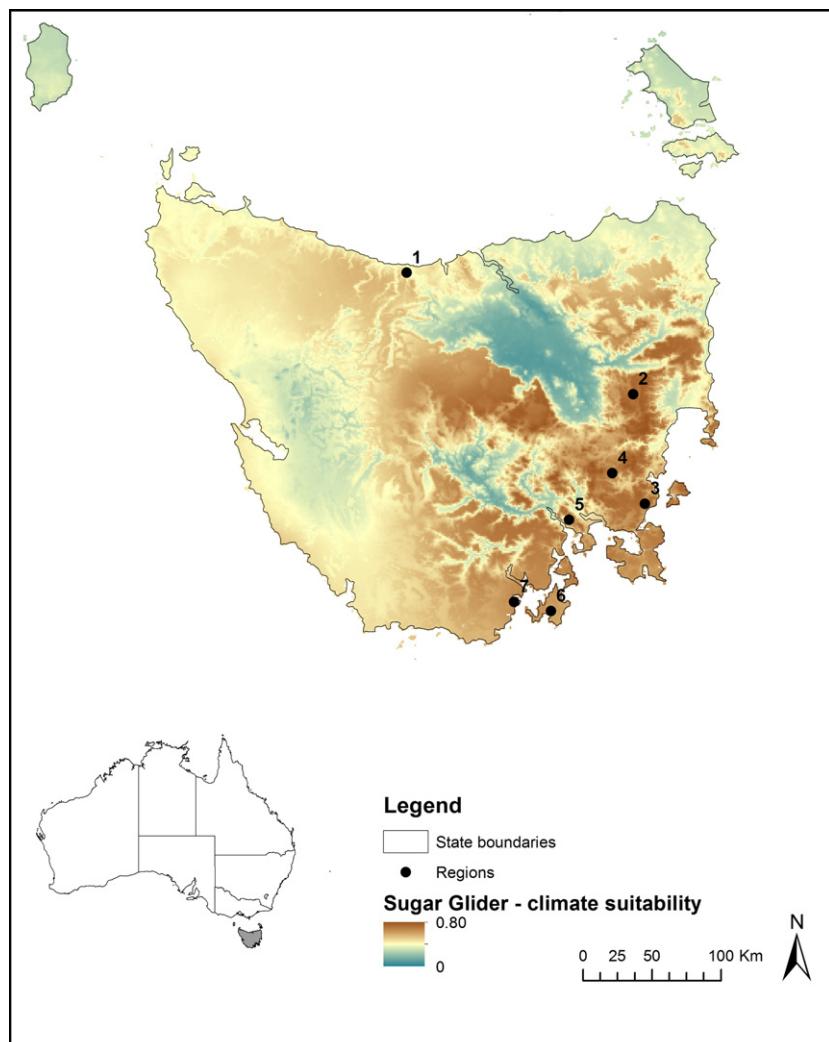


Figure 1 MAXENT model of bioclimatic suitability for sugar gliders across the study area, showing the location of the seven regions where swift parrot nests were monitored. The swift parrot nesting regions (and the number of nests included in the nest survival analysis from each) were as follows: (1) Devonport ($n = 7$), (2) Eastern Tiers ($n = 15$), (3) Wielangta ($n = 8$), (4) Buckland ($n = 3$), (5) Meehan Range ($n = 8$), (6) Bruny Island ($n = 16$) and (7) the southern forests ($n = 6$). Note the high suitability of islands offshore the east coast of Tasmania for sugar gliders (including Region 6). Offshore islands are important breeding habitat for swift parrots, and sugar gliders are absent from these areas.

swift parrot nests usually within 1 m of the tree cavity entrance and downloaded photographs weekly.

Estimating probability of sugar gliders occurrence

To determine whether the duration of camera deployments at each region was sufficient to detect sugar gliders if they were present, we calculated the probability of detecting a sugar glider in a single night at an active swift parrot nest. We fitted a single-season site-occupancy model within a removal design framework using PRESENCE (MacKenzie *et al.*, 2002, 2006). Nests were removed from the analysis after the first sugar glider detection which, except in one instance, always corresponded to a predation event. This approach assumed that a predation event would reduce the attractiveness to sugar gliders of a former swift parrot nest, thus lowering the likelihood of subsequent sugar glider detection. For swift parrot nests where no gliders were detected, we calculated the probability of sugar glider occurrence using the standard PRESENCE output, accounting for the number of nights that each nest was monitored.

Potential sugar glider distribution

We used MAXENT (Phillips *et al.*, 2006) to predict the bioclimatic space suitable for sugar gliders across Tasmania and nearby islands. We used 24 sugar glider records from this study and 68 records from the Atlas of Living Australia (ALA, <http://www.ala.org.au>, downloaded 31/5/2013). We only retained spatially validated ALA data, but manually mapped and removed nine doubtful records with low spatial accuracy. Four uncorrelated bioclimatic variables were selected using principal component analysis (PCA) in R software (R Development Core Team, 2008). The PCA was used to quantitatively assess variation in all bioclimatic variables for locations where sugar gliders were observed. The input vectors in the PCA correspond to all normalised bioclimatic variables (see Table 1 in Harris *et al.* 2013). We tested correlation coefficients between the variables using in R software (R Development Core Team, 2008). We used four uncorrelated bioclimatic parameters that accounted for more than 95% of the climate variability of the sites where sugar gliders were observed as follows: (1) BIO2, mean diurnal range

Table 1 Model selection for nest survival of swift parrots. Models are listed in ranked order according to AIC_c

Nest Survival Models	AIC _c	AIC _c weight	No. Par.	Deviance
Predation*Forest cover	130.63	0.98	2	126.62
Predation	138.75	0.02	2	134.74
Constant*Forest cover	161.11	0	2	157.12
Constant	162.91	0	1	160.9
Time	214.18	0	59	91.37
Predation*Time	325.39	0	118	69.51

No. Par., number of identifiable parameters.

[mean(period max-min)]; (2) BIO10, mean temperature of the warmest quarter in degrees Celsius; (3) BIO12, annual precipitation in mm; and (4) BIO15, precipitation seasonality (coefficient of variation). We ran two MAXENT models: one with 10 replicate runs calculated by cross-validation and the other with 10 replicate runs using bootstrapping, withholding 30% of the observations for validation. We used default values for all other parameters, for example a random set of 10 000 pseudo-absences as ‘background’ data. Results are presented as the relative probability of occurrence, with suitable climate being differentiated from unsuitable where this value is > 0.5 (Phillips & Dudík, 2008). Model performance was assessed using the area under the receiver operating curve (AUC), via the analysis of omission and commission provided by the MAXENT output and by checking the standard deviations of the predictions.

Forest cover and predation risk

The quality and extent of habitat at the regional scale is known to exert an influence on the likelihood of predation on forest-nesting birds (Malt & Lank, 2009; Tozer *et al.*, 2012). To assess regional scale effects of forest cover on swift parrot predation risk, we obtained the mean percentage cover of mature *Eucalyptus* forest by averaging forest cover within a 5 km radius of each individual swift parrot nest. We derived values of mature forest cover from a habitat map developed to inform the management of cavity-dependent species (Forest Practices Authority, 2011). The map provides a coarse estimate of mature *Eucalyptus*-dominated forest across Tasmania, and its limitations are discussed in detail elsewhere (Forest Practices Authority, 2011; Stojanovic *et al.*, in press). We chose a 5 km radius because this is a recommended management scale for logging operations near known swift parrot nests (Forest Practices Authority, 2010).

We used nest-survival analysis in program MARK to model the survival of swift parrot nests (White & Burnham, 1999). We excluded from the analysis nests that failed for reasons other than sugar glider predation ($n = 3$, two nests were flooded, and honeybees *Apis mellifera* killed chicks in another nest and usurped the cavity) or were only visited once because nests were found soon after they had already been destroyed by sugar gliders ($n = 4$). We estimated the

daily survival rate (DSR) of swift parrot nests using program MARK (White & Burnham, 1999). The influences of three biological factors on nest survival were included in our model comparisons: time, the extent of forest cover (as a covariate) and the exposure to predation (as a group effect, i.e. whether the nest was located on a predator-free island or on the mainland). We used AIC_c ranking to select the preferred model (Jehle *et al.*, 2004) from the six candidate models considered (see Table 1 for details) and calculated the DSR of swift parrot nests using the parameters from the best model.

RESULTS

We monitored a total of 70 swift parrot nests across seven regions used by the birds from 2010 to 2012. One of those regions (Bruny Island) was an offshore island, while the remaining six were spread across mainland Tasmania (Fig. 1). Other than Bruny Island (where three nests were found in 2011, and 13 nests were found in 2012), swift parrots nested in a new location each year, thus each region was only used once over the study period.

Due to different nest fates, deployment of camera traps was longer on Bruny Island (mean: 50.9 days, range: 6–98 days) than on mainland Tasmania (mean: 18.1 days, range: 2–73 days). Cameras recorded 10 species attempting to access swift parrot nests and, including the number of nests where they were detected, these were as follows: the sugar glider ($n = 24$), *Colluricincla harmonica* (grey shrike thrush, $n = 20$), *Strepera fuliginosa* (black currawong, $n = 3$), *Falco berigora* (brown falcon, $n = 2$), *Ninox novaeseelandiae* (southern boobook, $n = 1$), *Corvus tasmanicus* (forest raven, $n = 1$), *Accipiter fasciatus* (brown goshawk, $n = 1$), *Trichosurus vulpecula* (common brushtail possum, $n = 1$), *Pseudochelirus peregrinus* (common ringtail possum, $n = 1$) and *Cercartetus lepidus* (little pygmy possum, $n = 1$). Apart from sugar gliders, the small entrance or deep internal chamber of nest cavities foiled all other potential predators. In total, we recorded 24 predation events perpetrated by sugar gliders (Fig. 2). These occurred a mean 10.1 (± 1.8 SE) days after eggs were laid. Sugar gliders consumed all eggs in predated swift parrot nests, but in 83.3% of cases (20/24), the adult female swift parrot was also killed and eaten (Fig. 2). Of nests where sugar glider predation occurred, only 20 were inspected on more than one occasion (the other four were discovered soon after the nest had already been destroyed by sugar gliders, hence were only inspected once). At Region 2 (Fig. 1), *Petrochelidon nigricans* (tree martins) occupied tree cavities after sugar gliders destroyed the swift parrot nest. At each tree martin nest ($n = 3$), sugar gliders killed and ate the incubating female martin and all eggs in the nest.

Predation risk was not uniform across regions. The estimated probability of detecting a sugar glider on a single night at a swift parrot nest was 0.3 (± 0.1 SE) across all regions. Our deployment of camera traps for extended periods on Bruny Island (Fig. 1, Region 6) and total lack of predation events, combined with an apparent lack of records of

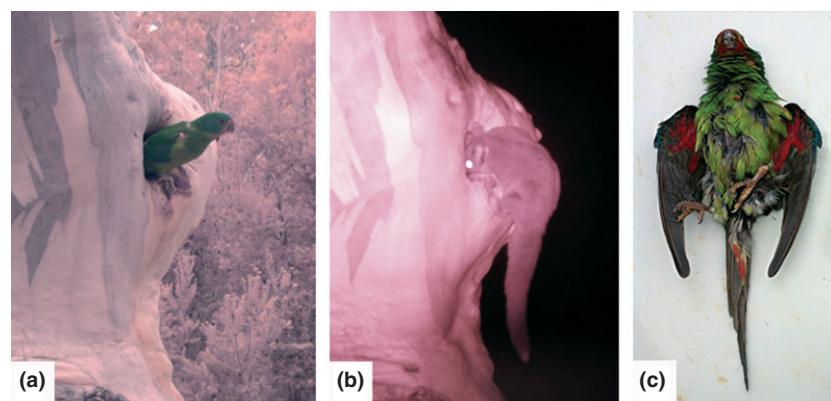


Figure 2 A sugar glider predation event captured by a camera trap at Region 2. The panel shows (a) an adult female swift parrot at her nest cavity at 1900 h, then (b) at 2300 h on the same day, a sugar glider entering the cavity, where it caused the failure of that nest. (c) Adult female swift parrots are killed and eaten by sugar gliders.

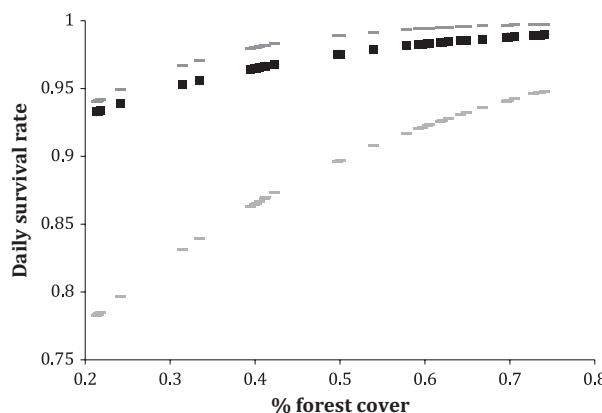


Figure 3 Modelled daily survival rates ($\pm 95\%$ confidence intervals) of mainland Tasmanian swift parrot nests as a function of landscape-scale forest cover. Estimates were generated using the parameters from the model of best fit and show that DSR improved as regional forest cover increased. In contrast, DSR was 1 for nests on islands where sugar gliders do not occur (not illustrated). DSR, daily survival rate.

this species provides strong evidence that sugar gliders are absent from this region. At Region 4 (Fig. 1), where we did not detect sugar gliders, all nests were successful.

We modeled survival of 63 swift parrot nests across Bruny Island ($n = 16$) and the Tasmanian mainland ($n = 47$). The preferred model of nest survival was one in which the DSR of swift parrots was constant over time and was influenced by the extent of forest cover and the presence of sugar gliders (Table 1). Using the parameter estimates from this model, we calculated that for swift parrot nests on islands, DSR was 1. In contrast, swift parrot nests exposed to predation on mainland Tasmania had a much reduced DSR of 0.97, equating to a true nest-survival rate of 0.17 over the course of the 60-day nesting period. Our model also indicated that there was a positive relationship between regional forest cover and DSR of swift parrot nests (Fig. 3). At mainland Tasmanian regions where forest cover was low, sugar gliders preyed on 100% of the nests and female swift parrots that we monitored (e.g. Region 1), but where forest cover was higher (e.g. Region 3), survival improved (Fig. 3).

Our two MAXENT models were not significantly different, and both suggested that most of Tasmania and its nearby offshore islands are potential sugar glider habitat (results for the cross-validation model presented in Fig. 1). Importantly, all of the areas used by swift parrots on mainland Tasmania were bioclimatically suitable for sugar gliders. Although our camera trap and ALA data indicate that Bruny Island does not support a sugar glider population, the MAXENT model indicates that the entire island is bioclimatically suitable (Fig. 4). The model AUC = 0.993 and the analysis of omission and commission errors indicate little bias, and standard deviation of the prediction was lower than 0.08. The contribution of each variable in explaining the current distribution of sugar gliders (percentage contribution in parentheses) were as follows: BIO10 (86.9%), BIO2 (8.2%), BIO15 (4.1%) and BIO12 (0.8%).

DISCUSSION

Our study reveals severe, but also highly variable, rates of predation on adult females and eggs in a migratory bird with low nest-site fidelity. We provide the first evidence that introduced sugar gliders act as the principal cause of breeding failure for an endangered bird. The DSR of swift parrot nests on sugar glider free islands was 1, whereas on the mainland where gliders occur, the average DSR was 0.97. Over the 60-day nesting period of mainland Tasmanian nests, the average true likelihood of survival for swift parrot nests was only 0.17. In most predation events (83.3%), the adult female swift parrot was killed in addition to her eggs. This intense predation pressure equated to an overall annual mortality rate of 42.6% for breeding adult females across Tasmania, although our nest survival analysis indicates that this number is likely to be an underestimate of true female mortality. We also show that predation of adult females and eggs ranges from 100% at some breeding sites on mainland Tasmania to zero predation on at least one major offshore island where sugar gliders are absent. Further, our results reveal that on the Tasmanian mainland, survival of swift parrot nests is a function of mature forest cover in the surrounding landscape. Importantly, our results demonstrate that likelihood of sugar glider predation decreases with increasing forest cover.

Because food tree flowering is ephemeral, patchy and unpredictable across the breeding range, swift parrots tend to aggregate to breed in just a few regions in each year (Webb *et al.*, 2012). In years when swift parrots are enticed by abundant tree flowering to breed in areas where introduced sugar gliders occur, large proportions of the remaining population may be exposed to predation. This dramatic spatio-temporal variation in predation pressure appears to be driven by the complex interplay of pulsed resource availability, habitat loss and presence-absence of sugar gliders.

Although many species were observed attempting to access swift parrot nests, only introduced sugar gliders were successful. Swift parrots select tree cavities with small entrance diameters and deep chambers (Stojanovic *et al.*, 2012), and these nest-site characteristics effectively excluded all other potential predators. However, even the largest sugar gliders only have a mean skull width of 24.8 ± 1.4 mm (Jackson, 2000) and can easily squeeze past the small entrances of swift parrot nest cavities. Other studies have recorded sugar gliders occasionally preying on birds (Holdsworth, 2006), and in this study, sugar gliders preyed on two cavity-nesting bird species. Our results confirm that sugar gliders are a major opportunistic predator of cavity-nesting birds and are likely to constitute a severe threatening process for endangered swift parrots and other small cavity-nesting birds. This is especially true in light of the predation of eggs and adult females. Mortality of adult females is a major factor contributing to extinction risk in small populations (Grubler *et al.*, 2008; Reidy *et al.*, 2009), and the low rate of female survival we report is similar to other highly threatened species of parrot (Moorhouse *et al.*, 2003; Holdsworth *et al.*, 2011). Importantly, the high female mortality reported here likely resulted in underestimation of sugar glider predation on mainland Tasmania because nests were likely to have failed before they could be discovered.

In the context of the significant predation pressure reported here, islands are likely to be important source habitats for the remaining swift parrot population because their nesting success and adult female survival are dramatically higher than on mainland Tasmania. Ensuring that islands remain sugar glider free is very likely to be critical to conserving swift parrots. Although naturally protected by their isolation, island-breeding birds are extremely vulnerable to predator introductions (Blackburn *et al.*, 2004). We did not detect sugar gliders at swift parrot nests on Bruny Island despite long camera deployments, indicating that gliders have so far failed to colonize Tasmanian offshore islands. However, our MAXENT model indicates that these islands support suitable bioclimatic conditions. This has important implications for the management of other cavity-nesting birds sympatric with sugar gliders. For example, sugar gliders have previously been implicated as predators of the critically endangered orange-bellied parrot (*Neophema chrysogaster*) at their nests (Holdsworth, 2006). Further, endangered forty-spotted pardalotes (*Pardalotus quadragintus*) have gone

extinct across most of their mainland Tasmanian range, but are still abundant on sugar glider free offshore islands (Threatened Species Section, 2006).

Where we detected sugar gliders on mainland Tasmania, there was a positive relationship between nest survival and regional cover of mature forest. At Region 1 where mature forest cover was very low, surviving swift parrots quickly abandoned the area after sugar glider predation caused complete breeding failure. In contrast, swift parrots that nested in contiguous forest in other regions experienced substantially lower predation rates. These results are similar to those of other studies where predation risk is correlated with landscape-scale habitat loss (Malt & Lank, 2009; Vetter *et al.*, 2013). Our study provides evidence for cascading trophic effects of forest loss on swift parrots. Many of our study sites are subject to ongoing logging, agriculture and urban development, so urgent research is required to understand whether forest loss favours the introduced predator and exacerbates predation risk on swift parrots. Our study points to more complex interactions between these processes than have been previously supposed.

Swift parrots are representative of the threats faced by migratory birds, and our study is a cautionary tale for the management of other mobile, difficult to study species. Sugar gliders represent an unexpected, but severe new threatening process that appears to interact synergistically with other, better known threats. Given the ongoing anthropogenic loss of forest across Tasmania, our results highlight the importance of detailed ecological research in revealing unexpected species-habitat interactions in modified landscapes.

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BIOSKETCH

Dejan Stojanovic is a conservation biologist, and this research was undertaken as part of his PhD research on the swift parrot. His research focuses on the conservation and management of threatened species and their habitat, with a focus on how threatened species cope with habitat loss.

Author contributions: D.S. conceived the idea, D.S. and M.W. collected the data; D.S., R.H., L.L.P. and R.A. analysed the data; and D.S., M.H.W. and R.H. led the writing.

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