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Pauline Palmas, Hervé Jourdan, L. Debar, Edouard Bourguet, Frédéric Rigault, et al.. A conservation paradox: endangered and iconic flightless kagu (*Rhynochetos jubatus*) apparently escape feral cat predation. *New Zealand Journal of Ecology*, 2020, 44 (1), pp.3394. <10.20417/nzj ecol.44.1>. <hal-02545324>

HAL Id: hal-02545324

<https://hal.science/hal-02545324v1>

Submitted on 8 Mar 2024

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A conservation paradox: endangered and iconic flightless kagu (*Rhynochetos jubatus*) apparently escape feral cat predation

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Published online: 7 February 2020

Abstract: The kagu (*Rhynochetos jubatus*) is an iconic endemic flightless bird from New Caledonia, red-listed as endangered according to the International Union for Conservation of Nature (IUCN) criteria. Feral cats are among the most successful and damaging invaders for island biodiversity. They have been directly responsible for the extinction of numerous birds worldwide, especially small- and medium-sized flightless species. Our study evaluates the feral cat threat to the kagu by analysing 772 cat scats from the two main sites housing major remaining populations (eight quarterly sampling sessions conducted per site over 2 years). Surprisingly, we detected no predation evidence against this endangered species (including chicks) although it falls within the cats' prey size range and exhibits life-history traits typical of island endangered naïve birds. We recommend a multi-species approach to invasive mammal management to mitigate direct and indirect pressures against remaining kagu populations.

Keywords: bird, conservation 'loser', *Felis catus*, invasive predator, island conservation, island ecosystems, threatened species, New Caledonia

Introduction

Domesticated thousands of years ago (Driscoll et al. 2007) and subsequently introduced by humans to islands worldwide, the domestic cat *Felis catus* has generally reached sustainable and even flourishing feral populations (Nogales et al. 2013). Feral cats are known to prey intensively upon native fauna, leading to numerous island species extinctions, extirpations and endangerment (e.g. Medina et al. 2011; Doherty et al. 2016). Feral cats feed on a wide range of prey, from large birds and medium-sized mammals exceeding 1–2 kg to small invertebrates (e.g. Bonnaud et al. 2011; Doherty et al. 2015). Cats are involved in the recent extinction of 63 insular vertebrate species (40 bird, 21 mammal, and 2 reptile species; 26% of all recent extinctions) (Doherty et al. 2016).

The dramatic loss of native island species has been mainly attributed to island prey naïveté (Carthey & Banks 2014). Endemic island flightless and ground-nesting birds are extremely vulnerable to introduced predators, especially feral cats (Roots 2006; Steadman 2006; Woinarski et al. 2017). Among the 40 worldwide bird species recently extinct (since AD 1500) partly or totally due to cat predation, at least 12 were flightless (Doherty et al. 2016); see Table S1 in Supplementary Material.

Cats were introduced to New Caledonia around 1860 by European settlers and are now present in a wide range of habitats, even in the most remote areas (Beauvais et al. 2006; Palmas et al. 2017). Throughout the New Caledonian archipelago, feral cats prey upon at least 44 native vertebrate species ranging from small insects to medium-sized birds and mammals (Palmas et al. 2017). Surprisingly, no remains of a flightless New Caledonian endemic bird, the kagu (*Rhynochetos jubatus*), were found among all the 5356 cat scats collected from the 14 study sites of a previous larger study (Palmas et al. 2017). This intriguing result motivated us to focus on cat scat sampling and analysing in the two major bastions for this bird species.

The kagu is an iconic endangered flightless ground-nesting forest bird endemic to New Caledonia (South Pacific) (see Figure S1 in Supplementary Material). Weighing c. 900 g, it combines all the vulnerability traits typical of island conservation 'losers': flightlessness, K-selected traits, and absence of shared evolutionary history with mammalian predators (Hunt 1997; Roots 2006; Steadman 2006). Today, kagu populations are mainly found in inland forested mountainous regions of the New Caledonia main island (Grande Terre) and appear fragmented among patches of rainforest

remnant habitat (Hunt 1997; BirdLife International 2016). During the last century, a general decline was observed for this species, mainly due to habitat loss, forest fragmentation, and potentially direct and indirect impacts of invasive species like dogs, rats, pigs and deer (Warner 1948; Hunt et al. 1996). The kagu has been IUCN red-listed as endangered. In 2016, whole-island monitoring reported c. 2000 wild kagu individuals (BirdLife International 2016), with 75.3% of the recorded individuals distributed in two major nature reserves (BirdLife International 2016), the focused sites of our study. Until the arrival of the first human settlers, 3200 years ago, and without the presence of native mammalian predators, the kagu was among the top native predators in natural forests, and thus, may not have developed anti-predator behaviour. All potential mammalian predators against the kagu were introduced to New Caledonia by humans, either Austronesian settlers 3200 years ago (Polynesian rat, *Rattus exulans*) or European colonisers during the first half of the 19th century (dogs, cats, black rats *Rattus rattus*, brown rats *Rattus norvegicus*, pigs; Beauvais et al. 2006). Feral cats are now widespread throughout the kagu distribution range and considered a major threat to this species (BirdLife International 2016), although the literature shows no clear evidence of cat predation (Hunt 1997; Rouys & Theuerkauf 2003; Gula et al. 2010).

Here, we used scat sampling and analysis to assess feral cat predation on the two main remnant populations of kagu, seeking to list the feral cat among the threats endangering this iconic endemic bird. We also studied feral cat diet according to kagu breeding cycle to detect any cat predation patterns that can differently affect kagu survival and productivity. To complete this trophic approach, we then examined, across all worldwide island bird and mammal species known to be preyed upon by feral cats, their morphological traits (i.e. weight and flight ability) to better understand the kagu's catchability.

Methods

Study sites

We conducted this study in the two New Caledonian nature reserves housing the two major remaining kagu populations

(BirdLife International 2016; Fig. 1). The Parc des Grandes Fougères (PGF) covers 45.45 km² of mainly rain forest vegetation on metamorphic soil. This forest has a high canopy (20–30 m) with a dense understorey, dominated by *Arecaceae*, *Sapindaceae*, *Meliaceae* and *Monimiaceae* (Ibanez et al. 2014). The floral endemism rate reaches 83% (Morat et al. 2012). The mean annual rainfall is between 1500 and 2000 mm (Meteo France 2007). This habitat covers 1800 km² of New Caledonia. The Parc Provincial de la Rivière Bleue (PPRB) covers 220.68 km² of mosaic habitat composed of rain forest vegetation and maquis shrubland on ultramafic soil (Isnard et al. 2016). The forest canopy reaches from 20 to 30 m. Mean annual rainfall is between 2500 and 3500 mm (Meteo France 2007). The maquis has heathy or scrubby vegetation with a low woody stratum (50 cm to 7 m). The maquis mosaic and rain forest flora endemism rates are respectively 96.9% and 96.4% (Isnard et al. 2016). This mosaic habitat is dominated by *Arecaceae*, *Sapindaceae*, *Meliaceae* and *Monimiaceae* (Ibanez et al. 2014) and covers 5600–5700 km² of New Caledonia.

Cat diet study according to kagu breeding cycle

Scat sampling at both sites took place in areas where kagu presence had been confirmed and mapped (Meriot et al. 2009; Boissenin 2012) and kagu were regularly observed during scat sampling.

There are two main periods that affect the kagu's degree of vulnerability to predators: the breeding period (June–December), and non-breeding period (January–May) (Létocart & Salas 1997). The breeding period corresponds to the highest vulnerability for kagu and includes the main laying period and juvenile rearing duration. We studied the feral cat diet by analysing scats collected along paths used by cats (Turner & Bateson 2014; Bonnaud et al. 2015) over 2 consecutive years, with samples collected every 3 months to cover the overall kagu breeding cycle, considering that scats reflected the two previous months of cat predation at most (Bonnaud et al. 2007). For each field session the cumulative sampling length effort cover 30.2 km for PPRB and 12.1 km for PGF. Cat scats were georeferenced, stored in individual Ziploc bags, and frozen until analysis. We analysed 335 scats for PGF and 437 scats for PPRB, representing a robust and significant sampling effort

New Caledonia archipelago

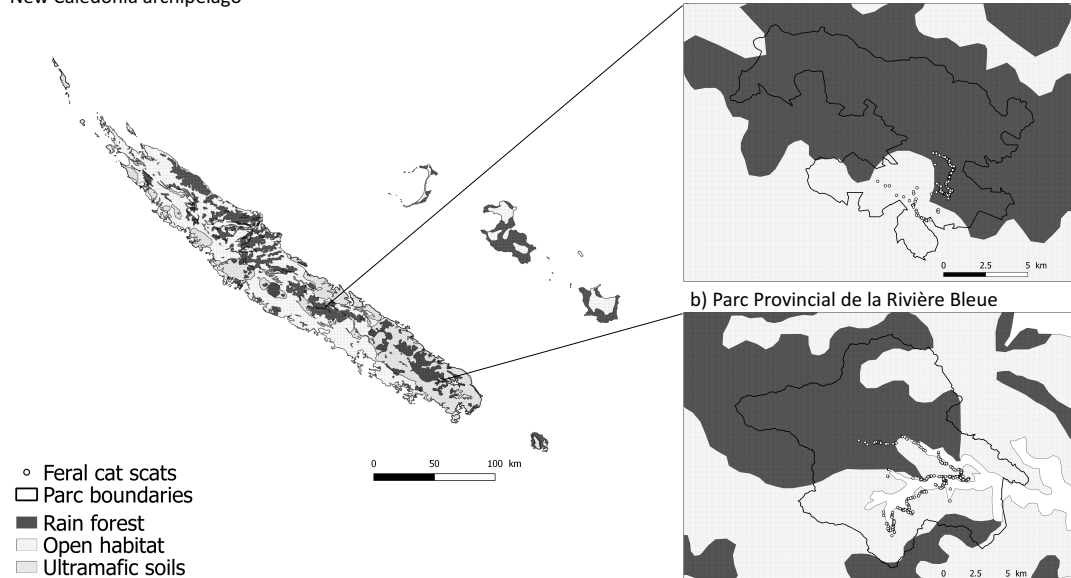


Figure 1. Location of the two New Caledonian nature reserves housing the main kagu populations; a) The Parc des Grandes Fougères (PGF); b) The Parc Provincial de la Rivière Bleue (PPRB). Circles indicate the location of collected and analysed feral cat scats.

($n > 100$) to track even rare prey remains (Bonnaud et al. 2011). Scats were dissected by washing over a 0.5 mm mesh size sieve and separating items like hair, feathers, bone fragments, claws, teeth, beaks, jaws, skink scales and arthropod chitin fragments. We compared each item to reference materials for assignment to one of the six main prey categories: introduced rodents, bats, birds, squamates, invertebrates and fish. Kagu remains available in our reference collection included beaks, claws, different types of feathers for adults and down for chicks.

Data analyses

For each type of cat prey, we calculated the frequency of occurrence (FO) per scat (Bonnaud et al. 2015). We used Levins' standardized formula for trophic niche breadth (Levins' SNB; Krebs 1999):

$$SNB = (B-1)/(n-1) \tag{1}$$

where $B = 1/\sum p_i^2$ with p_i the fraction of prey item i in the diet ($\sum p_i = 1.0$) and n the number of prey categories in the predator's diet. SNB ranges from 0 to 1, where a value close to 0 represents a narrow niche and one close to 1, a broad niche.

Statistical analyses

We conducted all statistical analyses with R 3.0.3 software (R core Team 2014) using 'pROC' (Fawcett 2006). We ran (1) Chi-square tests for homogeneity to test site effect on overall cat diet composition by comparing the FO of six prey categories; and (2) generalised linear models (GLM) to test site effect of occurrence of each prey in cat diet [in R: glm (response ~ site), family = binomial (link= "cloglog")]. We used area under the ROC-curve plot (AUC) to assess the accuracy of our model predictions (Fielding & Bell 1997). AUC values commonly range from 0.5 to 1.0 prediction, corresponding respectively to a random and perfect prediction.

Feral cats' prey sizes on islands

We compiled across all island bird and mammal species known to be preyed upon by feral cats according their morphological traits (i.e. median adult weight and flight ability). We produced

body-size frequency distribution by considering prey species with adult median body weight over 400 g (prey species and median weight from Bonnaud et al. 2011; Doherty et al. 2015; Avibase 2017; Birdlife International 2017; Myers et al. 2017). We considered only medium sized birds and mammals over 400 g in order to range the kagu within the cats' medium prey size range.

Results

Feral cat diet according to study site

Surprisingly, no remains of either adult or young kagu were found among the 772 feral cat scats collected within these two bastions of this species.

Overall cat diet composition differed between the two sites ($p < 0.001$) (Fig. 2). Cats had a wider standardised Levins' niche breadth in PPRB (Levins' SNB = 0.52) than in PGF (Levins' SNB = 0.30).

The GLM describing prey occurrences in cat diet for each site correctly predicted presence and absence of main prey groups (AUC ranging from 0.57 for birds to 0.78 for fish) (Fig. 2; Table 1). All studied prey groups showed significant differences: higher FO of rodents and squamates for PGF and higher FO of bats (mainly flying foxes), birds, invertebrates and fish for PPRB (Fig. 2; Table 1).

For PGF and PPRB, passerines were the predominant bird prey (in 14.3% and 14.8% of the scats containing bird remains respectively; Table 1), followed by seabirds for PGF (in 9.5% of scats containing bird remains). For PPRB, no seabird remains were found in cat scats.

Feral cat diet according to kagu breeding cycle

Cats had the widest standardised Levins' niche breadth in the kagu breeding period in PPRB (Levins' SNB = 0.62), and in the non-breeding period of the second sampling year in PGF (Levins' SNB = 0.36) (Fig. 3).

In PPRB, FO of rodents and squamates are much lower

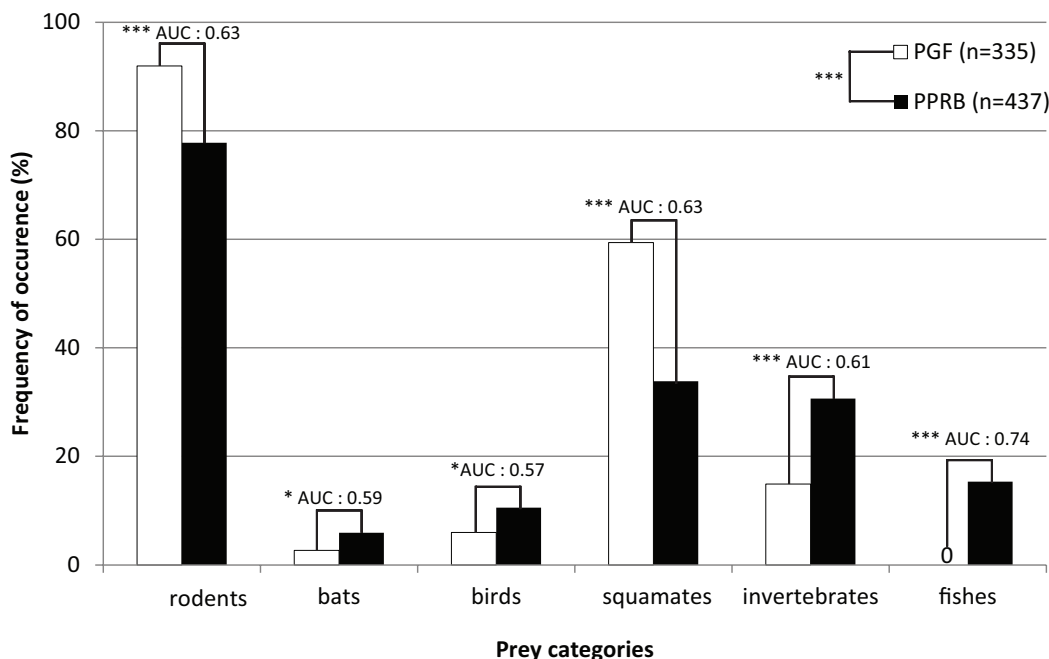


Figure 2. Frequency of occurrence (FO) of feral cat prey categories in the two study sites (n = 772); * $p < 0.05$, ** $p < 0.01$, and *** $p < 0.001$; the area under the ROC-curve plot (AUC) ranging from 0.5 to 1.0 indicates the accuracy of model predictions.

during the kagu breeding period (respectively 69.6% for breeding period vs 83.7% non-breeding period for rodents, and 30.4% vs 48.9% for squamates), while FOs of birds (14.3% vs 3.7%), invertebrates (36.2% vs 30.3%), fish (21.2% vs 10.2%) and bats (6.7% vs 2.9%) are higher.

In PGF, FOs of rodents, birds and bats are similar between periods (respectively 91.0% vs 92.6% for rodents, 7.0% vs 5.2% for birds and 2.7 vs 2.3% for bats), while FO squamates and invertebrates (respectively 52.0% vs 69.7% and 5.6% vs 30.2%) are the highest during the kagu non-breeding period.

Kagu vulnerability: body weight of known bird and mammal preyed upon by feral cats

On worldwide islands and considering only birds over 400 g, island birds preyed upon by feral cats include at least 46 species, of which 14 are flightless, belonging to Sphenisciformes (10), Gruiformes (2), Apterygiformes (1), Casuariiformes (1) and weighing from 850 to 4000 g (Fig. 4). For island mammals, feral cats are known to prey upon at least 33 species over 400 g (Bonnaud et al. 2011; Doherty et al. 2015; Fig. 4).

Table 1. Results of (a) Chi-square tests for homogeneity to test site effect on overall cat diet composition by comparing the FO of the six prey categories (b) GLM to test site effect on occurrence of each prey in cat diet including AUC values for assessing the accuracy of our model predictions.

	Chi-squared	df	p-value
(a)	112.1	5	$< 2.2 \times 10^{-16}$

	Deviance explained	Pr(> Chi)	AUC
(b)			
Rodents	0.044	0.000	0.629
Bats	0.017	0.026	0.593
Birds	0.012	0.023	0.572
Squamates	0.047	1.29×10^{-12}	0.627
Invertebrates	0.032	2.21×10^{-07}	0.607
Fish	0.178	$< 2.2 \times 10^{-16}$	0.738

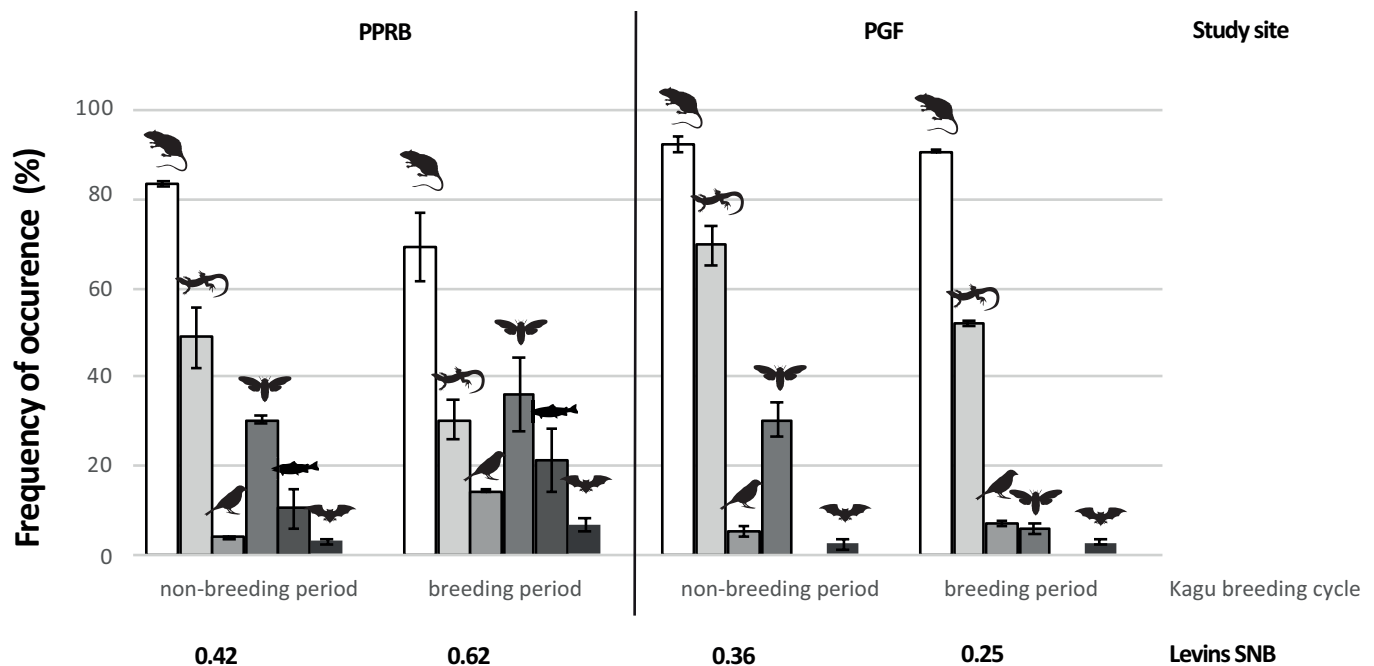


Figure 3. Cat diet and Levins SNB index for PPRB and PGF according to kagu breeding cycle; mean FOs of rodents, squamates, birds, invertebrates, fish and bats for the 2 consecutive sampling years.

Discussion

Pattern of feral cat diet according to study sites and kagu breeding cycle

Counter-intuitively, no kagu remains were found in the 772 feral cat scats analysed, despite the relatively abundant kagu populations recorded in both study sites (around 1000 and 500 individuals respectively for PGF and PPRB) (Meriot et al. 2009; Boissenin 2012) and the high diurnal activity observed for both kagu and cats (Palmas et al. unpubl. data). The apparent absence of predation by feral cats on kagu, even during their breeding period, is concordant with previous video-monitoring

of nests that did not record any feral cat visits (Rouys 2008).

From our diet results, feral cats exhibited a broader trophic niche in PPRB than in PGF, preying upon a wider range of species, all with higher FOs, except for introduced rodents and squamates. FOs of flying fox remains were higher in PPRB than in PGF despite the fact that no flying fox colonies are known in these parks (Le Goff & Brescia 2011). Predation on stranded fish (*Tilapia* sp.) in PPRB occurred over a short period corresponding to a massive seasonal drop in water levels of surrounding lakes. Such high FO (15.3%) for this prey group is striking and rarely mentioned in other cat diet studies. Cat predation on invertebrates (mostly insects) is frequent and comparable to the FO found previously on islands for PPRB

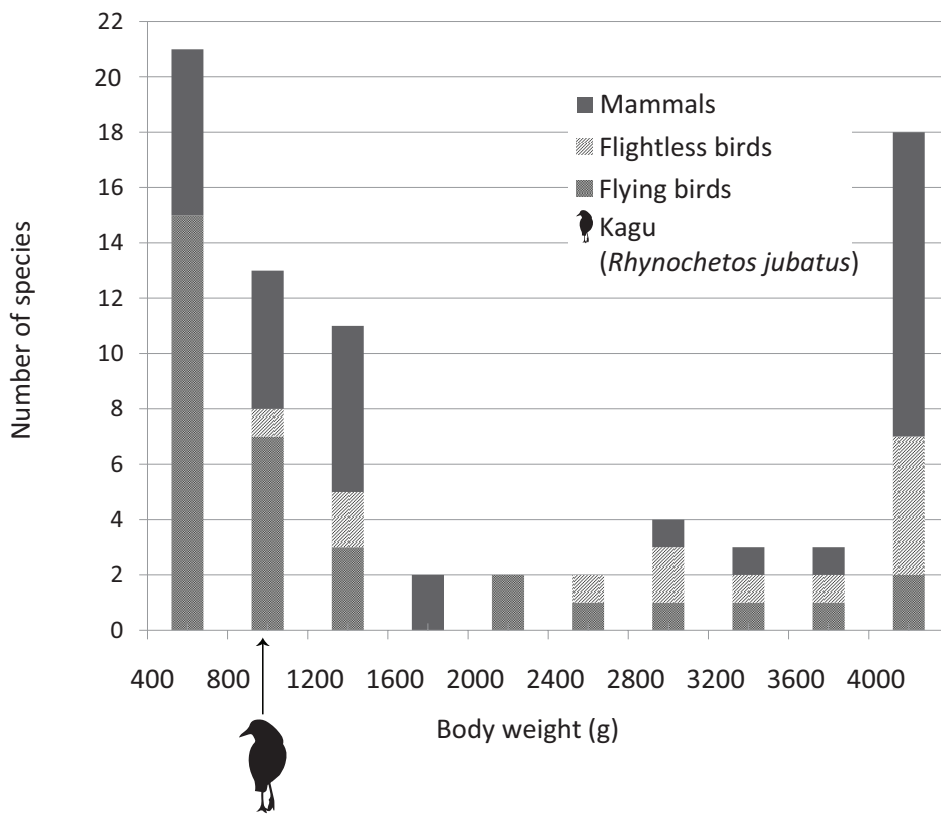


Figure 4. Body-size frequency distribution of medium- to large-sized bird and mammal species known to be consumed by feral cats on islands (weight \geq 400 g) (preyed upon species and median weight from Avibase 2017; Birdlife International 2017; Bonnaud et al. 2011; Doherty et al. 2015; Myers et al. 2017). The arrow indicates the position of kagu according to median adult weight.

(mean of 32.57% (SD 4.9) in Bonnaud et al. 2011; mean of 36.15% (SD 2.78) for Australia in Doherty et al. 2015; FO: 30.7% in PPRB) despite the poor nutritive value of this small, unpalatable prey (Turner & Bateson 2014). These diet patterns, particularly in PPRB, suggest that feral cats look for additional food resources apart from rodents. This finding is consistent with the hypothesis of a lower productivity of ultramafic soils present in PPRB, which could imply a lower productivity and a subsequent lower prey availability than PGF (Guilbert 1997; Theuerkauf et al. 2017), and thus could lead to a higher foraging effort for cats in PPRB.

In PPRB feral cats showed a broader niche in kagu breeding period. Cats preyed upon a wider range of prey with higher FOs for birds, invertebrates and bats according to a lesser FO of rodents and squamates. The decrease of rodents in feral cat diet could be correlated to a decline in rodent abundance that could occur at this period in this type of habitat (Rouys 2008). Feral cats preyed upon more birds, invertebrates and bats during the kagu breeding period, indeed this period corresponds to the breeding period for terrestrial birds and flying foxes (Létocart & Salas 1997; Rouys 2008; Barré et al. 2013; Brescia; Boissenin & Brescia, unpubl. reports, see <http://www.iac.nc/ressources-publications/catalogue-en-ligne-gaiac>) leading to a higher abundance and vulnerability of these prey. Rather, the increase of invertebrates on feral cat diet during this period appears when invertebrate populations are at the lowest densities (Guilbert 1997). These diet patterns showed that feral cats look for alternative resources to rodents during this period (birds, invertebrates and bats), which possibly involved higher foraging effort whereas kagu are abundant and most vulnerable to predation.

In PGF feral cats showed a faintly broader niche in kagu non-breeding period, despite a constant predation on rodents. Feral cats preyed upon a slightly wider range of prey in the kagu non-breeding period with higher FOs for squamates

and invertebrates. These patterns showed the opportunistic predatory behaviour of feral cats, that prey more upon these two groups when they are more abundant between January and June (Cohic 1950; Guilbert et al. 1994; Guilbert 1997; Jourdan pers. comm.).

Kagu traits: vulnerability and management implications

On worldwide islands, cats prey upon a large range of vertebrate species weighing from few grams to several kilograms (e.g. Bonnaud et al. 2011). Considering only birds and mammals over 400 g, known prey include at least 79 different species (46 birds and 33 mammals) (Bonnaud et al. 2011; Doherty et al. 2015; Fig. 4). Cat consumption of prey over 4000 g could be related to scavenging (Forsyth et al. 2014), as mean feral cat weight is from 2400 to 4000 g (Burbidge & McKenzie 1989; Moseby & Read 2006; Goltz et al. 2008). Cats prey upon a total of 14 flightless bird species weighing from 850 to 4000 g. (Fig. 4).

Consequently, the kagu (adults around 900 g) falls within the feral cat prey range even though the highest likelihood for a bird to be killed by cats is to show intermediate body mass (c. 60–300 g; Woinarski et al. 2017). In addition, the kagu’s flightlessness, ground foraging and ground nesting behaviours strongly increase vulnerability to predation, for instance by wild dogs (e.g. Hunt et al. 1996; Woinarski et al. 2017). Kagu were also regularly seen at short distances during scat sampling, that demonstrated their naïve and confident behaviour. However, adult kagu may have developed effective defensive behaviour against aggressive approaches, which further investigations could confirm. One defensive strategy is ‘opening their wings to display their black and white banded primary feathers’ (Hunt et al. 1996), thereby conveying their large size as a deterrent to cats. In addition, authors observed adult kagu in the nest, or chicks flapping their wings on the ground, that could be distractive or a deterrent for cats. Another strategy

is using cooperative breeding behaviour, which may help to reduce predation on chicks (Theuerkauf et al. 2009). Indeed, breeding kagu and their helpers could use the behaviours mentioned above to defend chicks from cat predation. Kagu have been described attacking dogs as they captured other kagu (Hunt 1997). This defence behaviour seems inefficient against dog predation (e.g. Sarasin 1913) but could probably be efficient against cat predation, given the smaller size of feral cats than wild dogs, and given the solitary habits of cats contrasting with the dog pack behaviour for hunting. This defence behaviour seems also particularly efficient against rodent predation, without any predation events on eggs or chicks as revealed during a dedicated study (Rouys 2008). One additional explanation to this striking absence of cat predation is that feral cats in New Caledonia exhibit a rather small size (mean weight for trapped males 2.23 ± 0.83 kg ($n = 17$) and for females 1.64 ± 0.55 kg ($n = 37$); unpubl. data) that could reduce their predation capacity on medium-sized prey like the kagu.

Some studies reported interesting results about feral cat impacts on large ground dwelling birds. In New Zealand, kiwi (*Apteryx* spp.) are vulnerable to feral cat predation during chick and juvenile stages. Indeed, McLennan et al. (1996) revealed that feral cats were largely responsible for the death of young kiwi, whereas ferrets and dogs are the main predators for adults. On the contrary the malleefowl (*Leipoa ocellata*) in Australia apparently escape feral cat predation (Dickman 1996) while red foxes (a larger predator) have been confirmed as the primary cause of failure of reintroduction for this bird species (high predation rate in fragmented habitats).

While morphological diet studies have greatly contributed to our understanding of invasive species' diets, this method may be constrained by resolution detection and identification, particularly for rare prey (Zarzoso-Lacoste et al. 2016). Using DNA-based methods (e.g. metabarcoding) would help to confirm the absence or extreme rarity of kagu in cat diet.

Even though predation by cats has by far the strongest deleterious effect on native island bird wildlife (e.g. Medina et al. 2011; Bonnaud et al. 2015), to date this flightless, endangered and endemic bird seems to have escaped this direct threat. However, cats could potentially affect kagu survival and fitness by killing and not consuming them or by frequently attempting to capture individuals that actually escape but are injured (Lloyd et al. 2013; McRuer et al. 2017). Furthermore, cats were found to prey extensively upon skinks and terrestrial arthropods, two of the main prey groups for the kagu (Létocart & Salas 1997). Cats may thus be an indirect threat considering competition for food (e.g. Medina et al. 2014), especially when resources are limited (Guilbert et al. 1994; Barré et al. 2010).

We conclude that feral cat predation is not yet a major issue for kagu conservation. However, we recommend multi-species management to mitigate the direct and indirect threats of invasive mammals (Griffiths 2011) to the remaining kagu populations, still fragile and confined to limited areas.

Acknowledgments

We are very grateful to civil and provincial authorities for allowing us to conduct this research in Parc Provincial de la Rivière Bleue and Parc des Grandes Fougères. The authors sincerely acknowledge the Société Calédonienne d'Ornithologie (SCO) and the Parc Zoologique et Forestier

(PZF) for kagu corpses used as reference materials for this study. The experiments comply with the current laws of France and New Caledonia (permission for sampling protocol n°2155-2012/ARR/DENV). We thank Hélène de Méringo for helping during fieldwork and trophic analyses. Our thanks to M. Sweetko for English language revision.

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Editorial board member: Al Glen

Received 5 December 2018; accepted 9 July 2019

Supplementary material

Additional supporting information may be found in the supplementary material file for this article:

Figure S1. Previous (a) and current (b) banknote of French Pacific territories showing pictures of kagu.

Table S1. List of flightless bird species extinct due (at least partially) to cat predation.

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Supplementary material

Figure S1. Previous (a) and current (b) banknote of French Pacific territories showing pictures of Kagu (1000XPF = 8.99 USD).



Table S1. List of flightless bird species extinct due (at least partially) to cat predation (derived from Doherty et al. 2016).

Extinct bird species	Synonyms	References (see below)
<i>Aphanapteryx bonasia</i>		a
<i>Cabalus modestus</i>		b
<i>Gallinula nesiotis</i>		c
<i>Hypotaenidia dieffenbachii</i>	<i>Gallirallus dieffenbachii</i>	d
<i>Hypotaenidia owstoni</i>		e
<i>Hypotaenidia pacifica</i>		f
<i>Hypotaenidia poeciloptera</i>	<i>Nesoclopeus poecilopterus</i>	g
<i>Mundia elpenor</i>		h
<i>Pezophaps solitaria</i>		i
<i>Traversia lyalli</i>		j
<i>Upupa antaios</i>		k
<i>Zapornia sandwichensis</i>		l
<i>Dryolimnas augusti</i> *		m
<i>Porphyrio paepae</i> *		n

* flightless character probable only

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