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Article

Invasive rats strengthen predation pressure on bird eggs in a South Pacific island rainforest

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Abstract

Invasive rats (*Rattus* spp.) are known to have pervasive impacts on island birds, particularly on their nesting success. To conserve or restore bird populations, numerous invasive rat control or eradication projects are undertaken on islands worldwide. However, such projects represent a huge investment and the decision-making process requires proper assessment of rat impacts. Here, we assessed the influence of two sympatric invasive rats (*Rattus rattus* and *R. exulans*) on native bird eggs in a New Caledonian rainforest, using artificial bird-nest monitoring. A total of 178 artificial nests containing two eggs of three different sizes were placed either on the ground or 1.5 m high and monitored at the start of the birds' breeding season. Overall, 12.4% of the nests were depredated during the first 7 days. At site 1, where nests were monitored during 16 days, 41.8% of the nests were depredated. The main predator was the native crow *Corvus moneduloides*, responsible for 62.9% of the overall predation events. Rats were responsible for only 22.9% of the events, and ate only small and medium eggs at both heights. Our experiment suggests that in New Caledonia, predation pressure by rats strengthens overall bird-nest predation, adding to that by native predators. Experimental rat control operations may allow reduced predation pressure on nests as well as the recording of biodiversity responses after rat population reduction.

Key words: bird-nest predation, forest birds, invasive rodents, island conservation, rat management.

Invasive species are recognized as one of the greatest threats to biodiversity worldwide, especially for island ecosystems (Blackburn et al. 2004). Island ecosystems are particularly vulnerable to species invasion for several reasons: first, their simplicity, i.e., a limited number of species and lower redundancy of different functional types; second, their uniqueness, i.e., high levels of endemism and presence of novel forms; and third, the existence of fewer trophic levels, particularly the virtual absence of terrestrial top predators (Simberloff and Rejmanek 2011). As native island species have generally evolved in the absence of mammalian predators, they have developed slow life history traits and lack appropriate anti-predator

responses, making them particularly vulnerable to invasive alien predators (Le Corre 2008; Carthey and Banks 2014).

Invasive rats represent a major threat to native island biodiversity, having been introduced by humans to more than 80% of the world's islands (Atkinson 1985; Towns et al. 2006; Harris 2009). *Rattus rattus* (Linnaeus, 1758; the black rat), *Rattus norvegicus* (Berkenhout, 1769; the Norway rat), and *Rattus exulans* (Peale, 1848; the Pacific rat) are considered to be among the most damaging of invasive species (Towns et al. 2006; Capizzi et al. 2014). These omnivorous and opportunistic rodent species have strong deleterious effects on overall island ecosystem functioning (Fukami et al. 2006;

Towns et al. 2009), as well as on various island taxa such as plants (e.g., Meyer and Butaud 2008; Pender et al. 2013), invertebrates (e.g., Wagner and Van Driesche 2010), reptiles (Towns 1996), and birds (e.g., Brown 1997; Robinet et al. 1998; Vanderwerf 2009).

Over recent decades, the pervasive negative impacts of invasive rats on island birds in particular have been documented, both for seabirds (e.g., Jones et al. 2008; Harper and Bunbury 2015) and for land birds (e.g., Brown 1997; Robinet et al. 1998; VanderWerf 2001; O'Donnell and Hoare 2012). Numerous species from different families and genera varying widely in ecology and size are impacted directly by rats, especially through predation of eggs, chicks, and adults (Atkinson 1985). Rats can also have indirect effects on birds via competition for food (Shiels et al. 2014), competition for shelter (Matsui et al. 2010), or even by inducing changes in bird behavior through predation risk perception (Massaro et al. 2008). As birds play a key role in several ecosystem processes (e.g., plant pollination, plant dispersal, nutrient depositing, etc.), bird decline may also cause major disruption to many important ecosystem functions, making it important to protect bird populations not only for their own sake, but also to preserve the ecosystem functions that they mediate (Sekercioglu 2006; Whelan et al. 2015).

To cope with these threats, many islands undertake invasive rat control or eradication projects to conserve and restore bird populations (e.g., Côté and Sutherland 1997; Howald et al. 2007; O'Donnell and Hoare 2012). The positive effects of rat control or eradication on bird populations are frequently cited, particularly on nesting success (e.g. Vanderwerf 2009; Jones et al. 2008; Pascal et al. 2008; Smith et al. 2010). For example, on Lavezu Island, the average breeding success of the Cory's shearwater *Calonectris diomedea* doubled when rats were controlled or eradicated (Pascal et al. 2008). In Hawaii, rodent control decreased predation on artificial and real nests placed on trees and the ground to mimic O'ahu 'Elepaio (*Chasiempis sandwichensis ibidis*) nests by 45% and 55%, respectively (VanderWerf 2001). However, the nature of rat impacts on birds is not always clear, and in some cases, bird populations may remain unaffected (Amar and Esselstyn 2014; Hervías et al. 2014). It is important to remember that the impacts of rats can vary according to ecological context (bird species, habitat, presence of other invasive predators, etc.), making generalization difficult (Ruffino et al. 2015). While most rat management projects have been conducted with the aim of protecting birds, they have not always been based on clear evidence of rat impacts on birds (Towns et al. 2006; Harris 2009). Since management projects involve a huge investment of time, resources and effort, assessing the effects of removal operations on native biodiversity is critical to ensuring optimal adaptive management (Westgate et al. 2013).

Rat impact is often assessed either by monitoring bird nesting success, by analyzing rat diet or by estimating bird population size via various methods [e.g., bird point counts, capture-mark-recapture (CMR), etc.; Towns et al. 2006; Ruffino et al. 2015]. Contrary to population size estimation, which requires long-term monitoring to record bird population responses, nest success monitoring can help evaluate the short-term effects of rat removal on birds, and may be a good proxy for bird population dynamics (Jones et al. 2008). However, a large number of nests have to be monitored to obtain accurate results, and checking nests may disturb bird reproduction. This is especially problematic for forest birds, access to whose nests is limited, and monitoring can lead to unexpected nest abandonment (Major & Kendal 1996). For this reason, artificial nests are a good option when assessing rat-induced risk to bird nests, affording larger sample sizes over a shorter period of time, and avoiding the risk of

disturbing reproduction (for reviews, see Major and Kendal 1996; Moore and Robinson 2004). In addition to revealing relative predation percentages before and after rat removal, artificial nests enable researchers to determine the influence of different factors such as egg size and nest height on nest survival (Stirnemann et al. 2015). Although rats are reported to impact all egg sizes, birds laying small eggs (e.g., passerines or small seabirds) are generally considered to be more vulnerable to rat predation than birds laying larger eggs (Prieto et al. 2003; Zarzoso-Lacoste et al. 2011; Latorre et al. 2013). Moreover, birds nest higher when predation risk is high (Thibault et al. 2002; Vanderwerf 2012), suggesting that predation risk decreases with nest height, even though rats are agile climbers (Foster et al. 2011).

Here, we sought to assess and better understand the influence of two sympatric invasive rats (*Rattus rattus* and *R. exulans*) on bird eggs in a dense evergreen rainforest of New Caledonia, using artificial nest monitoring. Our aims were to 1) assess the relative impact of invasive rats and other predator species on experimental nest survival, 2) estimate the relative sensitivity of experimental nests to predation in relation to egg size and nest height, and 3) inform stakeholders responsible for conducting adaptive management of potential impacts of rats on biodiversity.

Materials and Methods

Study site

This study was conducted in a dense evergreen rainforest (mean canopy height: 11 m) located between 550 and 950 m a.s.l. in the wilderness reserve of Mont Panié (20°37'30"S, 164°46'56"E, 5400 ha) in New Caledonia, South Pacific (Figure 1). Mont Panié reserve has been protected since 1950 because of its cultural importance and the high micro-endemism rates observed for most taxa (plants, insects, squamata) (Tron et al. 2013). The climate is moist subtropical, with a hot season between December and mid-April and a cool season between mid-May and September. The location of the study site, at the core of a primary rainforest, eliminated any possibility of edge effects influencing nest predation by altering nest visibility and accessibility to predators (Ruffell et al. 2014; Stirnemann et al. 2015).

Two species of invasive rats, *Rattus rattus* and *R. exulans*, are present in the study area. *R. exulans* was brought to New Caledonia around 3,000 years ago with the first Austronesian colonizers, while *R. rattus* arrived later with European settlers about 150 years ago (Beauvais et al. 2006). Rat population assessments were conducted previous to and after the study at different seasons in Mont Panié at the two sites where the artificial bird-nest experiment was carried out. The first trapping session was conducted on three line transects of 30 traps laid 20 m apart, 5 months before the artificial nest experiment. A total of four trapping sessions, each conducted over 5 consecutive nights, took place in May 2013, November–December 2013, September 2014, and April 2015. This sampling configuration represented a capture pressure low enough to be assumed not to interfere with the artificial nest experiment. A rat abundance index (number of captures per 100 trap-nights adjusted for the corrected number of trap-nights, Nelson and Clark 1973) ranging between 8.3 ± 9.2 and 46.8 ± 16.2 per 100 corrected trap-nights was reported (Figure 2). The proportion of *R. exulans* vs. *R. rattus* varied between 12.9 ± 18.1 and $30.6 \pm 37.2\%$, depending on the season.

Twenty-six species of birds breed in the study area (Tron et al. 2013 and Q. Duron, personal observations, 2014; Table 1), most of them between September and January. Fourteen of the species are

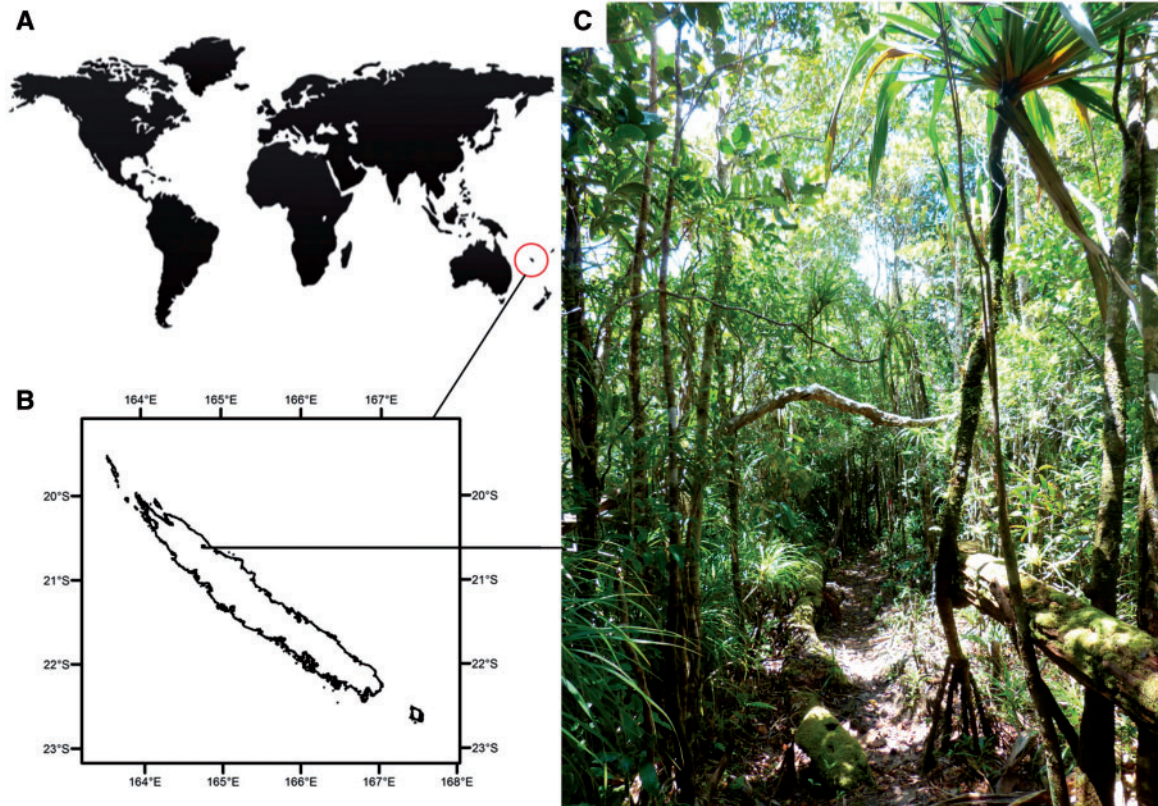


Figure 1. Location of the study in the wilderness reserve of Mont Panié, northern New Caledonia. (A) Location in the world. (B) Location in New Caledonia. (C) The dense evergreen rainforest of Mont Panié.

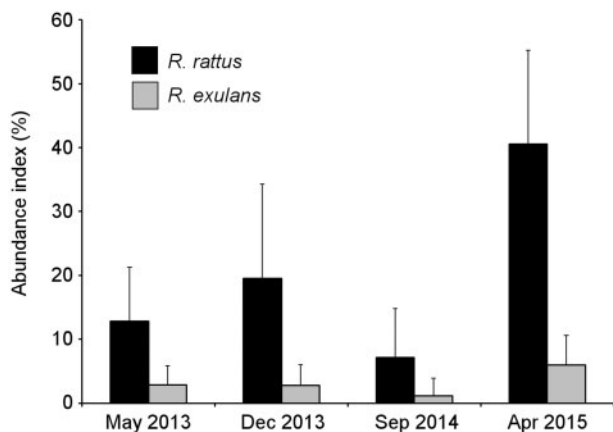


Figure 2. Abundance indexes of the two sympatric rat species during four trapping periods.

Abundance indexes (mean \pm 1SD), i.e., number of captures per 100 trap-nights, adjusted for the correct number of trap-nights, were provided for *R. rattus* and *R. exulans* during four 5-day trapping sessions (May 2013, December 2013, September 2014, April 2015) in the Mont Panié reserve.

small passerines, such as white eyes *Zosterops xanthochrous*, fantails (*Rhipidura* spp), and honeyeaters (Meliphagidae) all of which lay small eggs. Six are large species like raptors (Accipitridae), fruit doves (Columbidae), and crows *Corvus moneduloides*, which lay large eggs. The 6 remaining species, like cuckooshrikes *Chrysococcyx lucidus* and starlings *Aplonis striatus*, lay small-to-medium or medium-sized eggs. Depending on the species, bird-nest

location ranges from ground-level to high in the canopy, and nest construction ranges from no nest on the bare ground to complex constructions (Table 1).

Artificial bird-nest predation experiment

An artificial bird-nest predation experiment was conducted at two different sites (hereafter sites 1 and 2), located 500 m apart. The study was conducted over September/October 2013, i.e., the start of the reproduction period for most native birds in the area (Table 1, Barré et al. 2013). Artificial nests were constructed from wire mesh and garnished with moss, ferns, and leaves to mimic the real nests of a variety of native birds (from passerines to pigeons). Each artificial nest contained two eggs. Three different egg sizes were selected to represent the three size categories of native bird eggs (mean \pm 1SD of length \times width in mm taken from 30 eggs): Large, using hen eggs (*Gallus gallus*, $55.2 \pm 2.5 \times 42.7 \pm 0.8$); Medium, using quail eggs (*Coturnix japonica*, $33.9 \pm 1.5 \times 25.9 \pm 1.5$); Small, using zebra finch eggs (*Taeniopygia guttata*, $15.7 \pm 0.5 \times 11.5 \pm 0.4$). Nests were placed at two different heights, on the ground and in trees at a height of 1.50 m. Due to the extreme difficulty of fieldwork in Mont Panié area, it was impossible to set up nests higher in trees. Moreover, the nest height for passerine birds in Table 1 shows that around 9–10 bird species nest at very low heights (between the ground and 2–3 m high). In order to minimize the possibility of human scent affecting egg predation (Whelan et al. 1994), the eggs were handled with care after rubbing our hands in moss and leaf litter (Reitsma et al. 1990).

A total of 178 artificial nests was tested in five combinations (named hereafter “treatments”) of egg size and nest height: large eggs

Table 1. List of bird species present in the study area. Levels of endemism are ES = endemic species, WD = wide distribution, ESS = endemic sub-species. Reproduction period corresponds to the length of time from when eggs are first laid until chicks leave the nest. As no egg was measured in New Caledonia, measures were taken on related species (egg size proxy). L is the length of the egg and w is the width of the egg.

Family	Scientific name	Endemism	Reproduction period	Egg size category	Egg size proxy (L/w mm)	Nest height
Accipitridae	<i>Accipiter haplochrous</i>	ES	Oct–Mar	Large	No data	Canopy
	<i>Haliastur sphenurus</i>	WD	Oct–Jan	Large	No data	Canopy
Columbidae	<i>Columba vitiensis hypoenochroa</i>	ESS	June–Jan	Medium–Large	36–45/25–30	Low height or on ground
	<i>Ducula goliath</i>	ES	June–Dec	Large	50/30	Canopy
	<i>Drepanoptila holosericea</i>	ES	Aug–Jan	Medium–Large	No data	Low height 2–3 m
Psittacidae	<i>Trichoglossus haematodus deplanchei</i>	ESS	May–July, Nov–Dec	Medium	26–27/22–23	No data
Cuculidae	<i>Chrysococcyx lucidus layardi</i>	WD	no data	Small–Medium	No data	No data
Meliphagidae	<i>Myzomela caledonica</i>	ES	Nov–Feb	Small	No data	High in dense foliage
	<i>Philemon diemenensis</i>	ES	Aug–Feb	Small–Medium	No data	High in dense foliage
	<i>Phylidonyris undulata</i>	ES	Oct–Jan	Small	No data	Low height 0.5–2 m
	<i>Gerygone f. flavolateralis</i>	ESS	Sep–Jan	Small	No data	Low height 0–3 m
Eopsaltridae	<i>Eopsaltria flaviventris</i>	ES	Sep–Feb	Small	No data	Low height 0.7–2.2 m
Pachycephalidae	<i>Pachycephala caledonica</i>	ES	Sep–Jan	Small	No data	Low height 1–4 m
	<i>Pachycephala rufiventris xanthetraea</i>	ESS	Nov–Jan	Small	No data	Low height 0.3–1.5 m
	<i>Corvus moneduloides</i>	ES	Oct–Jan	Medium–Large	39–45/25–29	Medium height 2.5–10 m
Campephagidae	<i>Coracina analis</i>	ES	Sept–Jan	Medium	No data	Variable
	<i>Coracina caledonica caledonica</i>	ESS	Nov–Feb	Medium	32–36/22–23	Canopy
	<i>Lalage leucopyga montrosieri</i>	ESS	Nov–Jan	Small	No data	Canopy
Rhipiduridae	<i>Rhipidura fuliginosa bulgeri</i>	ESS	Sep–Jan	Small	15–16/11–12	Low height 1.5–3 m
	<i>Rhipidura spilodera verreauxi</i>	ESS	Oct–Jan	Small	No data	Low height 2–3 m
Monarchidae	<i>Clytorhynchus p. pachycephaloides</i>	ESS	Nov–Jan	Small	No data	High in dense foliage
	<i>Myiagra caledonica caledonica</i>	ESS	Nov–Jan	Small	18–19/13–14	Medium height 2.5–10 m
Sturnidae	<i>Aplonis striatus striatus</i>	ESS	Oct–Jan	Small–Medium	No data	Variable
Zosteropidae	<i>Zosterops xanthochrous</i>	ES	Sep–Feb	Small	16/12.5	Medium height 2–6 m
Megaluridae	<i>Megalurulus mariei</i>	ES	Nov–Jan	Small	No data	On ground
Estrildidae	<i>Erythrura psittacea</i>	ES	Oct–Jan	Small	No data	Trees hollows

on the ground, large eggs 1.5 m high, medium eggs on the ground, medium eggs 1.5 m high and small eggs 1.5 m high. Small eggs were not tested on the ground, as there is no small passerine species nesting on the ground in New Caledonia (Table 1). Along a line transect, at each location, spaced 50 m apart, a nest treatment was randomly selected from the five available and 20 nests per treatment were placed. However, because of the difficulty of obtaining small eggs, the “small egg 1.5 m high” treatment could only be tested at site 1. At site 1, 48 nests out of a total of 98 were placed on the rat trapping transect, the others being at least 50 m from the rat trapping transect. At site 2, 43 nests out of 80 were placed on the rat trapping transect. In order to verify that rat trapping (performed 5 months previously) had not interfered with the artificial nest experiment, we checked for a difference in rat predation between nests placed on rat transects and nests placed outside rat transects, with a χ^2 test for homogeneity.

Each nest was checked twice a day, at sunrise and sunset, to distinguish nocturnal from diurnal predation events over the first 7 days. Additional visits were then made, once a day, on days 11, 14 and 16 at site 1. If one of the 2 eggs was pierced, nibbled, or had disappeared, the nest was considered to be depredated (Martin and Joron 2003). When possible, egg fragments were used to identify the likely predators: tooth marks were clues of rat predation and perforation suggested bird predation.

In parallel with the artificial bird-nest predation experiment, 15 camera traps (11 Ambush Flash Cuddeback® and 4 Ambush IR Cuddeback®) were set-up at both sites to identify predator species by monitoring additional nests containing large or medium eggs

placed on the ground or 1.5 m high. Cameras were not placed near the nests used for the artificial bird-nest predation experiment, to avoid any possible influence on predator behavior (Richardson et al. 2009). The collected pictures, coupled with predation clues, helped to further identify the different species of predators involved. However, it was difficult to distinguish each rat species with certainty on pictures and predation clues were the same. Consequently, despite the fact that *R. exulans* and *R. rattus* may have different impacts on bird nests, we could not differentiate between egg predation events by *R. exulans* and by *R. rattus*.

To compare egg survival between the two sites, and according to egg size (three treatments) and nest height (two treatments), Kaplan Meier survival curves were drawn and their estimators were compared using Cox proportional hazards regression models and the Breslow χ^2 to test for significance, as described by McKinnon et al. (2010). To assess any differences in predator identity among the five treatments, Fisher’s exact test was used. These analyses were performed with R version 2.15.3 (R Core Team 2013).

Results

No difference in predation percentage was recorded between nests placed on rat trapping transects and nests placed outside rat transects ($\chi^2 = 0.033$, $df = 1$, $P = 0.856$). Overall, only 22 of the 178 artificial nests tested were depredated during the first seven days (12.4%). At site 1, where nests could be monitored over 16 days, 21 additional nests were depredated. For the purpose of comparison

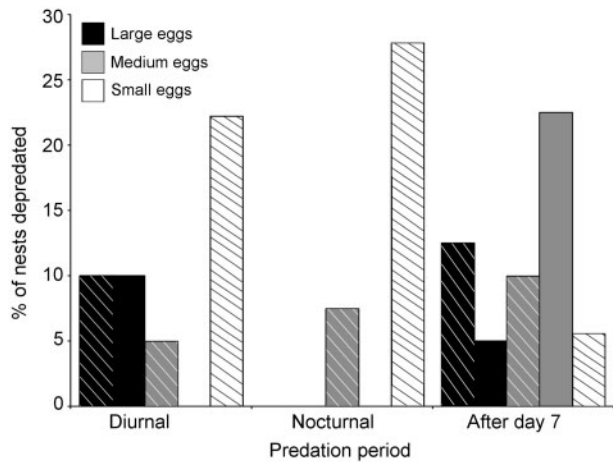


Figure 3. Proportion of nests depredated for the five treatments during each predation period. Proportion of nests depredated during day (diurnal) and night (nocturnal) over the first 7 days at sites 1 and 2, and day and night taken together thereafter at site 1 only. Nests located 1.5 meters high are hatched.

between sites, since the treatment involving small eggs at a height of 1.5 m could only be set-up at site 1, only medium and large eggs are considered hereafter. Predation at site 2 (3%, two nests) was significantly lower during the first seven days compared to site 1 (13%, 10 nests; Breslow $\chi^2 = 6.3$, $P = 0.012$).

For medium and large eggs only, over the 7 days of the experiment, nest survival was not significantly affected by the interaction between egg size and nest height but a trend was observed (Breslow $\chi^2 = 7.74$, $P = 0.052$, Figure 3). Medium eggs on the ground were not predated. The predation percentages were 10% for large eggs on the ground, 10% for large eggs 1.5 m high, 0% for medium eggs on the ground and 12.5% for medium eggs 1.5 m high. At site 1, over the 16 days of the experiment, for large, medium, and small eggs, nest survival was not affected by the interaction between egg size and nest height (Breslow $\chi^2 = 3.57$, $P = 0.467$, Figure 3). The predation percentages were 30% for large eggs on the ground, 40% for large eggs 1.5 m high, 45% for medium eggs on the ground, 40% for medium eggs 1.5 m high, and 50% for small eggs 1.5 m high.

Of the 22 nests depredated during the 7 days of daily monitoring, 14 nests were depredated in daytime and 8 at night (Figure 3). Nests with large eggs were only depredated in daytime (36.4%), while medium and small eggs were depredated both during the day (27.3%) and at night (36.4%). There was no distinction between predation during the day and at night from day 8 to day 16 at site 1 (Figure 3). Because of predation clues (shell remains, predator marks) and the timing of the event, a likely predator could be assigned to each of the 43 predation events. Predators identified were, by decreasing order of importance, New Caledonian crows (62.9%), rats (22.9%), ants (11.4%), and pigs (2.9%) (Figure 4). The 15 camera traps detected 14 nocturnal rat visits (but no predation) and one diurnal predation by a New Caledonian crow (*Corvus moneduloides*). Predators varied in their choice of prey from the five treatments ($P = 0.001$, Fisher's exact test). Crows ate all egg sizes (but mainly large eggs) at any height, rats consumed medium and small eggs at any height (but no large eggs), while ants ate only small eggs (Figure 4). Moreover, as far as medium and large eggs are concerned, both crows and rats predated more eggs placed 1.5 m high (respectively 14 and 3) than on the ground (respectively 6 and 1).

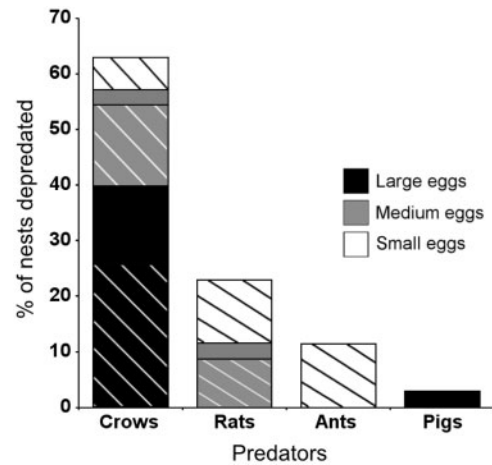


Figure 4. Nest predation for the five treatments showing the relative impact of the different predators. Nest predators were, by order of importance, crows, rats, ants, and pigs. Nests located 1.5 m high are hatched. Pigs only had access to nests on the ground.

Discussion

In this artificial bird-nest experiment carried out in a dense evergreen rainforest of New Caledonia, the main bird egg predators included a native bird, the New Caledonian crow *Corvus moneduloides*, and to a lesser extent invasive rats of genus *Rattus*. The percentage of nests preyed upon was slightly less than three times lower for rats than for native crows. Corvids are already known to be major predators of bird nests (Ekanayake et al. 2015; Madden et al. 2015), and in our case, the native crow's impact on native bird nests may be much higher than the impact of invasive rats. Further studies on real bird nests may be needed to corroborate this result. However, both corvids and rodents use distinctive cues to find nests and eggs, corvids being visual predators and rodents being olfactory predators (e.g., Ekanayake et al. 2015). Moreover, New Caledonian crows are known for their cognitive capabilities (Weir et al. 2002). We cannot, therefore, exclude the possibility that crows may have followed the investigators checking our nests, thereby finding the nests more easily than without a human presence.

Another possible limitation to our results is that artificial nests do not necessarily reflect predation percentages for real nests. Their use has been criticized (Major and Kendal 1996; Moore and Robinson 2004) on the grounds that artificial nests may not be recognized as real nests by predators, in part because of the absence of parents protecting their nest and thus giving away its location. However, here our camera traps detected invasive rats actually visiting the artificial nests, showing that they were able to find them even if they did not necessarily prey upon the eggs. A possible reason is that they may not always have the required skills to break and consume these eggs (Zarzoso-Lacoste et al. 2011). Moreover, Moore and Robinson (2004) emphasize that predation measured using artificial nests differs frequently from those measured monitoring real nests, which suggests that results of predation percentages need to be considered with caution. That said, artificial nests have been used successfully as a proxy for studying relative predation percentage among different treatments (e.g., Robinet et al. 1998; VanderWerf 2001; Thibault et al. 2002). Furthermore, artificial nest studies are currently the only means of obtaining large sample sizes without disturbing real nests, and of carrying out studies with

standardized parameters such as egg size and nest height (Stirnemann et al. 2015).

Similar artificial nest experiments conducted with quail eggs in Hawaii in mesic forests showed a predation percentage by rats two to three times higher than in our experiment (VanderWerf 2001). High predation by rats (51–87%) was also recorded during an artificial nest experiment conducted on Loyalty Islands (New Caledonia archipelago) (Robinet et al. 1998) and a 41% predation percentage was also registered in Tahiti Island forests (Polynesian archipelago) (Thibault et al. 2002). On Mediterranean islands, experiments with artificial nests used to mimic the pallid swift nest *Apus pallidus* were conducted on rat-invaded and rat-free islands. The nest predation percentage on the rat-invaded island was twice as high as that on the rat-free islands (93% versus 47%). On rat-free islands, most predation was by the raven (*Corvus corax*), gulls, and small birds (Penloup et al. 1997).

However, more in line with our results, in indigenous forests of New Zealand, predation percentages recorded in rat control areas showed smaller or no differences from areas without rat control (respectively 37% versus 12% in December and 20% for both areas in January) (Innes et al. 2015). Even lower predation percentages (4%) were recorded in a Hawaiian montane forest in presence of rats (Amarasekare 1993). These differences indicate that the intensity of rat impacts on bird reproduction can vary greatly and the ecological conditions affecting the magnitude of rat impacts on birds remain poorly known (Ruffino et al. 2015). Amarasekare (1993) attributed their low predation percentages either to low rat presence or to a great abundance of alternative foods. In our setting, the hypothesis of abundance of alternative food resources (Townes et al. 2006; Catry et al. 2007; Ruffino et al. 2015), i.e., plants, invertebrates, and squamata, is plausible. Species composition and relative abundance of plants and animals in the environment can influence the rat diet (Catry et al. 2007; Russell and Ruffino 2012; Shiels et al. 2013). Forest birds, contrary to colonial seabirds which breed in high densities and may be more attractive for rats, are less abundant and scattered. Consequently, alternative food resources may be more abundant and less costly to find and forage upon than forest birds breeding in low densities.

The second purpose of our artificial bird-nest experiment was to detect differences in rat predation risk according to egg size and nest height. As very few eggs were actually eaten by rats, we were unable to accurately compare predation risk among the five treatments tested. However, we did determine that these few occurrences of rat predation concerned medium and small eggs alone. This result is consistent with other studies showing that predation risk decreases with increasing egg size (Zarzoso-Lacoste et al. 2011; Latorre et al. 2013). Regarding the effect of nest height on rat predation, in most cases predation occurred at a height of 1.5 m. Consequently, even if our results do not allow us to test statistical significance, we hypothesize that nesting at low-height does not allow reducing predation risk compared with ground nesting. Rats are able to climb and forage in trees, especially *R. rattus* (Foster et al. 2011). In the same way, Robinet et al. (1998) showed that the highest nest sites of a parakeet species did not offer better protection against *R. rattus* and *R. exulans* than lower nests, and Stirnemann et al. (2015) observed that birds nesting both high and low in the canopy were at similar risk of predation by *R. rattus* in Samoan forests.

To conclude, even though invasive rats do not appear to be the main bird-nest predators, their presence in Mont Panié forest area seems to strengthen overall bird-nest predation, adding to that by native predators. Moreover, invasive rats may also impact bird communities via other processes not investigated here. First, rats may also predate

birds at chick and adult stages (Atkinson 1985; Jones et al. 2008). In addition to direct impacts by predation, invasive rats may have indirect impacts through food competition, particularly with frugivorous and insectivorous birds (Shiels et al. 2014), or by inducing changes in bird behavior due to predation risk perception (Massaro et al. 2008; Vanderwerf 2012). Contrary to predation, competition between invasive rats and birds is poorly documented. It may, however, be responsible for some bird population declines. For example, trophic niche overlap between the critically endangered Tuamotu Kingfisher *Todiramphus gambieri* and invasive rats (*R. rattus* and *R. exulans*) may induce competition for resources, particularly invertebrates and lizards, and may be a cause of depletion of Tuamotu Kingfisher populations (Zarzoso-Lacoste 2013). Latham (2006) suggested possible food competition between North Island brown kiwi chicks *Apteryx mantelli* and *R. rattus* on Ponui Island, New Zealand. The perception of predation risk may also strongly influence bird reproduction. For example, Zanette (2011) found that, in song sparrows *Melospiza melodia*, playback of predation calls reduced the number of offspring produced yearly by 40%. Similarly, the mere presence of rats may limit the suitability of some Mediterranean islets for breeding by Yelkouan shearwaters (*Puffinus yelkouan*, Bourgeois et al. 2013). All of this highlights the need for a more holistic ecosystem approach to studying rat impacts (Ruffino et al. 2015).

Rattus exulans and *R. rattus* are long- or medium-term standing inhabitants of New Caledonia, introduced respectively 3,000 years ago and 150 years ago. We therefore cannot discard the hypothesis that invasive rats were responsible for an initial fall in bird community diversity when they colonized New Caledonia (Harper and Bunbury 2015). A “filter effect” (Balmford 1996) may have favored bird species that are relatively less sensitive to rat impact. Indeed, the current New Caledonian forest bird community has been described as depauperate. For example, in three New Caledonian caves, 32 bird fossil species of which 11 are currently extinct were found in deposits contemporary with human and *R. exulans* arrival (Balouet and Olson 1989). Thus, ancient rat introductions may already have helped deplete the indigenous bird community. From that perspective, rat control could have positive effects on the bird community by limiting actual predation (VanderWerf 2001), perceived risk of predation (Massaro et al. 2008, Vanderwerf 2012), competition (Shiels et al. 2014), and indirect influences through the disruption of ecosystem function (Townes et al. 2009).

It seems that, in New Caledonian rainforests, there are justifications for implementing and continuing rat control projects. Rats strengthen the overall predation on bird eggs and impact other endemic and threatened taxa such as macro-insects (wetas, stick insects) or squamata (Duron et al. unpublished data). Experimental rat control operations may allow the recording of biodiversity responses after rat population reduction (VanderWerf 2001; Le Corre et al. 2015), which would pave the way towards optimal adaptive management (Westgate et al. 2013). Scientists and managers need to work together to ensure that rat control operations will enhance our knowledge of rats, which should lead to more effective conservation measures (Ruffino et al. 2015).

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