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Is there a competition between endemic pink pigeon (*Nesoenas mayeri*) and invasive Madagascar turtle-dove (*Nesoenas picturata*) in lowland Mauritius?

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Is there a competition between endemic pink pigeon (*Nesoenas mayeri*) and invasive Madagascar turtle-dove (*Nesoenas picturata*) in lowland Mauritius?

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Abstract

Mauritius, one of the Mascarene islands in the Indian Ocean, was identified as a biodiversity hotspot by IUCN and as an Important Bird Area by BirdLife International, mostly because of its endemic species richness. Habitat destruction and introductions of many alien invasive species already caused extinctions and reduction of populations to critical low levels. The endemic pink pigeon (*Nesoenas mayeri*), one of Mauritius emblematic species, has recovered from less than 20 birds in the mid 1970s to 343 free-living individuals in 2014 among which the subpopulation established on Ile aux Aigrettes, a Nature Reserve offshore islet. This study investigated if pink pigeons were competing with exotic Madagascar turtle-dove (*Nesoenas picturata*), a sister species widespread on the island, for food and nesting sites. The reproductive success of both species was also investigated by nests monitoring. Significant differences in the diet, foraging behaviour and nesting preferences of pink pigeon and Madagascar turtle-dove were found on Ile aux Aigrettes. Pink pigeon was predominantly eating leaves and favouring areas of mature canopy forest, preferring tall ebony trees *Diospyros egrettarum* for nesting. Madagascar turtle-dove was mostly a fruit eater and was nesting at lower levels, with no big preference in the plant species choice, and in open areas or forest edges. Proportion of successful nests was 3 times higher for the exotic *N.picturata*. Differing ecological requirements indicate that divergence between these congeners may be sufficient for them to coexist and exploit contrasting resources on this restored islet. Nevertheless, we discuss the implications of such coexistence in relation to pathogen *Trichomonas gallinae* transmission which can affect pink pigeon long-term recovery programme.

Key words: Endemism, threatened species, invasive alien species, foraging behaviour, nesting preferences, breeding success

1. Introduction

Oceanic islands are characterized by high levels of biodiversity and species endemism (Alder, 1994). These islands are also more vulnerable facing exotic species introductions (Baillie et al., 2004). Invasive alien species may threaten native species as direct predators or competitors, as vectors of disease, or by modifying the habitat or altering native species dynamics. Indeed, they may out-compete native species, repressing or excluding them and, therefore, fundamentally change the ecosystem of the island (MA, 2006). On small islands, exotic species introduction is now comparable with habitat degradation as the lead cause of biodiversity loss (Dulloo et al., 2002; Wanless, 2002; Baillie et al., 2004; Norris & Harper, 2004; Watson et al., 2004).

Mauritius, one of the Mascarene Islands in the south-west Indian Ocean, 890 km east of Madagascar, is one of the highest priorities for conservation of threatened species because of its biological richness and the high degree of threat to its wildlife (Collar & Stuart, 1988; Myers et al., 2000; Brooks et al., 2002). Actually, Mauritius was designated as an Important Bird Area by BirdLife International on one hand and the World Conservation Union (IUCN) identified no more than 49 invasive alien species on the other hand (IUCN/SSC/ISSG, 2004). This introduction of many exotic species added to the 95% reduction of native vegetation (Safford, 1997) have already caused the extinction of 17 endemic bird species (BirdLife International, 2014), including that of the dodo *Raphus cucullatus* (Cheke, 1987) and population reduction to critical levels in 9 others (BirdLife International, 2014). In fact, the Mauritian kestrel *Falco punctatus*, echo parakeet *Psittacula eques* and the pink pigeon *Nesoenas mayeri*, have been considered among the world's rarest and most endangered birds (Jones, 1987).

The last remaining endemic columbid species, the pink pigeon *Nesoenas mayeri* (Prévost, 1843), is an endangered (IUCN Red List, 2013) forest dwelling pigeon which feed mostly on leaves of trees. It was probably once widespread on the island, but by the early 1980s the population was restricted to 30 km² of relict forest habitat (Collar & Stuart, 1985; Jones, 1987; Jones & Owadally, 1988). In 1975, the total population size was estimated at 10-20 birds (Collar & Stuart, 1985; Jones, 1987) and by 1990 only 9 or 10 birds remained. This grim situation has attracted considerable conservation efforts (Jones, 2007). Therefore, a restoration programme has comprised captive-breeding, reintroduction and management of wild and free-living populations. A captive population was established on Mauritius in 1976 and at Jersey Zoo in 1977 (Jeggo, 1978; Jones & Owadally, 1988; Jones, 1995), and reintroduction into native forest began in 1987 (Jones et al., 1992). Then, the species and habitat recovery programme has successfully increased the pink pigeon population size. In April 2014, the known free-living population, divided into 6 subpopulations, was estimated at 343 birds (Currooah, 2014).

In addition to the endemic *Nesoenas* pink pigeons, confined to Mauritius and Reunion, *Nesoenas* (formerly *Streptopelia*) turtle-doves once occurred on all three Mascarene Islands. In Mauritius and Reunion, all but the Mauritius pink pigeon *N. mayeri* had disappeared during the 18th century. Introductions of Madagascar turtle-dove *Nesoenas picturata* (Temminck, 1813) took place on Mauritius and Reunion after the extinction of the native birds, and present populations of *N. picturata* are all introduced and now widespread across Mauritius (Hume, 2013). *N. mayeri* and *N. picturata* are sister species, closely phylogenetically related (Johnson et al., 2001), and are both present on Ile aux Aigrettes where one of the pink pigeon subpopulation is established as part of the conservation programme. The present research sets out to examine the possible interaction between endemic pink pigeons and introduced Madagascar turtle-doves occurring sympatrically in lowland habitat on the offshore islet of Ile aux Aigrettes. The specific aims of this study were: (1) to investigate reproductive success, food and nesting site preferences of the two species (2) to compare these parameters in order to know if they compete for resources and if exotic *N.picturata* is out-competing *N.mayeri* or is acting as a brake to its recovery (3) to consider the implications of the results for the long-term restoration of the pink pigeon.

2. Materials and methods

2.1. Study area and species characteristics

2.1.1. Study area

Fieldwork was carried out from October 2013 to March 2014 on Ile aux Aigrettes (20°25’12”S, 57°43’58’’E), a small 26 ha coralline limestone islet located 700 m off the south-east coast of Mauritius (Fig.1). It was declared a Nature Reserve in 1965 and is under active management of the Mauritian Wildlife Foundation since 1986. The islet contains the remnants of a unique coastal vegetation type that once existed on the coastal and lowland areas of Mauritius.

A continuing habitat recovery programme has re-established this wide range of indigenous Mauritian flora where shallow soils restrict forest canopy height to fairly low levels (Parnell et al., 1989). Much of the island is covered by coastal scrub vegetation, dominated by small trees and shrubs including *Ehretia petiolaris*, *Tarenna borbonica* and *Scaevola taccada*, with an average height of 2.5 m. Areas of mature canopy forest, with an average height of 4-5m but some trees reaching 7-8m, are dominated by lowland ebony *Diospyros egrettarum*, together with *Dracaena concinna*, *Gastonia mauritiana* and *Eugenia lucida*, and have an almost continuous ground cover of the native fern *Phymatodes scolopendria* (Parnell et al., 1989). *Leucaena leucocephala* is the most problematic exotic species, forming monospecific stands which out-compete the native flora, but is kept under control by regular weeding. Exotic mammalian predators (black rat *Rattus rattus*, mongoose *Herpestes auropunctatus*, feral cat *Felis catus* and crab-eating macaque *Macaca fascicularis*), have been eradicated (Varnham et al., 2002) or were never present. The island is marked into a 12.5 m^2 grid system with pegs driven into the surface substrate (Garrett et al., 2007).

2.1.2. Species characteristics

On Ile aux Aigrettes, pink pigeon subpopulation counted 39 birds in April 2014 (Morgan, 2014). As a result of intensive monitoring, these birds have been individually marked with metal ID and unique plastic colour combination leg rings (Jones, 2004; Bunbury et al., 2008). Concerning the exotic Madagascar turtle-doves, their density on the island was estimated to be 55 individuals per hectare in February 2014 using the “strip transects” sampling method, by walking 16 transects of 36*6 m^2 which locations were randomly chosen (Sutherland, 2000; Buckland et al., 2008). Madagascar turtle-dove population size can be estimated to approximately 1429 in February 2014.

2.2. Nest searching and monitoring

For pink pigeons, nests were found by following adults carrying nesting material, flying back to the nest for the change-over during incubation or by searching in known pairs’ territories. Madagascar turtle-doves nests were found by doing random searches as they were widespread on the island. To determine outcome, all the nests were monitored every 3 days during the whole breeding attempt. When access was not possible, nests were checked with a pole and mirror. In addition, the following nest characteristics were noted: plant species, height of plant and height of nest.

Based on this data collection, hatching, breeding and nesting success were calculated. For pink pigeons, as nests were always monitored from earliest stage to fledgling, hatching success was defined as the number of young in relation to the total number of eggs per nest (hatchability was calculated for non-predated clutches only). Breeding success refers to the number of fledglings in relation to the total number of eggs and nesting success represents the number of nests with at least one fledgling in relation to the total number of nests (Förschler & Kalko, 2006). Madagascar turtle-dove nests were often discovered after egg-laying has started and were not always followed until completion. Moreover, it seems that successful nests were found with a higher probability than unsuccessful ones. That is why another method was used to calculate the breeding parameters in order to avoid any bias while taking the entire dataset into consideration. In fact, Mayfield (1961, 1975) pointed out that under these circumstances the proportion of successful nests is biased high relative to actual nesting success. Therefore, for Madagascar turtle-dove's breeding parameters calculation, the appropriate sampling unit would be the number of days the nests were exposed to the hazards of predation, human disturbance and/or bad weather conditions (i.e during a cyclone).

2.3. Diet assessment

2.3.1. Feeding observations

For both species, feeding observations were taken on the field with the random method, which was identified as the best method to get the more data on IAA (Edmunds, 2006). All feeding observations made during the everyday routine were taken into account. Food item consumed and feeding height were noted.

2.3.2. Stomach contents

In the framework of invasive alien species control, Madagascar turtle-doves were killed when trapped on the islet. It was thus interesting to do postmortem and to study stomach contents in order to collect more information about their diet. In most cases, seeds and other contents were easily identified.

2.4. Statistical analysis

All statistical analyses were performed using R version 3.1.0 (R Development Core Team, 2014). Results are expressed as means ± SE. The differences in trees height, nests height and feeding height between the two species were tested using Mann-Whitney *U*-tests. Fisher's exact tests were done in order to compare plant species chosen for nesting and dietary composition between the two bird species. Results were considered significant if *p*-value < 5%.

3. Results

3.1. Reproductive success

On Ile aux Aigrettes, between January 2013 and February 2014, pink pigeons built 46 nests, layed 58 eggs and raised 28 squabs among which 9 successfully fledged. Between October 2013 and February 2014, 63 nests of Madagascar turtle-doves were monitored for a total of 106 eggs and 49 squabs among which 39 birds fledged. All the three breeding parameters were greater for exotic Madagascar turtle-dove than for pink pigeon, respectively hatching success : 51.1% vs. 31.1%, breeding success : 36.8% vs. 15.5% and nesting success : 62.0% vs. 19.6%.

3.2. Nesting sites

For nesting, the two species were targeting different plants (Fisher's exact test: $P < 0.001$; Fig.2). In fact, pink pigeons targeted only 7 tree species such as predominant *Diospyros egrettarum* (50%), *Eugenia lucida* (28%) and *Tarenna borbonica* (11%), whereas Madagascar turtle-doves were nesting in 13 species among which *Maytenus pyria* (23%), *Eugenia lucida* (22%), *Diospyros egrettarum* (12%), *Tarenna borbonica* (10%) and *Gastonia mauritiana* (7%). Moreover, pink pigeons used significantly taller trees than Madagascar turtle-doves. Mean ± SE height (meters) of pink pigeons nesting trees was 4.55 ± 1.2 compared to 3.41 ± 0.87 for Madagascar turtle-doves (Mann-Whitney *U*-test: $U = 2283.5$, n = 109, $P < 0.001$). Pink pigeons were also building nests higher than Madagascar turtle-doves with respectively 3.80 ± 1.07 vs. 2.70 ± 0.87 meters (Mann-Whitney *U*-test: $U = 2330$, n = 109, $P < 0.001$; Table 2).

3.3. Foraging behaviour

Foraging behaviour was significantly different between the two species as pink pigeons were feeding in taller trees than Madagascar turtle-doves (mean ± SE, pink pigeon: 4.68 ± 0.3, Madagascar turtle-dove: 2.47 ± 0.15; Mann-Whitney *U*-test: $U = 5094.5$, n=196, $P < 0.001$; Table 3) and were feeding higher (mean ± SE, pink pigeon: 3.83 ± 0.29, Madagascar turtle-dove: 0.29 ± 0.07; Mann-Whitney *U*-test: $U = 7128$, n = 196, $P < 0.001$; Table 3). In fact, 64% of Madagascar turtle-doves fed on the ground.

Dietary composition also differed between pink pigeons and Madagascar turtle-doves (Fig.3). Pink pigeons were predominantly eating leaves whereas Madagascar turtle-doves were more fruits and seeds eaters. Pink pigeons feeding observations found that 71 of 102 (70%) foraging events targeted leaves whereas fruits contributed to the largest part of the Madagascar turtle-doves dietary intake (70/94, 74%; Fig. 3). At the same time, the stomach contents study and seeds identification of these contents revealed that Madagascar turtle-doves were also feeding on fruits that were not found of the islet. Watermelon seeds were found in 14 of 14 post mortem, bitter melon in 2 of 14, pomegranate in 2 of 14 and papaya in 1 of 14.

4. Discussion

4.1. Reproductive success

Endemic pink pigeon has a lower reproductive success than exotic Madagascar turtle-dove with, respectively, 31.1% vs. 51.1% hatching success, 15.5% vs. 36.8% breeding success and 19.6% vs. 62% nesting success. The proportion of successful nests is 3 times higher for exotic Madagascar turtle-dove. It is not surprising as reproductive traits are crucial for the establishment and maintenance of populations in new areas, and therefore for the invasion process (Correia et al., 2014). Concerning the low productivity of pink pigeon, one hypothesis is the high inbreeding depression which is influencing its reproduction and which effect is known to be more severe in the wild than in captivity where eggs are artificially incubated and chicks hand-reared and so to compensate (Swinnerton et al., 2004). Moreover, there were only few pink pigeons breeding attempts which can be linked with the subpopulation advanced age and with the considerable unbalanced sex-ratio which is male dominant (Males: 27, Females: 10, Juveniles: 2, in April 2014; Mauritian Wildlife Foundation, unpublished report) that creates a high number of single males which are not breeding.

4.2. Nesting sites

The two species do not have same habitat requirements concerning nesting. Pink pigeons are selecting higher trees and favours two main species: the ebony tree *Diospyros egrettarum* and *Eugenia lucida*, while Madagascar turtle-doves are nesting in more different plant species, at lower levels and even in open areas and forest edges. This exotic species seemed less demanding regarding nesting conditions, in fact open areas and edges are usually linked with higher disturbance or predation rate. In the case of this predator-free islet, it is humans' disturbance that can impact these nests. Madagascar turtle-doves were also seen using pink pigeons' old and abandoned nests, whereas the contrary is not verified. Pink pigeons were always seen building their nests from scratch and were putting more time into building. One hypothesis can be that Madagascar turtle-dove has a different strategy and that their nests and nest sites quality is less important as they have more and quicker breeding attempts as an invasive species (Correia et al., 2014). It is known that ambient temperature determines numerous aspects of bird biology, such as breeding biology (Cotton, 2003; Broggi et al., 2004; Cooper et al., 2005; Tieleman, 2007). Thus, another hypothesis could be that the height of nests is a response to heat exposure, as temperature and nest heat exposure affect nestling growth and adult stress during incubation (Salaberria et al., 2014). Pink pigeons could nest high due to an adaptation to the wet forests that were covering half inland Mauritius once, to find a balance between having enough sun exposure in this cool and wet forest. But it could also be a recent adaptation, in order to protect themselves against the exotic predators that were not present before (i.e the black rat, brown rat, crab-eating macaque and mongoose).

4.3. Foraging ecology

Feeding observations indicated that pink pigeon is primarily folivorous (70% of diet), mostly targeting endemic *Hilsenbergia petiolaris* (38%) aswell as invasive *Leucaena leucaena* (22%), but is also eating berries of *Ficus reflexa, Hilsenbergia petiolaris* and

Passiflora suberosa (28%). Madagascar turtle-dove is predominantly feeding on fruits and seeds (74% of diet) of various species among which *Dodonea viscosa* (20%), *Gastonia mauritiana* (12%), *Hilsenbergia petiolaris* (12%) and *Euphorbia hirta* (11%) and also on flower parts fallen on the ground (11%). Pink pigeons are staying on the islet, feeding high in the trees whereas Madagascar turtle-dove is mostly feeding on the ground, except when feeding on *Hilsenbergia petiolaris* berries, going up in the trees. In Seychelles, where Madagascar turtle-doves can be found, the same observations were done. They were always found on the ground, foraging among grasses or under thick bushes but not in the trees present on the island (Rocamora et. al, 2003). Despite their ability to fly over 100 meters (Rocamora et. al, 2003), as it can be observed on one occasion, they were reluctant to take off when disturbed and preferred to run, sometimes with a few wings flapping but always keeping very close to the ground. On the other hand, it is now known that the species also fly to the mainland to find more food according to the stomach contents study (salted peanuts, watermelon, papaya, bitter melon and pomegranate). The two species do not have the same diet nor the same foraging behaviour, it would appear that they do not exploit the same feeding resources and do not compete for it on Ile aux Aigrettes.

4.4 Conclusion and perspectives

This study found significant differences in the diet, foraging behaviour and nesting preferences of pink pigeon and Madagascar turtle-dove on Ile aux Aigrettes. Pink pigeon *Nesoenas mayeri* is predominantly eating leaves and favouring areas of mature canopy forest with ebony trees *Diospyros egrettarum* for nesting. These requirements must be linked with the fact Mauritius was once almost entirely covered by forest and particularly by a wet one on the higher and wetter grounds (Florens, 2012; Parnell et al., 1989). In contrast, the Madagascar turtle-dove *Nesoenas picturata* is feeding on fruits and seeds, at ground level. It is more generalist for nesting tree species preference and it can nest lower and in areas of open, immature forest and forest edges, like a grassland bird. Moreover, the stomach contents study revealed Madagascar turtle-doves were going to the mainland to search for food and coming back to feed their chicks staying on Ile aux Aigrettes. This, and the fact they were highly abundant between October and February, seemed to show they were coming to the predator-free islet in order to breed and raise squabs. The offshore islet must be seen as an advantageous place to breed but with a lack of resources, as they were going to the mainland to feed, apparently around market places according to human wastes and fruits found during necropsies.

According to these results, the two species do not seem to compete for food nor for nesting sites, the divergence between them being sufficient for coexistence and exploitation of different resources on this islet. Nevertheless, the increase of Madagascar turtle-dove population on Ile aux Aigrettes, due to a greater reproductive success, could lead to saturation of the islet carrying capacity. Moreover, there is the problem of birds being vectors of pathogens. In fact, *Trichomonas gallinae*, protozoan parasite which causes avian disease Trichomonosis, is one of the major population limiting factors for pink pigeons (Bunbury et al., 2008).

Pink pigeon restoration program permits to increase the range and security of this threatened species, but it is still important to make sure the exotic species expansion is not acting as a brake to its recovery. Total eradication of Madagascar turtle-doves could not be done as the islet is close enough to the mainland for birds to fly by, but managing population by eggs removal or by trapping could probably maintain the population at lowest level (Solow et al., 2008).

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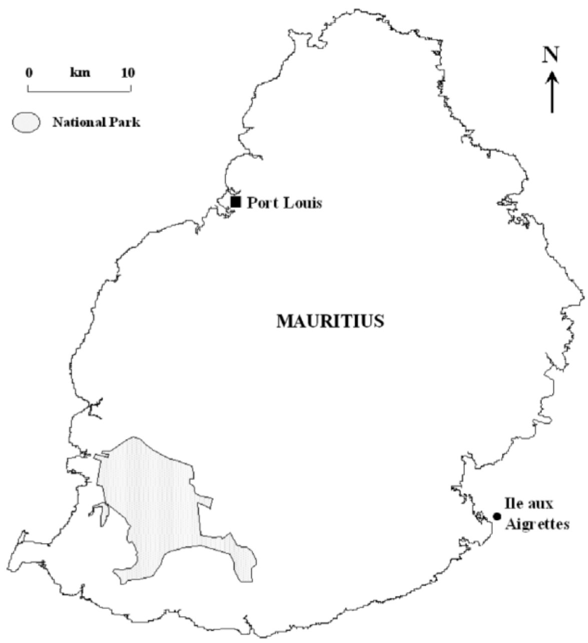
0 km 10
National Park
N
Port Louis
MAURITIUS
Ile aux Aigrettes

Fig. 1.

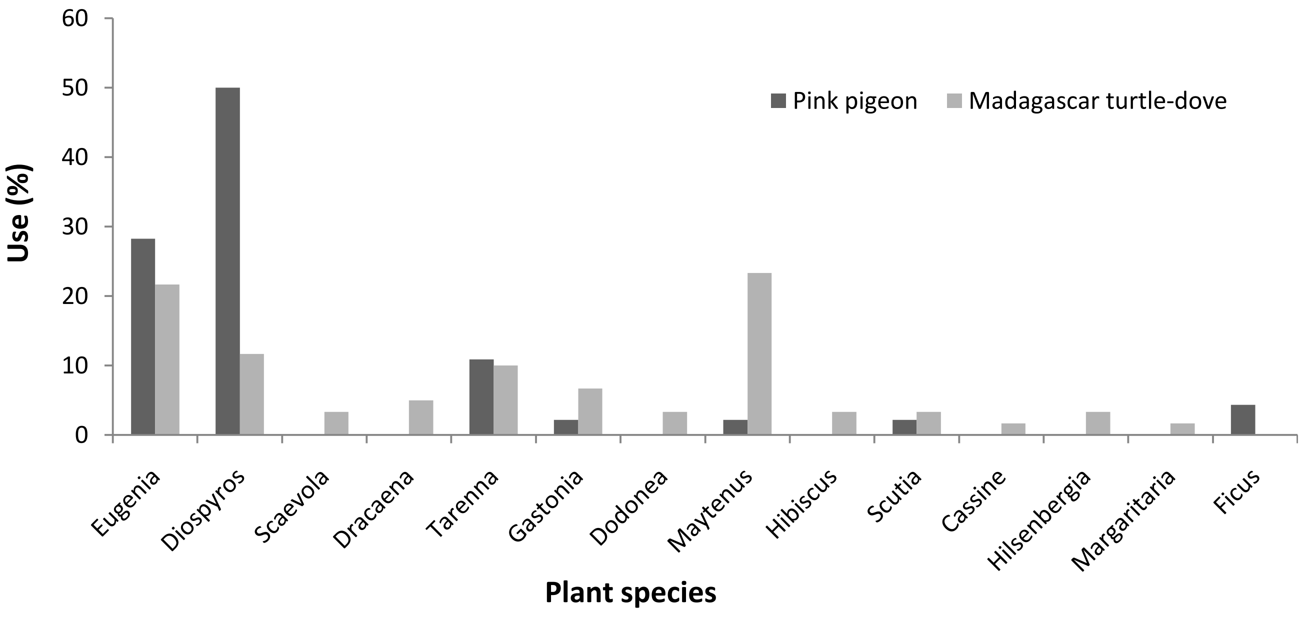
60
50
40
30
20
10
0
Use (%)
Pink pigeon
Madagascar turtle-dove
Eugenia
Diospyros
Scaevola
Dracaena
Tarenna
Gastonia
Dodonea
Maytenus
Hibiscus
Scutia
Cassine
Hilsenbergia
Margaritaria
Ficus
Plant species

Fig. 2.

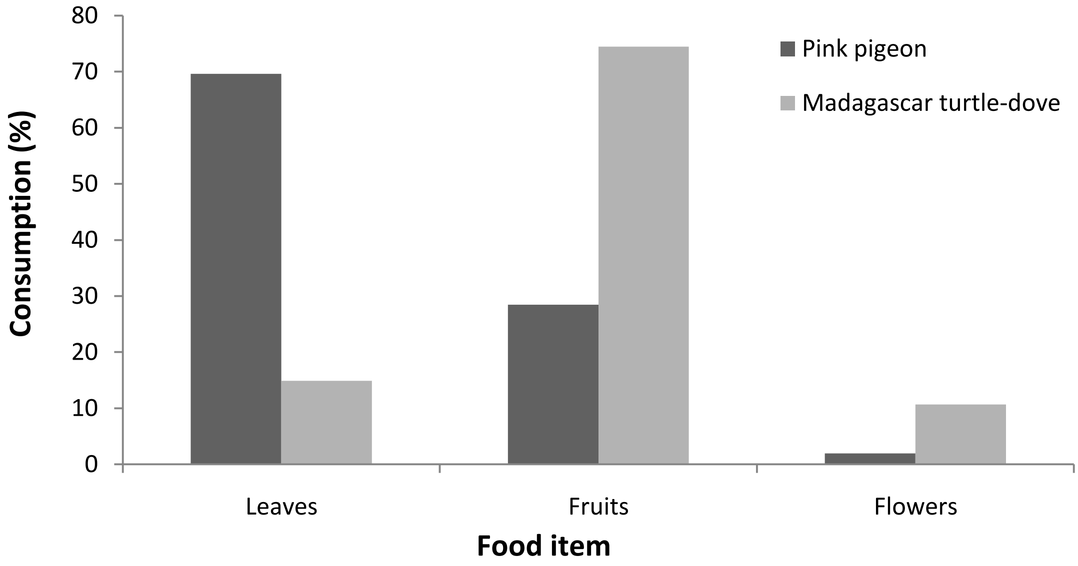

Fig.3.

Table 1 – Comparison of reproductive parameters between pink pigeon and Madagascar turtle-dove

Variable	Pink pigeon	Madagascar turtle-dove
Hatching success (%)	31.1	51.1
Breeding success (%)	15.5	36.8
Nesting success (%)	19.6	62.0

Study period was January 2013-January 2014 for Pink pigeons and October 2013-February 2014 for Madagascar turtle-doves.

Table 2 – Comparison of nesting sites parameters between pink pigeon and Madagascar turtle-dove

Variable	Pink pigeon mean ± SE	Madagascar turtle-dove mean ± SE	*U*	n
Tree height (in meters)	4.55 ± 1.2	3.41 ± 0.87	2283.5*	109
Nest height (in meters)	3.80 ± 1.07	2.70 ± 0.87	2330*	109

*Significance to the $p < 0.001$ level.
Study period was January 2013-February 2014 for Pink pigeons and October 2013-February 2014 for Madagascar turtle-doves.
Mann-Whitney *U*-tests compared each parameter for Pink pigeon and Madagascar turtle-dove nests.

Table 3 – Comparison of foraging behaviour between pink pigeon and Madagascar turtle-dove

Variable	Pink pigeon mean ± SE	Madagascar turtle-dove mean ± SE	*U*	n
Tree height (in meters)	4.68 ± 0.3	2.47 ± 0.15	5094.5*	196
Feeding height (in meters)	3.83 ± 0.29	0.29 ± 0.07	7128*	196

*Significance to the $p < 0.001$ level.
Study period was June 2013-February 2014 for Pink pigeons and October 2013-February 2014 for Madagascar turtle-doves.
Mann-Whitney *U*-tests compared each parameter for Pink pigeon and Madagascar turtle-dove feeding events.