

Understanding the decline and extinction of monarchs (Aves) in Polynesian Islands

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Abstract

Understanding the decline and extinction of species has become critical to conservation biology. The five monarch species of the genus *Pomarea*, endemic to the southeastern Pacific, are all listed as threatened. Introduced mammals and birds are believed to be responsible for their rarefaction. We analyzed the historical and current distribution of monarchs and introduced animals and found no relation between presence of Polynesian rats (*Rattus exulans*) and monarch distribution. There was a highly significant correlation between the arrival of the black rat (*Rattus rattus*) and the decline and extinction of monarch populations. The extinction of monarch populations after colonization by black rats tended to take longer on larger islands than on smaller ones. On islands without black rats, monarchs persisted even where forests have been reduced by more than 75%. After an island was colonized by black rats the number of monarch pairs with young decreased dramatically. Eggs in artificial nests placed in sites used by monarchs were only preyed upon by black rats. No eggs were preyed upon by Polynesian rats (*Rattus exulans*) or introduced birds. Monarch nests were mainly placed on horizontal branches inside the canopy and were more accessible than nests of Polynesian warbler (*Acrocephalus caffer*), a species still locally abundant. Warbler nests were placed higher up on vertical branches near the top of trees. These studies suggest that nest predation by black rats has been the main cause of monarch decline. However observations of direct aggression of adult monarchs by introduced red-vented bulbuls (*Pycnonotus cafer*), especially when monarchs raise their young, suggest that introduced birds could aggravate the decline of monarch populations already weakened by black rats. We discuss the practical implications of these findings for monarch conservation. © 2002 Elsevier Science Ltd. All rights reserved.

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1. Introduction

The introduction of alien animals has followed from the development of long distance trade, and has played an increasing role in species extinction, especially on islands (e.g. Elton, 1958; Diamond, 1984; Atkinson, 1985, 1989). The higher susceptibility of island species to invasives has been related to the limited area of islands. What would be a local effect on a continent, will affect the entire area of distribution of an island endemic. The relatively small size of island populations also increases extinction risk (Pimm et al., 1988). Islands and archipe-

lagos vary in the length of time from first exposure to human colonization (Atkinson, 1985) and thus often to species introductions. For ancient introductions, the current assemblages have often adjusted to the introduced species (e.g. Martin et al., 2000). This frequently resulted in the extinction of the most sensitive species. Where introductions have occurred more recently, species assemblages are currently subject to rapid change. This paper uses such an opportunity to tease out the relative impact of different introduced species and of other environmental changes on native species.

The islands of the Pacific have lost and are losing a high proportion of their avifauna following prehistoric (e.g. Milberg and Tyrberg, 1993; Pimm et al., 1994; Steadman, 1995) or historical (Greenway, 1967; Johnson and Stattersfield, 1990) colonization by humans.

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Predation on eggs, nestlings, or adults by introduced rats has been identified by Atkinson (1985), Seitre and Seitre (1992) and Robertson et al. (1998) as a potentially important cause of extinction of island birds especially in the Pacific where three rat species (the black rat *Rattus rattus*, the Norway rat *Rattus norvegicus* and the Polynesian rat *Rattus exulans*) have become widespread.

The Polynesian monarchs, passerines of the genus *Pomarea* (Corvidae family, Monarchini tribe, Sibley and Monroe, 1990) provide a dramatic example of a group of species endemic to the Pacific that is currently driven close to extinction after a process that started at the end of the eighteenth century (Thibault and Meyer, 2001). In addition to rats two exotic land birds, the Indian myna (*Acridotheres tristis*) and the red-vented bulbul (*Pycnonotus cafer*) have become established on islands within the known distribution range of monarchs. For most of these islands, we were able to collect data on the status and process of colonization by the two arboreal rats (the Polynesian rat and the black rat) and by the two land birds. We documented the status of the monarchs at different stages of colonization by these introduced species. We use this situation (1) to analyze the historical and current distribution of monarchs and introduced animals and their relation with island characteristics, (2) to assess the relative impact of introduced mammals and birds on monarch reproductive success, (3), to understand the sensitivity of monarch nests to predation by introduced mammals, and (4) to look for direct interactions between monarchs and introduced birds.

2. Methods

2.1. Past and current distribution of native and introduced species and their relation to island characteristics

2.1.1. Native species and their habitats

The five species of monarchs (genus *Pomarea*) are restricted to islands in the southeastern Pacific (Holyoak and Thibault, 1984): Rarotonga, Cook Is. (*P. dimidiata*), Tahiti, Society Is. (*P. nigra*), and formerly most of the Marquesas Is. (*P. iphis*, *P. mendozae* and *P. whitneyi*) (Fig. 1). They are all listed as threatened (BirdLife International, 2000). An additional extinct species (*Pomarea pomarea*) occurred on Maupiti in the Leeward Society Is. (Holyoak and Thibault, 1984). The distribution and abundance of monarchs has been reviewed by Robertson et al. (1993) for the Rarotonga monarch and by Thibault and Meyer (2001) for the remaining species. Monarch populations have a large elevational distribution, from lowland to high inland valleys up to the upper limit of the forest (Table 1).

They occupy all wooded areas, except high ridges and summits covered by shrubland plant communities.

For each island with extant or extinct populations of monarchs, we recorded total area and maximum elevation. Data on vegetation type, dominant canopy species, percentage of forest left and main threats were obtained from both the literature and botanical field investigations (JYM, unpublished data). We also documented the past and current status and distribution of the Polynesian warblers for the same set of islands.

2.1.2. Introduced species

The Polynesian rat occurs on all islands, except perhaps on Mohotani (Fig. 1). Archaeological studies (Roberts, 1991) and genetic analyses (Matisoo-Smith, 1994) confirm that it was intentionally introduced by Polynesians (see Belwood, 1978, for chronology). The black rat (also called roof rat or ship rat) was introduced by Europeans as early as the eighteenth century on the Society Is. (Orliac, 1997). On the Marquesas, it colonized most islands in the late nineteenth, or in the course of the twentieth century. It colonized Ua Pou and Fatuiva only recently, and a few islands such as Ua Huka are still rat free (Thibault and Meyer, 2000). Both rats occupy cultivated areas and inland forests. Norway rats are restricted to urban areas on a few islands (Tate, 1935).

The Indian myna was introduced to Tahiti in the early twentieth century (Wragge, 1906), and later on other islands (Holyoak and Thibault, 1984). The red-vented bulbul was introduced to Tahiti in the late 1970s (Bruner, 1979). On Tahiti the ranges of the myna and bulbul in the 1990s covered most of the island (Monnet et al., 1993), penetrating every valley, reaching 1500 m asl for the myna and the highest peaks for the bulbul (recorded at 2000 m, Anon., 1996). Their numbers can be estimated at several tens of thousands (JCT, unpublished data). We collected and synthesized all information available on their past and current status in Polynesia.

2.2. Reproductive success

2.2.1. Direct evidence of changes in reproductive success

To directly assess the impact of introduced black rat on monarch reproductive success, we recorded the number of monarch pairs accompanied by juveniles in three relict populations from the Marquesas, before and after the introduction of rats. This was done during systematic surveys of monarch distribution ranges on each island. We recorded for each sighting whether the birds were in pair, territorial, nesting, or feeding juveniles. Clutch size in Polynesian monarchs is two eggs; breeding is seasonal on Tahiti, occurring in summer, and occurs probably all-year round on the Marquesas Is. (Holyoak and Thibault, 1984; JCT, personal observation).

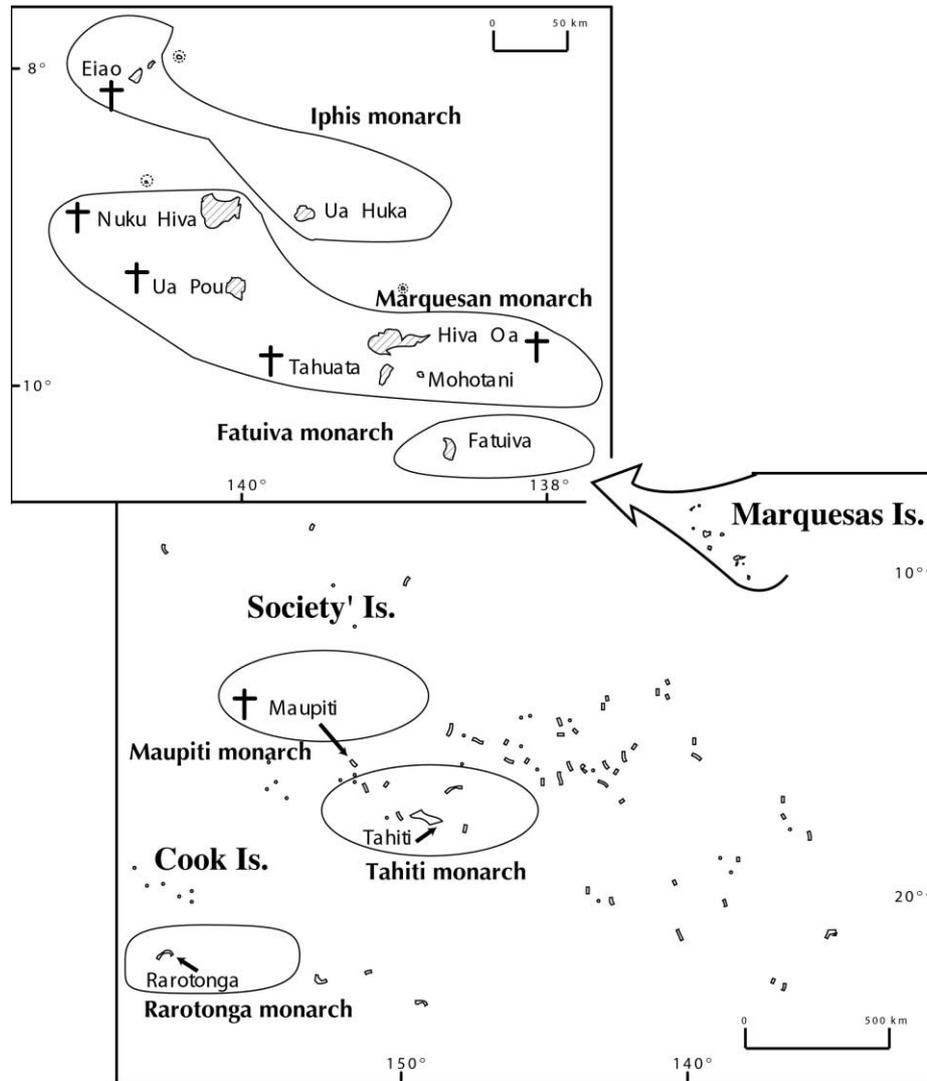


Fig. 1. Distribution of monarch species in eastern Polynesia.

2.2.2. Artificial nest experiments

Although predation rates on artificial nests do not necessarily give an accurate estimate of the predation risk for natural nests (Willebrand and Marcström, 1988; Reitsma et al., 1990; Major and Kendal, 1996; King et al., 1999), they have been extensively used to study variation in predation risk among localities or nest sites (Wilcove, 1985; Yahner and Cypher, 1987; Martin, 1995; Penloup et al., 1997). We used wicker nests similar to those used by Penloup et al. (1997). Nests were baited with two Japanese quail (*Coturnix japonica*) eggs. Experiments were set up on Tahiti Island during the rainy season from 17 January to 21 February 1998, corresponding to the end of the breeding season of the Tahiti monarch. Nests were placed in (1) three small forested valleys on the west coast, where black rat, Polynesian rat, red-vented bulbul, Indian myna and Tahiti monarch were present, and (2) a garden owned by a research institute (I.R.D.) surrounded by other

gardens, at sea level near Pape'ete. There, rats are absent because of systematic rat control by poisoning, but red-vented bulbul and Indian myna were common.

Elevation for the forest study sites ranged from 85 to 160 m asl. The canopy was dominated by the native trees *Hibiscus tiliaceus* and *Neonauclea forsteri* with few *Ficus prolixa*, along with the exotics *Spathodea campanulata* and *Inocarpus edulis*. The understory was dominated by native ferns and gingers—*Zingiber zerumbet* and *Etilingera cevuga*—with the native liana *Freycinetia impavida*, the endemic shrub *Ixora setchellii* and naturalized *Coffea arabica*. The habitat can be considered as low elevation secondary moist valley forest, belonging to the hygrophilous vegetation type (see Florence, 1993).

In each valley we installed three replicates along a single transect. Each transect followed trails stretching along the river banks and regularly used by locals. These trails crossed the rivers at regular intervals. Replicates consisted of 10 stations separated by 30 m.

Table 1
Location, area and elevation of islands with extant or extinct monarch populations

Island	Monarch population	Lat S /Long W	Area (km ²)	Elevation (m)	Elevation range for breeders (m)
Tahiti	<i>Pomarea nigra</i>	17°48'/149°30'	1045	2241	65–950 ^a
Nuku Hiva	<i>P. mendozae nukuhiuae</i> ^b	8°52'/140°06'	339	1224	?
Hiva Oa	<i>P. m. mendozae</i> ^b	9°46'/139°00'	315	1276	30–750?
Ua Pou	<i>P. mendozae mira</i> ^b	9°24'/140°05'	105	1203	30–730
Fatuiva	<i>P. whitneyi</i>	10°29'/138°39'	85	1125	50–700 (775)
Ua Huka	<i>P. i. Iphis</i>	8°55'/139°33'	83	884	30–640 (840)
Rarotonga	<i>P. dimidiata</i>	21°14'/159°46'	67	653	50–260
Tahuata	<i>P. m. mendozae</i> ^b	9°55'/139°05'	61	1050	?
Eiao	<i>P. iphis fluxa</i> ^b	8°00'/140°42'	40	577	?
Mohotani	<i>P. mendozae motanensis</i>	9°59'/138°50'	13	520	140–500
Maupiti	<i>P. pomarea</i> ^b	16°27'/152°16'	12	372	?

From Sanders (1993), Robertson et al. (1994), Meyer (1996b), Bonvallot (1993), Thibault and Meyer (2001), Service de l'Urbanisme, Papeete (personal communication). Islands are listed in order of decreasing area.

^a Possibly higher formerly.

^b Extinct populations.

Adjacent stations were placed on alternate sides of the transect. In order to get an idea of where and how much artificial eggs were exposed to predation by introduced species we placed three nests at each station at 10 m or more from the transects. One of these nests was placed on the ground and two in the trees at a height of 1 and 3.5 m respectively. The minimum height of 1 m was selected as it was the minimum height at which we observed natural monarch nests. It was not possible to place artificial nests in trees at heights matching those we observed for the highest natural monarch nests (> 15 m). The nest-sites in trees were selected so as to be similar in placement to those built by monarchs. There were ca. 100 m between adjacent replicates, which were placed on opposite river banks in two of the three valleys.

The experiment installed in the gardens consisted of 20 stations at only 10 m intervals for lack of sufficient space. Two nests were placed at each station, one on the ground, and one at a height of 1 m. Higher nest sites were not available in sufficient number. Nests and eggs were handled only during installation.

Using a mirror mounted on a perch, we checked the 310 nests every fourth day for 16 days, approximating the incubation period of monarchs. The use of a mirror, the regular rains and the use of the main trail by local people as well as the crossing of rivers, all minimized the risk of scent trails being used by rats to locate the nests. Despite the obvious differences in vegetation we used the garden and forest sites as the best way to estimate the relative impact of introduced rats and birds on egg predation. The comparison of predation risk between valleys, replicates, and nest sites helped identify how these variables affected predation risk.

To further clarify the respective role of the four potential nest predators we used automatic cameras connected to an artificial nest and equipped with a modified version (Penloup et al., 1997) of the electromagnetic

system designed by Garner and Garner (personal communication). A picture was taken when the introduced egg was removed. Five such cameras connected to artificial nests were installed within the three replicates in valley No. 1, at 1–4 m from the ground. Similarly, automatic cameras were installed in the garden locality. These nests were checked daily early in the morning. Nests and cameras were moved to a different spot after 2–3 days, or earlier if a predation had taken place.

2.3. Nest site selection

Species with different nest-site preferences may vary in their sensitivity to a given nest predator [e.g. Van Riper (1978) cited by Amarasekare (1993); Sieving and Willson (1998); Reed (1999), for natural nests, and Penloup et al. (1997) for artificial nests]. To investigate whether there is a difference between monarchs and warblers in their susceptibility to nest predation, we compared the position of the natural nests for these two species groups on Ua Huka (30 July–20 August 1998) and Fatuiva (13–29 February 2000), Marquesas Is., with additional data from Tahiti. Both species groups breed in trees and build cup-shaped nests made of plant material fastened to twigs. Warbler nests are deeper than monarch nests (Holyoak and Thibault, 1984). On all islands, we searched nests systematically in the areas occupied by the birds. Once the nest was found, its placement was described (height of nest and tree, and angle of branch with horizontal line at nest level).

2.4. Interaction of introduced bird species with adult breeding monarchs

In addition to nest predation, predation or aggression of adults by introduced species can affect population trends. In response to anecdotal evidence of agonistic

behaviour between fledged or adult monarchs and red-vented bulbuls we studied the frequencies of interactions between monarchs and introduced birds on Tahiti during two seasons in 1990, and 1998–1999 (Thibault et al., 1999). We used our own or published data collected by continuous focal animal sampling (Altman, 1974) near occupied monarch nests, checking interactions between the Tahiti monarch and other bird species. Once an occupied nest was located, it was monitored at the laying, incubation, feeding and post fledging stage until the young were emancipated. The number of visits per nest during the period best sampled (feeding of young) varied between four and eight and observation time per visit between 1 and 6 h, averaging 2.3 h/visit).

2.5. Statistical methods

We used generalized linear models (Payne, 1985; Aitkin et al., 1989; Lebreton et al., 1992 and application in Penloup et al., 1997, Martin et al., 2000; GENMOD procedure, SAS, 1993) to analyze how the presence of introduced rats, introduced birds and island area affected monarch abundance. In the experiments with artificial nests we used the GLM procedure to analyze the effect of study area, valley, replicates and nest site on nest predation.

3. Results

3.1. Historical analysis of distribution of native and introduced species

We were able to reconstruct the chronological sequence of the presence and abundance of introduced species, monarchs and warblers for all but two of the 11 islands studied (Table 2). The Polynesian rat was present on all islands since the earliest record, with the possible exception of Mohotani, for which proper data are missing (Thibault and Meyer, 2000). Its presence was not documented on Tahuata until the beginning of the twentieth century, but it has been recorded since. The black rat has colonized nine of these 11 islands between the eighteenth and twentieth centuries. The Indian myna has been introduced on five of the 11 islands, and the red-vented bulbul, as mentioned, occurs only on the largest, Tahiti. The status of the monarchs and of the warblers before the arrival of the black rat and of the introduced birds is known for all islands except Tahiti.

During the same period the extent of forested habitat was dramatically reduced on all islands with reductions ranging from 25–50% on Fatuiva to 90–95% on Maupiti (Table 3). On about half of the islands the integrity of the remaining habitat is threatened by alien invasive plants or introduced herbivores.

3.2. Consequences of species introduction and island characteristics on monarch and warbler distribution

On all islands with only Polynesian rats, there has been no documented decline in monarch and warbler abundance in suitable habitats. On all islands colonized by black rats, monarchs declined or went extinct (Table 2). The longer the black rat has been present on an island, the lower the abundance of the monarch. Islands colonized by Indian mynas and red-vented bulbuls already had black rats at the time of colonization making their effect on native passerines harder to identify. However neither in the forest sites nor in the garden site did we document any case of egg predation by bulbuls or mynas. The GLM analysis confirms that the black rat is the only introduced species that had a significant effect on the abundance of the monarchs ($\chi^2 = 7.99$, d.f. = 1, $P < 0.01$).

There is also a marginally significant interaction effect between presence of black rats and island area (black rat \times area) on the abundance of monarchs ($\chi^2 = 3.71$, d.f. = 1, $P < 0.054$), but no significant effect of the area of native habitat left (Table 2).

There was no significant effect in the GLM analysis of any of the introduced species on the distribution and abundance of Polynesian warblers.

3.3. Reproductive success of monarchs and presence of black rat

3.3.1. Reduced number of young per pair

On the two islands without rats there was no difference in the proportion of monarch pairs with young between years (Table 4). On Fatuiva the proportion of pairs with young decreased significantly after the colonization of the island by rats: none of the 20 pairs observed in the latter period had young. The same pattern of low proportion of adults with juveniles was observed on Tahiti (Thibault et al., 1999; Blanvillain, 2000).

3.3.2. Predation of artificial nests

The predation risk of artificial nests averaged 41% in the forest study areas and zero% in the garden study area (Table 5). In the forest habitats predation varied from 21 to 61% between valleys, from 0 to 93% between replicates and from 0 to 100% between nest sites. The effect of valley and replicate on predation risk was significant in the GLM analysis (Table 6). The effect of the interactions between valley and replicate and between replicate and site were also significant. Nest site had no significant effect as such. Thus, in a given valley and a given replicate, predation risk was similar for all nest-sites.

In the forest of valley No. 1, the five automatic cameras were set up for a total of 115 days of nest exposure.

Table 2
Past and current distribution of introduced rats and birds on islands with extant or extinct monarch and warbler populations

Islands	Year or period	Polynesian rat ^a	Black rat ^b	Bulbul ^a	Myna ^a	Monarchs ^c	Warblers ^c
Tahiti	19th century	1	1	0	0	3	3
	Early 20th century	1	3	0	0	2	1
	1970s	1	3	0	1	2	1
	1990s	1	3	1	1	1	1
Nuku Hiva	19th century	1	0	0	0	3	3
	1920s	1	1	0	0	1	3
	1990s	1	3	0	0	0	3
Hiva Oa	19th century	1	0	0	0	3	3
	1922	1	1	0	1	3	3
	1975–2000	1	3	0	1	0	1
Ua Pou	1920s	1	0	0	0	3	3
	1975	1	1	0	0	1	3
	1998	1	2	0	0	0	3
Fatuiva	1923–1975	1	0	0	0	3	3
	2000	1	1	0	0	2	3
Ua Huka	1922	1	0	0	0	3	3
	1975–1999	1	0	0	0	3	3
Rarotonga	Late 19th century	1	0 ^d	0	0	1 ^d	
	1970–1980s	1	1	0	1	1	
	From 1988	1	0 ^e	0	1	3 ^e	
Tahuata	1922	?	?	0	0	3	3
	1975	1	1	0	0	0	3
Eiao	1922	1	0	0	0	3	3
	From 1980	1	1 ^f	0	0	0	3
Mohotani	1922	?	0	0	0	3	3
	1975–1999	? ^g	0	0	0	3	3
Maupiti	1823	1	0	0	0	3	
	1973	1	1	0	1	0	

From Tate (1935), Holyoak and Thibault (1984), Seitre and Seitre (undated), Dubois (1991), Robertson et al. (1994), Orliac (1997), Thibault and Meyer (2000, 2001), Gerald McCormack (personal communication), J.-C. Thibault and I. Guyot (unpublished data).

^a Polynesian rat, red-vented bulbul, Indian myna: 0 = absent, 1 = present, ? = presence unconfirmed.

^b Black rat: 0 = absent or control, 1 = first record, 2 = present for several decades, 3 = present for more than 50 years.

^c Monarchs and warblers: 0 = extinct, 1 = rare, 2 = declining, 3 = high density.

^d Presence of the black rat between 1850 and 1880 (Gill, 1885, cited by Robertson et al., 1994) was inferred by Robertson et al. (1994) from the observed decline of the Rarotongan monarch and McCormack and Künzle (1990) indicate that it arrived within the last 100 years. However, direct observation of the black rat date only back to the 1970s.

^e Rat control from 1988 in Takitumu area led to a decrease in rat abundance and an increase of monarch number (Robertson et al., 1994).

^f Rat identified as black rat after building of shelters by military in 1972–1973 (J.-L. Candelot, personal communication).

^g Not caught with trap, possibly owing to an important population of feral cat (Thibault and Meyer, 2000).

Fifty-six predation incidents occurred leading to 52 photographs. Black rat was the predator identified on all pictures. Although red-vented bulbuls and Indian mynas were common in these forests they were never observed preying upon nests. In the garden study area where only bulbuls and mynas were present, the nests with electromagnetic cameras were never preyed upon.

3.4. Nest placement and differences in sensitivity to predators

There was no significant difference in the height of trees in which monarchs and warblers placed their nests (*t*-test, n.s., $P=0.16$; Table 7). But warbler nests were significantly closer to the top of trees, while monarch nests were placed inside or at the base of the canopy (*t*-test = 3.60, $P<0.001$; Table 7). Monarchs nests were

mostly placed on horizontal or close to horizontal branches (79%) and warbler nests were placed significantly more on vertical branches (67% of the nests; Fig. 2; Newman–Keuls = 7.06, $P<0.05$). Finally the range of heights at which nests were found varied from 1 to 15.5 m on Ua Huka, where black rats are still absent, from 4 to 14 m on Fatuiva which has been colonized by black rats recently, and from 8 to 25 m on Tahiti, where rats were present already in the nineteenth century.

3.5. Interference of introduced bird species with adult breeding monarchs

After the colonization of Tahiti by red-vented bulbuls had been completed, antagonistic behaviour towards monarchs significantly increased between 1990 and

Table 3
Characteristics and status of the habitats used by extant or extinct monarch populations

Island/monarch population	Vegetation type	Dominant canopy species	% Native forest left	Main threats to the forest
Tahiti/ <i>P. nigra</i>	Low and mid elevation secondary moist and wet valley forest	<i>Hibiscus</i> , <i>Neonauclea</i> , <i>Ficus</i>	25–30	Invasive plants (<i>Miconia calvescens</i> , <i>Spathodea campanulata</i> , <i>Tecoma stans</i>)
	Upper elevation native wet forest and high elevation native cloud forest	<i>Crossostylis</i> , <i>Cyathea</i> , <i>Metrosideros</i> , <i>Weinmannia</i>		
Nuku Hiva/ <i>P. mendozae nukuhivae</i> ^a	Low and mid-elevation native moist and wet valley forest	<i>Hibiscus</i> , <i>Pandanus</i>	25–50	Invasive plants (<i>Leucaena leucocephala</i> , <i>Psidium guajava</i> , <i>Syzygium jambos</i>)
	High elevation native wet and cloud forest	<i>Crossostylis</i> , <i>Cyathea</i> , <i>Metrosideros</i> , <i>Weinmannia</i>		
Hiva Oa/ <i>P. m. mendozae</i> ^a	Mid- and upper elevation wet native forest	<i>Crossostylis</i> , <i>Cyathea</i> , <i>Weinmannia</i>	25–50	Invasive plants (<i>Psidium cattleianum</i> , <i>Syzygium cumini</i>), feral goats
Ua Pou/ <i>P. mendozae mira</i> ^a	Low and mid-elevation native moist and wet forest	<i>Hibiscus</i> , <i>Fagraea</i> , <i>Pandanus</i>	25–50	Invasive plants (<i>Leucaena leucocephala</i>)
Fatuiva/ <i>P. whitneyi</i>	Low and mid-elevation native moist and wet valley forest	<i>Hibiscus</i> , <i>Pandanus</i>	50–75	Fires, Invasive plants (<i>Psidium cattleianum</i>)
Ua Huka/ <i>P. i. Iphis</i>	High elevation native wet and cloud forest	<i>Crossostylis</i> , <i>Cyathea</i> , <i>Metrosideros</i> , <i>Weinmannia</i>	25–50	Feral goats and horses
	Low and mid-elevation native moist and wet forest	<i>Hibiscus</i> , <i>Cyclophyllum</i> , <i>Pandanus</i>		
Rarotonga/ <i>P. dimidiata</i>	Upper elevation native wet and cloud forest	<i>Crossostylis</i> , <i>Cyathea</i> , <i>Weinmannia</i>	5–25	Fires
	Low-elevation native moist valley forest	<i>Homalium</i> , <i>Hernandia</i> , <i>Bischofia</i> , <i>Elaeocarpus</i>		
Tahuata/ <i>P. m. mendozae</i> ^a	Mid-elevation ridges	<i>Fagraea</i> , <i>Fitchia</i>	25–50	Fires, feral goats, and introduced plants
	Low and mid-elevation native moist and wet valley forest	<i>Hibiscus</i> , <i>Pandanus</i>		
Eiao/ <i>P. iphis fluxa</i> ^a	High elevation native wet and cloud forest	<i>Crossostylis</i> , <i>Cyathea</i> , <i>Metrosideros</i> , <i>Weinmannia</i>	ca. 9	Feral sheep
	Low elevation dry native and secondary forest	<i>Pisonia</i> , <i>Hibiscus</i> , <i>Pandanus</i> , <i>Thespesia</i>		
Mohotani/ <i>P. mendozae motanensis</i>	Low and mid-elevation dry native and secondary forest	<i>Pisonia</i> , <i>Cordia</i> , <i>Thespesia</i>	15–20	Feral sheep
Maupiti/ <i>P. pomarea</i> ^a	Mid-elevation moist native forest (300–500 m)	<i>Hibiscus</i> , <i>Pandanus</i> , <i>Ficus</i>	ca. 9	Hurricanes, Invasive plants (<i>Leucaena leucocephala</i> , <i>Mangifera indica</i> , <i>Tecoma stans</i>)
	Low and mid-elevation native and secondary moist forest	<i>Hibiscus</i> , <i>Ficus</i>		

From Robertson et al. (1994), Meyer (1996b), Florence and Lorence (1997), Mueller-Dombois and Fosberg (1998), Thibault and Meyer (2001), J.-Y. Meyer (unpublished data).

^a Extinct populations.

Table 4
Number of pairs with juveniles at two different periods in the three relict monarch populations in the Marquesas islands

Species/island	Number of pairs ^a				<i>P</i>	Period with rats
	1975		1998–2000			
	Total	With young	Total	With young		
<i>Pomarea iphis</i> /Ua Huka	Several tens ^b	20–30%	35	11	n.s.	None
<i>P. mendozae</i> /Mohotani	25 ^c	8	21	8	n.s.	None
<i>P. whitneyi</i> /Fatuiva	8	3	20	0	*	1998–2000

^a Pairs followed during enough time to be sure of their accompanied or not by juveniles.

^b Exact number not recorded, but ratio recorded in our field notes.

^c Count restricted to March 1975.

* $P < 0.05$.

Table 5
Percentage of nests lost by predation during the experiments using artificial nests (n = sample size per cell)

Locality	Replicate	Nest site	n	% Predated/site	% Predated/ replicate	% Predated/ valley
Valley 1	A	Ground	10	50	26	21.2
		1 m	10	30		
		3.5 m	10	0		
	B	Ground	10	30	40	
		1 m	10	45		
		3.5 m	10	50		
	C	Ground	10	0	0	
		1 m	10	0		
		3.5 m	10	0		
Valley 2	A	Ground	10	20	23	44.5
		1 m	10	20		
		3.5 m	10	30		
	B	Ground	10	0	13	
		1 m	10	10		
		3.5 m	10	30		
	C	Ground	10	90	93	
		1 m	10	100		
		3.5 m	10	100		
Valley 3	A	Ground	10	30	23	61.2
		1 m	10	10		
		3.5 m	10	30		
	B	Ground	10	60	76	
		1 m	10	80		
		3.5 m	10	90		
	C	Ground	10	70	83	
		1 m	10	80		
		3.5 m	10	100		
Garden		Ground	20	0	0	0
		1 m	20	0		

1998/1999 (Table 8). The interactions observed ranged from alarm to pursuits and fights. Fights were especially frequent with the larger red-vented bulbul [26–45g (Long, 1981), against 24–26 g for Monarchs (JCT, six individuals)]. They were always initiated by the red-vented bulbul. The frequency of aggressions increased significantly being lowest during monarchs' incubation period and highest immediately after fledging (Table 9).

4. Discussion

4.1. Black rats and the decline of monarchs

Changes in the distribution of monarchs and artificial nest experiments suggest that nest predation by introduced black rats has been a key factor in the extinction of four monarch subspecies on five islands in the

Marquesas and in the decline of two other monarch species on Tahiti and Rarotonga. The dramatic reduction in the proportion of monarch pairs with young when rats were present, and the increase in monarch reproductive success after rat control on Rarotonga (Robertson et al., 1994), is further evidence that black rats prey upon monarch eggs and nestlings. Finally the trend of a decreasing proportion of natural monarch nests placed low in trees with increasing time since rat colonization suggests that, in presence of black rats, active nests are progressively restricted to sites least accessible to rats, a result already shown by Martin et al. (2000) in a study on the effect of black rats on pallid swifts (*Apus pallidus*). Robertson et al. (1994) indicated, however, that estimates of adult survival of Rarotonga monarchs increased after rat control. The role of the black rat remains uncertain in only two cases of monarch extinction: on Eiao, where the presence of the black rat is only suspected, and on Maupiti, where extinction occurred in the nineteenth century, without proper documentation. The direct role of black rats in the extinction of small land birds has also been suggested on Hawaii (Atkinson, 1977) and demonstrated in New Zealand (Atkinson, 1973; Bell, 1978).

While the monarch populations on the Marquesas Is. have vanished from Ua Pou, Nuku Hiva, Tahuata and Hiva Oa after their colonization by black rats, the warbler populations have remained vigorous on these islands (JCT, unpublished data). Our analysis of nest

placement suggests that monarch nests could be more accessible to black rats than warbler nests. While monarchs built their nests on horizontal branches, which our photographs showed to be accessible to black rats at least for heights ranging from 1 to 4 m, warblers built their nest on vertical branches situated close to tree tops. On Tahiti, the warbler does not breed in trees, but seems to build its nests exclusively at the top of vertical bamboo ($n=10$) (Holyoak and Thibault, 1984; C. Monnet, personal communication). Several authors (Atkinson, 1985; Penloup et al., 1997) reached similar conclusions on the role of nest placement on the risk of nest predation by black rats.

4.2. Impact of the Polynesian rat

The Polynesian rat probably coexisted with monarchs (and warblers) for centuries suggesting that it had little or no effect on monarch populations. It is considered less arboreal than the black rat (Storer, 1962; Lindsey et al., 1998) but has been observed in trees on the Marquesas, especially near nests of Iphis monarchs on Ua Huka (JCT, unpublished data; see also McCartney, 1970). We did not record a single egg predation that we could attribute to the Polynesian rat in experiments with artificial nests. Similar results have been obtained in experiments on the Loyalty Is. (Robin et al., 1998). However, in some instances predation by Polynesian rats has been the subject of controversial conclusions (Seitre and Seitre, 1992; Atkinson, 1996; Meyer, 1996a; Holdaway, 1999) or has been demonstrated for eggs of small seabirds breeding on the ground at high density (Kepler, 1967; Imber, 1978; Brooke, 1995; Booth et al., 1996), or for eggs of small passerines nesting in shrubs or trees (Flack and Lloyd, 1978; Lovegrove, 1996).

4.3. Effect of island area on the impact of black rats

The marginally significant effect of island area on monarch decline in the presence of rats in the GLM analysis suggests a longer delay to extinction on larger islands. This could reflect the longer time necessary for the entire settlement of larger islands by black rats. Rats

Table 6
GLM analysis of variation in predation risk of artificial nests placed in native forests (d.f. = degree of freedom)

Effect	Deviance	χ^2	d.f.	<i>P</i>
Valley	337	31.03	2	***
Replicate	308	29.07	2	***
Nest site	307	2.18	2	0.34
Valley×replicate	227	78.39	4	***
Replicate×site	207	13.68	4	**
Valley×site	221	6.40	4	0.17
Valley×replicate×site	204	3.01	8	0.93

** $P < 0.01$.

*** $P < 0.001$.

Table 7
Data on nest placement of monarch and warbler species on Tahiti and Marquesas Island

Species	Tree height (m)			Nest height (m)			Branch angle (degrees)		
	Mean	S.D.	<i>n</i>	Mean	S.D.	<i>n</i>	Mean	S.D.	<i>n</i>
Tahiti monarch	20.7	6.9	13	14.6	4.3	17	38.4	34.2	19
Iphis monarch	11.9	3.15	16	9.4	4.1	16	20	31.7	16
Fatuiva monarch	15.7	1.15	3	10.5	5.6	3	23.3	20.8	3
Marquesan warbler	13.2	6.1	15	12	6.0	15	76.3	24.2	15

From Thibault et al. (1999) for the Tahiti monarch, and J.-C. Thibault and I. Guyot, unpublished data for other species. Branch angle = angle made by the branch on which the nest is placed relative to a virtual horizontal line; n = number of nests.

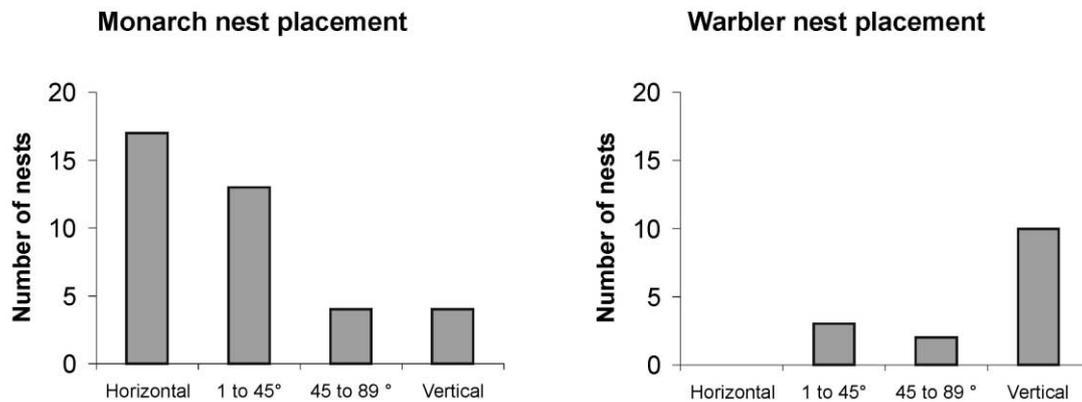


Fig. 2. Nest placement of monarch and warbler nests in relation to angle of branch relative to horizontal at nest level.

Table 8

Number of interactions between males of Tahiti monarchs and native (n) and introduced (i) birds

Species	November–December 1990 (16 h)	<i>I/H</i>	October 1998–February 1999 (39 h)	<i>I/H</i>
Unknown	0	0	8	0.20
Australian Harrier (i)	0	0	1	0.02
<i>Circus approximans</i>				
Tahiti swallow (n)	0	0	3	0.08
<i>Hirundo tahitica</i>				
Indian myna (i)	3	0.16	19	0.49
<i>Halcyon venerata</i>				
Red-vented bulbul (i)	Lacking	0	42	1.08
Tahiti kingfisher (n)	7	0.44	0	—
Total	10	0.62	73	1.87
χ^2 on difference between periods		$\chi^2 = 26.6$, d.f. = 1, $P < 0.001$		

The red-vented bulbul was lacking during the first period; from Thibault et al. (1999). *I* = number of interactions, *H* = number of hours of observation.

first colonize coastal areas around their landing point (e.g. Thorsen et al., 2000, in the case of the Norway rat) where food resources tend to be more abundant, partly because of more intense human activity. The colonization of inland forests would occur later. Thibault and Meyer (2001) showed that even on the smaller islands monarchs first vanished from coastal areas, and only later from inland areas. Another reason for an area effect could be the existence, on larger islands, of extensive areas at higher elevation where rat densities are lower. Amarasekare (1993), for instance, found few black rats and low predation risk on artificial nests at high altitude on Hawaii. The data available for several other tropical Pacific islands also suggest higher black rat density in lowland areas (Jackson, 1967; Tomich, 1970; Tamarin and Malecha, 1971).

4.4. Habitat loss or change and monarch decline

The proportion of native vegetation left on the different islands varies greatly (Table 3). Our results suggest, however, that reduction of forest cover alone has not caused the extinction of monarch populations although reduced population size (e.g. on Mohotani where only 15–20% of the native forest is left) increases the risk of

stochastic extinction (MacArthur and Wilson, 1967). But native forests are also changing in composition and structure. On the Society and Marquesas Is., forests are increasingly invaded by alien trees, which form dense monotypic stands even in inland valleys and on slopes. In mesic habitats the main invading trees are *Spathodea campanulata* and *Tecoma stans* (Bignoniaceae), in wet habitats *Miconia calvescens* (Melastomataceae), *Psidium cattleianum* and *Syzygium jambos* (Myrtaceae) and in dry habitats *Leucaena leucophala* (Leguminosae) and *Psidium guajava* (Myrtaceae). The impact of such habitat changes on monarch populations remains unknown.

4.5. Possible impacts of introduced birds?

Biological invasion is an ongoing and dynamic process (Vitousek et al., 1997). Islands of eastern Polynesia are no exception. Not only did the colonization by the black rat progress during the period of this study, but new exotic species, such as the red-vented bulbul and the Indian myna, reached these archipelagos. So far, documentation of nest predation by these two species is restricted to a very few cases [see Long (1981); Heather and Robertson (1996); also Barré et al. (1996) for predation by the red-whiskered bulbul (*Pycnonotus*

Table 9
Number of interactions with other bird species during the breeding period of the Tahiti monarch

Breeding period	<i>H</i>	<i>I</i>	<i>I/H</i>
Laying	4	3	0.75
Incubation	8	7	0.87
Rearing	39	86	2.2
Feeding after fledging	8.5	20	2.35
Before and after hatching	$\chi^2 = 3.88$, d.f. = 1, $P < 0.05$		

Most observations concern the red-vented bulbul (from Thibault et al., 1999). *H* = number of hours of observation, *I* = number of interactions.

jocosus]). This is confirmed by our experiments with artificial nests in which no egg predation by bulbuls was documented. However, aggressive behaviour of red-vented bulbuls against native passerines has been noticed on Hawaii (Berger, 1981) and Fiji islands (Watling, 1982; Clunie, 1984). On Fiji, Watling (1982) reported competition for nectar between the red vented bulbul and the wattled honeyeater (*Foulehaio carunculata*). Our behavioural data showed that frequent fights occur between the larger red-vented bulbul and the Tahiti monarch during the breeding period. The causes that trigger these fights remain obscure and the consequences of this energy investment on monarch reproductive success is unknown. However, the present decline of the relict monarch population that survived in the 1970s in the highland forest on Tahiti coincided with its colonization by the red-vented bulbul (Thibault et al., 1999) suggesting a possible negative impact of bulbuls on the small monarch population already weakened by black rats.

On Rarotonga, mynas have not been considered a threat to monarchs (McCormack and Künzle, 1990; Saul et al., 1998). The same may not be true for warblers. Holyoak and Thibault (1984) provided evidence that a decrease or extinction of warblers (*Acrocephalus*) occurred on the Marquesas and Society Is., precisely after mynas were introduced. On Tahiti, where both the myna and the bulbul occur, warblers are now confined to 12 valleys (31% of surveyed valleys; Monnet et al., 1993), whereas they were widespread in the early twentieth century (Whitney South Sea Expedition cited by Holyoak and Thibault, 1984). A similar pattern obtains for Hiva Oa.

The bulbul and the myna have penetrated the native habitat, often thought to act as a refuge resisting invasion by exotics [Lack (1976) in Lesser Antilles; Diamond and Veitch (1981); Simberloff (1992) on La Réunion, Indian Ocean]. The open structure (small trees with small leaves) of the vegetation on many of these oceanic islands has been suggested to facilitate their invasion by introduced animals [the red-whiskered bulbul at la Réunion (Mandon-Dalger et al., 1999); the brown tree snake (*Boiga irregularis*) on Guam (Savidge,

1987)] and plants (*Miconia calvescens* on Tahiti; Meyer and Lavergne, 2001). Moreover, exotic birds disperse alien plants that have edible fleshy berries such as *Miconia calvescens*, which is dispersed by silvereyes (*Zosterops lateralis*) and red-vented bulbuls (Meyer and Florence, 1996) potentially fueling whatever impact habitat change has on native species.

5. Recommendations

Two general management recommendations follow from our results. (1) Every effort should be made to prevent black rats colonising the last islands they have not reached (e.g. Ua Huka, for the Iphis monarch). This means, for instance, monitoring permanent baiting stations on landing wharves to prevent the establishment of any individuals. Established rat populations are hard to tackle even at an initial stage (see e.g. Thorsen et al., 2000). (2) Local rat control is nevertheless a worthwhile effort on islands with black rats, as it can help stabilise or restore monarch populations (Robertson et al., 1994, 1998). Such control should be rapidly initiated on significant areas of Fatuiva (for Fatuiva monarch), an island recently colonised by rats. On Tahiti, long term rat control in sites where monarchs still survive has become a priority (Blanvillain, 2000) and should aim to conserve the monarch population. They can sustain interference with introduced red-vented bulbuls. Defining such a population threshold will need research on the ecology of introduced birds and on their interaction with indigenous land-birds in all insular habitats.

Our analysis of the status of native habitats suggests that, on some islands, remnant patches of native forests should be protected from browsing by introduced mammals through fencing (e.g. sheep grazing on Mohotani, for Marquesan monarch) in order to maintain available monarch habitat in the future.

Translocation to predator-free islands has often been proposed as a solution to save threatened island populations (Powersland et al., 1992, 1995). The principle of such translocations could be considered for the Tahiti monarch (e.g. to Mehetia) or for the Iphis monarch (e.g. to Eiao). But such attempts will necessitate the elimination of grazing animals to restore some native forest or the elimination of black rats on some of these small islands before translocation should be considered.

Finally, we suggest further studies on the behavioural and ecological relationships between native and introduced birds on Polynesian islands.

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