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Breeding biology and impact of introduced birds and predation on reproductive success of the Tahiti monarch (*Pomarea nigra*)

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Summary

1. We studied the demography and breeding biology of the Tahiti Monarch, a critically endangered forest bird endemic to Tahiti (French Polynesia) as part of a recovery program aimed at protecting nests from rodent, from 1998-2012.

2. During the 15 years of the program, only 4-13 pairs were present each season and species decrease was halted when both basal and high populations were protected against rodent and introduced birds.

3. Nest building was seasonal and occurred between June and March and peaked in October.

4. A total of 159 nests were found. 49% of nest protected against rodent produced fledgling against 10 % of unprotected nest. Only 50 % of nests were incubated. Of 80 incubated nests, 83% were successful and produced a total of 66 fledglings. Only between 48 and 53 of them survived longer than one month

5. The percentage of pair which produced fledgling was negatively correlated with the percentage of young adults in the population between 1999 and 2007 ($r = -0.87$). Breeding success of breeding pairs increased to nearly 90-100 % since 2009 (and regular introduced bird control). On the 35 failures documented on incubated nest since the start of the program 34 % (12) were caused by introduced birds, 14 % (5) due to climatic event and 40 % (14) on unknown factors.

6. Incubation averaged 13.7 days (n=8). Both sexes incubated, and the average daily incubation period was 96 %. Females spent more time incubating than males (55 % vs. 38 %; $P < 0.004$). The nestling period was 14.2 days (n=9). Both parents fed the nestling, and feeding frequency by male and female was similar.

7. Breeding success was 1) positively correlated with nestling feeding frequency ($P = 0.01$) and 2) negatively correlated with the number of interactions observed each hour between the breeding pair and all other birds, including conspecifics, during incubation and nestling stages ($P = 0.01$ and 0.05).

8. Overall, our results suggest that five factors limit Tahiti Monarch nesting success and fledging survival: depredation by rats and by introduced birds; lower parental efforts due to disturbance by other birds; climatic factors, and percentage of young birds in the population when introduced bird control is not performed.

Introduction

On many oceanic islands, native animal and plant species have become extinct since discovery by Europeans, while introduced species have become established (Atkinson 1985). Island populations account for most modern extinction and many currently endangered species (Stattersfield & Capper 2000). The cause of the native extinctions and their relation to the introductions are much debated (Diamond & Veitch 1985). Suggestions include five main points.

1. Predation by introduced mammals such as rats, cat, dog, pig, mustelids, monkeys and brown-tree snake (Aitkinson 1985; Johnson & Stattersfield 1990; Seitre & Seitre 1992; Roberston *et al*. 1994; Blanvillain *et al*. 2002).
2. Reduction in forest area by clearing, which is considered to be the most common cause of extinction and the most important factor currently affecting island birds (Johnson & Stattersfield 1990).
3. Changes in forest structure by invasive plant species and depletion of native food plants important for birds by introduced browsers such as ungulates, rabbit, pig, rats and Australian possum (Steadmann 1987; Johnson & Stattersfield 1990; Dirzo & Miranda 1990).
4. Diseases, documented for the Hawaiian avifauna only (van Riper et *al.* 1986).
5. Finally, competition from introduced bird species. Despite the numerous bird species introduced from island to island in the pacific and elsewhere, few studies have tested the idea that introduced bird species, with the exception of birds of prey, may also have an impact on native island bird survival. In New Zealand at least 143 exotic species were introduced and about 34 remain established (Diamond & Veitch 1981), in French Polynesia at least 55 species have also been introduced and 11 are still present today (Holyoak & Thibault, 1984), in most of Hawaii one sees mainly introduced birds (Berger 1972). Did competition from exotic birds contribute to extinctions of natives ? (Diamond & Veitch 1981). Are island communities ecologically saturated, such as exotics can become established only at the expense of natives ? (Lack, 1976). These questions are of practical importance for conservation as well as theoretically interesting.

The Tahiti Monarch or O’mamao (*Pomarea nigra,* Sparrmann 1786 in Holyoak & Thibault 1984), is a critically endangered monarch monarch endemic to the island of Tahiti, French Polynesia (Stattersfield & Capper 2000). Previously very common throughout the island (Peale 1848), its range was restricted to 4 valleys in 1998 (Gaze 1998), each containing an isolated population of 5-7 birds for a total of only 25 birds (Blanvillain, *et al*. 2003). A high population containing 33 birds was discovered in 2002 (Blanvillain, et al. 2002). This recovery program last since 15 year now. It focused first in rodent control during breeding season and collared trees (between 1998 and 2002, Blanvillain, *et al.*2003) on the basal population, then rodent control was performed all year round (Gouni, *et al*. 2004). It was intensified in basal population since 2008 and extended to high populations since 2010. At the start of the recovery programme, it was thought that the main threat was predation by ship rats (*Rattus rattus*), as was the case for the Kakerori (*Pomarea dimidiata*), a monarch endemic to Rarotonga, Cook Islands (Robertson *et al*. 1994). Since then, two introduced bird species: the Indian mynah (*Acridotheres tristis*) and Red-vented Bulbul (*Pycnonotus cafer*) have been identified as serious threats to the species survival because they decreased its reproductive success and predate nests (Blanvillain *et al*. 2003; Ghestemme 2011). This additional threat was addressed first by shooting introduced birds around nest using air-gun in 2009 and 2010 (Ghestemme et al, 2009, 2010) and by using air-gun, poisoning and trapping with an increasing known-well since 2011 (Ghestemme et al, 2011, Blanvillain et al 2012).

This work present our study of the breeding behaviour and parental effort of the Tahiti Monarch between 1998-2002 and 2008-2012 and the main results and observation collected during its recovery programme. The only information available about the breeding biology of other *Pomarea* monarchs in eastern Polynesia is for the Kakerori (Saul, Robertson & Tiraa 1998). To estimate parental efforts of the Tahiti Monarch we focused on indirect measures (Wright *et al*. 1998) such as activities during the nest-building and egg-laying phases, the rate of nest occupation during incubation, the parental food provisioning rate to the young during the rearing stage and the time budgets of both parents. The relative parental effort of both sexes was considered in detail. Factors potentially affecting breeding behaviour and success, and particularly the impact of interactions with other birds were also analysed and cause of nest failure documented.

Material and methods

Study areas

Tahiti (17° 38′ S 149° 30′ W), French Polynesia, is a tropical volcanic island, the highest and largest of the 14 islands of the Society Islands group. It reaches 2,241 m elevation and covers 1,042 km^2, with most of the rugged basaltic interior being covered in forest. On both the mainland and the peninsula, the shape of the ancient volcanoes has given a relatively regular distribution to valleys and their dividing ridges radiating from the central peaks.

Tahiti monarchs are now restricted to 4 valleys in the Paea and Punaauia districts in the southwest of the mainland. All Tahiti monarch territories are located between 80-400 m elevations with adjacent hillsides from 300 to 900 m high. Those four populations seem to be isolated from each other for a very long period as territorial calls differ between valleys and there is a poor reaction to recorded calls from other subpopulations.

Bird and nest studies

Since the start of the recovery program, in 1998 campaigns of 5-8 months duration (extended all year round since 2004) were undertaken to:

- survey and determine the distribution and approximate number of surviving birds and the age structure of each population;
- carry out an intensive programme of rat poisoning;
- find nests, and determine nesting success in relation to conservation measures undertaken.

The Tahiti monarch has three distinct plumages: orange for the two first years, grey for the third year, and then black. Black and grey birds are territorial, at least during the reproductive season, whereas non-breeding orange birds are more mobile and thus more difficult to survey. Orange birds were adult as they were able to reproduce. In 1998, five Tahiti Monarchs were captured and marked with individual colour-ring combinations. Two of them are still in life in 2013. Between 2008 and 2012, 19 monarchs were also captured and marked.

An estimate of the population size was established during and just after the breeding period (5 to 8 months each year) by mapping the distribution of sightings of different colour forms (age classes), together with sightings of the 5 colour-banded birds (Bibby, Jones & Marsden 1988).

Due to nest situation in trees it was impossible to band nestlings. The same methodology was used during the nine years of the study of the breeding biology (which take place between 1998-2002 and 2008-2012). On arrival at each territory, the observer remained for 30-240 minutes and observed the bird’s behaviour in order to locate nests and to follow birds. Observations focussed on birds that were displaying behaviours related to reproductive activity (e.g. nest-building, egg-laying, incubation, nestling stage, fledged young) and territory guarding.

Laying and hatching date were determined by observing the behaviour of breeders at the nest. Nests that fledged one young were considered successful. Sex was determined for banded birds and for pairs of orange/black or orange/grey birds during mating. When mates could not be identified during data collection, only the overall parental behaviours could be considered. We therefore performed the analysis either by combining female, male, sex unknown data, or by considering each sex separately. The age of the breeding pair was also considered by comparing data collected on pairs of birds in mature plumage, i.e. pairs of black birds compared with data from pairs including at least one bird in immature orange plumage.

Observations were made between 07.00h and 14.00h using binoculars from vantage points, using the same locations for observations for every nest and minimizing the disturbance to the breeders. The temporal distribution of parental activities at the nest was surveyed, recording each parental trip from foraging sites to the nests, the times spent in the nest, interaction close to the nest (i.e. chasing and/or calls, airborne fighting, etc). Altogether, 263 hours of observation were conducted during those 4 breeding phases.

The impact of other bird species and conspecifics on breeding efforts was estimated through the aggressive interactions (alarm calls and chasing), observed between those birds and the owners of the territory (called 'interactions'). The other bird species present in the study areas were: 1) indigenous birds, such as Gray-green Fruit Dove (*Ptilinopus purpuratus*), Tahiti Kingfisher (*Halcyon venerata*), Pacific Swallow (*Hirundo tahitica*), Long-tailed Cuckoo (*Eudynamys taitensis*); 2) introduced bird species, such as Red-vented Bulbul, Indian Mynah, Silvereye (*Zosterops lateralis*) and Australasian Harrier (*Circus approximans*).

The history of recovery between 2003 and 2007 was issued from report analysis (Gouni 2003, Gouni & Noiret 2004, Gouni, *et al*. 2005, 2006 and 2007) and data collected directly by the authors between 1998 and 2002; 2008 and 2012.

Data analysis of the reproduction

We combined results from nine years of observations. Detailed analysis on inter-annual differences could not be carried out because of the paucity of the data set. We hope that our data are not biased by inter-annual differences in sampling effort.

Many nests were located in inaccessible tree-tops and our priority was to leave them undisturbed. As a consequence, the amount of time spent by adults at the nest during the nestling period could not be separated into feeding and brooding times. Following Laiolo, Bignal & Patterson (1998), the frequency of visits to the nest was used as a measure of feeding frequency during the nestling stages. As we also cannot check for clutch and brood sizes, food provisioning rate was calculated only with respect to brood (trips/hours per brood) and egg-laying time was estimated through the initiation of the incubation period or the hatching time.

Different breeding activities were considered for four distinct periods: (a) nest-building period: rate at which breeders visited the nest (trips/hour); nest attendance time (expressed as a percent of time spent into the nest); (b) egg-laying and mating time: idem; (c) incubation period: idem plus duration of complete incubation spell and duration of incubation recesses (d) nestling period: parental provisioning rate (trips/hour), nest attendance time.

The activities were compared between sex, age of the pair (pair of black birds or pair including at least one bird in orange plumage) and analysed with regard to hours of data collection and days from laying or hatching (i.e. nestling age).

Results

Bird census

At the start of the recovery program in 1998, a survey based on its historical range established that the species was still present in 4 valleys, but with a total of only 25 birds. The trends in numbers of its 'basal', accessible population, and of the difficult to access population located above several 10-30m waterfalls (known as the 'High' population) is presented in Table 1. In 2002, 14 birds were known in the basal population and 33 in the high population. In 2010, 22 birds were known in the basal population and 14 in the high pop. Decrease of total population that occurred between 2002 and 2009 was stopped by the progressive inclusion of the high population in the recovery effort and by the regular increase of young productivity that was achieved when rat control was intensified and introduced bird control initiated. The number of bird increased since.

Table 1 : Census of Tahiti monarch since the start of the recovery program

	1988	1999	2000	2001	2002	2003	2004	2005	2006	2007	2008	2009	2010	2011	2012*
Basal Pop.	19 (8) +2	25 (8) +6	23 (9) +3	19 (7) +1	14 (4) +1	12 (4) +1	17 (6) +2	16 (6) +3	17 (6) +1	17 (7) +5	20 (6) +2	23 (6) +4	22 (6) +5	22 (6) +4	22 (7) +4
High Pop.	2(1)	2(1)	4(1)	10(3)	33 +2	>2	>2	>2 +1	>2	>2	>1	12 (1) +1	14 (4) +1	18 (6) +3	22 (6) +4
Total Pop.					48 +3							35 +5	36 (10) +6	40 (12) +7	44 (13) +8-9

Legend : fixed adult birds (pairs number) + number of fledgling during the X breeding season (August X-April X+1)

***** 2012 breeding season will finish in March 2013. Our data are preliminary results for the ongoing breeding season

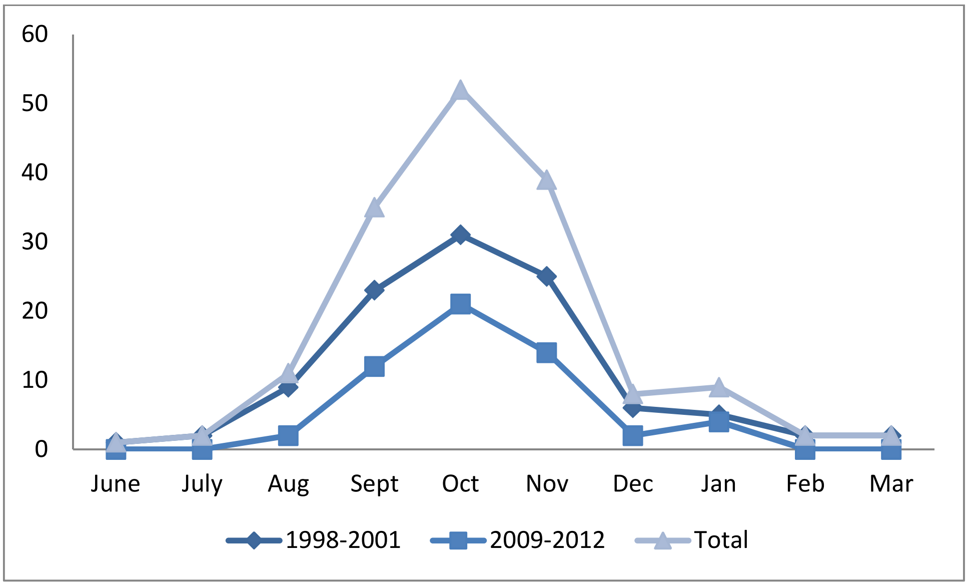
Nesting sites

Overall, 66 nests were described throughout the study period (data not show). The majority of nests were in native tree *Neonauclea forsteri* (62 %), *mara* in Tahitian, or in introduced and invasive African Tulip-tree *Spathodeae campanulata* (35 %), the two dominant tree species of the higher canopy of Tahiti monarch territory. The same individual tree could be used several times the same breeding season (up to 5 times for Mara, 3 times for Tulip-tree), but only Mara specimens were used by the same or different pairs several consecutive years. Most of the 66 nests were built in trees close to the river flow, although 15 of them (23 %) were on trees 6+ m high on valley ridges. The height of the nests above the ground averaged 13.0 ± 0.6 m. (range 5-21 m.).

Timing of breeding and factors affecting it

Nest building occurred between June and March with a peak lasting from September to November (Fig. 1).

Figure 1; Timing of nest building from 1998 -2001 and 2008-2012 in Tahiti Monarch



In case of nest failure, second broods were common (see below). First nest-building dates varied by 1-5 weeks each years (from 20 August ± 12 days in 2000 for the earlier breeding season onset to 16 November ± 22 days in 2008 for the latest one) P<0.003, H= 23.5, Kruskal-Wallis test). By combining all the data, first nests were built around 7 October ± 6 days.

No significant difference was observed in the timing of first nest building between pairs of black birds and pairs that included at least one bird in juvenile (orange/grey) plumage. This was similar for incubated nests.

Reproductive performance during the recovery period

Tahiti monarchs are monogamous, with pair bonds of unknown duration. It was sometimes difficult to establish if death or divorces caused pair shift. Sexes co-operate to incubate and raise nestlings. Second nests (up to seven nest-building attempts in one breeding season) were common. Second broods occurring after successful attempts were observed for two pairs of black bird only, on two occasions each.

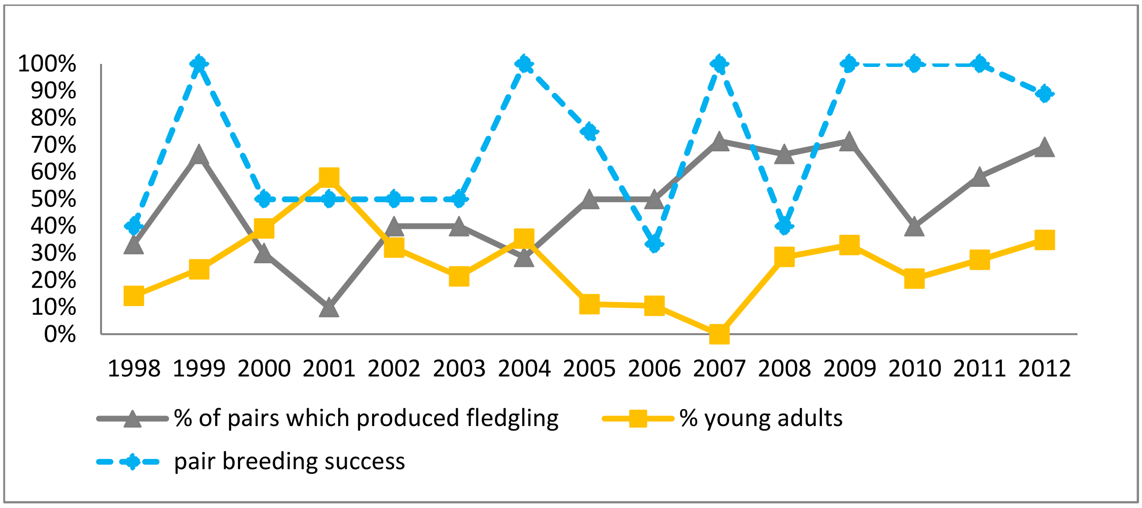
A summary of life history data are presented in Table 2. Each year, 5-13 pairs were present; 2-9 of them incubated at least one nest. 159 nests were found and 80 incubated from which 66 young fledged. 49 % of nest protected against rodent produced fledging against 10 % of unprotected nests. The mean number of fledged young per successful nest was 1 ± 0 (n = 66) and at the nestling stage, only one chick could ever be seen inside the nest. Between 20 to 27 % of the 66 fledgling died the first weeks after fledging, a critical period for its survival.

Table 2 : Summary of life history data in Tahiti Monarch

POPULATION BASSE	**1998**	**1999**	**2000**	**2001**	**2002**	**2003**	**2004**	**2005**	**2006**	**2007**	**2008**	**2009**	**2010**	**2011**	**2012**	**% ou Ṁ**	**Total**
Oiseaux Z basses connus	19	25	23	19	14	12	17	16	17	17	20	23	22	22	22	**19,2**	
Oiseaux Z hautes connus	2	2	4	10	33	2	2	2	2	2	1	12	14	18	22	**8,5**	
% young adults	14%	24%	39%	58%	32%	21%	35%	11%	11%	0%	29%	33%	21%	28%	35%	**26%**	
nb couples Z basses	8	8	9	7	4	5	6	6	6	7	6	6	6	6	7	**6,5**	
nb couples Z hautes	1	1	1	3	1	1	1					1	4	6	6	**2,4**	**26**
nb of pairs identifed	9	9	10	10	5	5	7	6	6	7	6	7	10	12	13	**8,1**	**122**
nb couples suivi	8	8	8	6	5	5	4	4	4	6	6	7	6	12	13	**6,8**	**102**
% orange mixtes ds couples suivis	6%	19%	25%	42%	25%	0%	10%	0%	13%	0%	16%	29%	33%	29%	35%	**0,2**	
nb de couples ayant incubé un nid	5	6	6	2	4	2	2	4	3	5	5	5	5	7	9	**4,7**	**70**
nb couples ayant produit des poussins à l'envol	3	6	3	1	2	2	2	3	3	5	4	5	4	7	9	**3,9**	**59**
nb couples protégés contre rats	5	9	7	6	4	5	4	4	4	5	6	7	6	11	13	**6,4**	**96**
nb nids trouvés	20	13	19	12	6	4	5	4	4	5	9	11	9	23	15	**10,6**	**159**
nb nest incubated	7	9	8	7	4	2	np	np	np	5	7	9	5	8	9	**50%**	**80**
% nids incubés	35%	69%	42%	58%	66%	50%				100%	78%	82%	56%	35%	60%	**50%**	
échec de l'incubation	2	1	0	2	1	0	np	np	0	0	2	4	0	0	1	**17%**	**13**
nb poussins nés	5	8	8	5	3	2	np	3	3	5	5	5	5	8	8	**5,2**	**73**
échec de l'élevage au nid	1	0	4	2	0	0	np	0	0	0	1	0	0	1	0	**12%**	**9**
nb of fledgling	4	8	4	3	3	2	2	3	3	5	4	5	5	7	8	**4**	**66**
échec post envol	2	2	1	2	1	1	0	0	2	0	1	0	0	0	0	**18%**	**12**
nb of successful fledgling	2	6	3	1	2	1	2	3	1	5	2	5	5	7	8	**53**	
J survie incertaine*	0	0	2	0	0	0	0	2	0	1	0	0	0	0	0	**9%**	**5**
nb envols/cp suivis	0,25	0,75	0,38	0,17	0,40	0,20	0,50	0,75	0,25	0,83	0,33	0,71	0,83	0,58	0,62	**0,50**	
nb envols/cp producteurs de poussins ayant survécu	1,00	1,25	1,00	1,00	1,00	1,00	1,00	1,00	1,00	1,00	1,00	1,20	1,20	1,00	1,00	**1,0**	
pair breeding success	40%	100%	50%	50%	50%	50%	100%	75%	33%	100%	40%	100%	100%	100%	89%		
% of pairs which produced fledgling	33%	67%	30%	10%	40%	40%	29%	50%	50%	71%	67%	71%	40%	58%	69%	48%	
nb envol /nid incubé	0,29	0,67	0,38	0,14	0,50	0,50				1,00	0,29	0,56	1,00	0,88	0,89	**0,6**	
dératisation	saison	saison	saison	saison	saison	saison	continue	continue	continue	continue	continue	continue	continue	continue	continue		
nb de nid protété contre les rats (couples connus)	9	9	16	8	6	4	5	4	4	5	8	11	8	11	15	**8,2**	**123**
nb nid protégé ayant produit des poussins	3	7	4	3	3	2	2	3	3	5	3	5	5	4	9	**50%**	**61**
nb de nid non protégés contre les rats	11	4	2	3	0	0	0	0	0	0	1	0	0	0	0	**1,5**	**21**
nids non protégé ayant produit des poussins	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	**10%**	**2**
lutte contre OI/tirs				2 ois/tirs								10	15	25	3		
lute conre OI/poison														15	30-50		
lutte contre OI/nasses tapette				23										5	2700		
Total échec (nid incubés et envol)	5	3	5	6	3	1			2	0	4	4	0	1	1		**35**
Failure due to introduced birds	2		3	1							3	2		1		**34%**	**12**
Failure due to climatic events				2	1							2				**14%**	**5**
unknow failure	3	3	2	3		1			2		1				1	**40%**	**14**

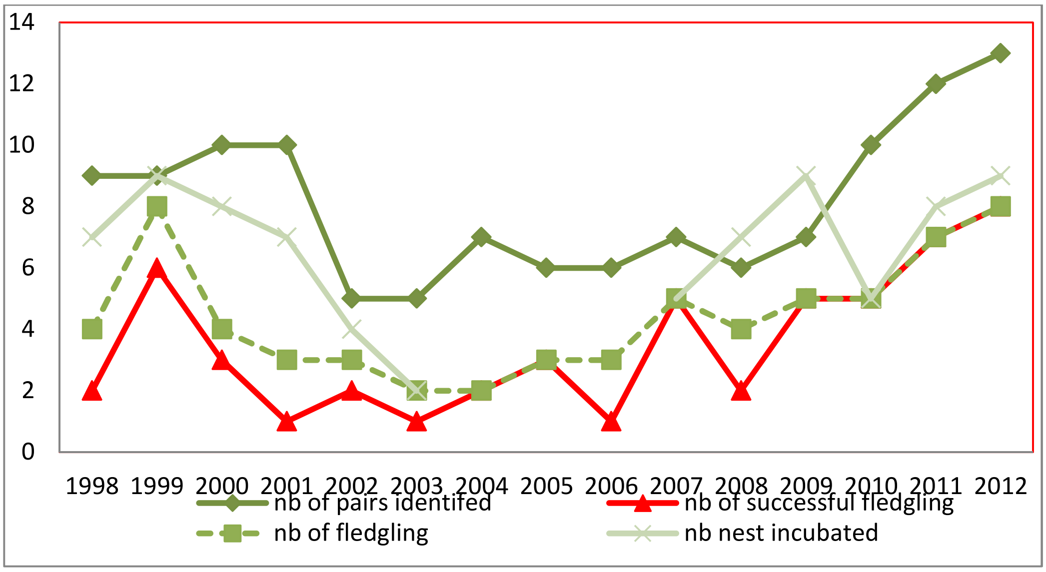
The percentage of pairs which produced fledgling was negatively correlated with the percentage of young adults in the population or in the pairs between 1999 and 2007 (r = - 0.87 and - 0.63 respectively). This correlation became weak if we include the entire period (from 1999 to 2012 r = - 0.46 and - 0.21). The pair breeding success (ie the number of pairs incubating a nest that produced fledgling) was erratic between 1998 and 2008 and remains elevated since 2009 (between 90 and 100 %) which coincide with the initiation of introduced bird control (Figure 2).

Figure 2: % of pairs wich produced fledgling, young adults and breeding success in Tahiti Monarch



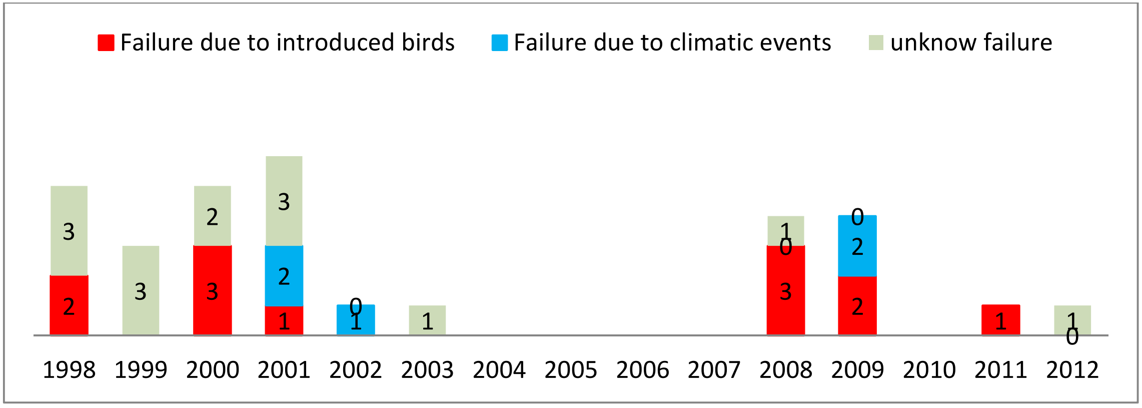
The increase of recovery efforts since 2009 and breeding success coincide with the increase of the number of pair identified, fledgling and successful fledgling (Figure 3).

Figure 3: number of pairs identified, fledgling, successful fledgling and incubated nest in Tahiti Monarch



35 nest failures were documented, 34 % of them were due to introduced birds (n = 12), 14 % to climatic event (n = 5) and 40 % were unknown failures (Figure 4).

Figure 4: origin of nest failure in Tahiti Monarch between 1998-2002 and 2008-2012



Breeding activities and factors affecting them

Nests building & nest structure

Tahiti monarch nests are constructed in a fork, usually of three twigs, a short distance from an umbrella of leaves which protects the nests from rain and sun. Their nests are open cups (about 9 cm across and 4 cm deep; 6 cm and 3 cm for internal measurements) and consisting of moss (*Aerobryopsis ?*). The nest cup is lined with small twigs of the thin ferns (*Adiantum trapeziforme* or *A. raddianum*). The nest contains a past composed of very small wood and leaf fragments which seemed to have been regurgitated by the birds. Scattered over the outer surface are white spiders' nests which camouflage the nests *and help its cohesion*.

We spent 22 hours observing 12 different nests during the nest-building stage. During this period, which lasted 8.0 ± 1.8 days (n=8), the nests were visited by breeding pairs at a mean rate of 13.6 ± 2.0 trips per hour (3 to 34 trips/hours). In total, they spent 21 ± 2 % of observation time inside the nest (Table 6). A positive correlation was found between the nest attendance time and the number of trips per hour (Kendall' correlation test; Tau = 0.4, Z = 2.5, P = 0.01). Both sexes visited the nest at the same rate (5.9 ± 1.3 for male vs. 5.1 ± 1.3 for female; 11 hours of observations; n.s., Wilcoxon test), but the male's nest attendance time was higher than the female's (12 ± 2 % vs. 8 ± 2 %; p = 0.04, Wilcoxon test). On 5 on 60 breeding attempts observed, they were re-using the precedent nest and bring some new material on it. This occurred 1) after egg-laying phase (n=3), after nest failure (n = 1), or using the nest of the preceding year (n=1) ; this lead to abandoned nest in two occasions or to the incubation and birth of a young (n = 3).

Mating and Egg-laying

After a mutual pursuit of each other, Tahiti monarchs mate on a branch near the completed nest or up to 15 m away, sometimes even on the ground. Mating was also observed outside the period of breeding activities and outside the breeding season. Occasional courtship feeding was observed. Several beak to beak contacts were also observed between the sexes. Courtship displays involved the male flapping his wings near the female (as for the mounting posture during which the male mounts the female for a few seconds) and in the same position but with the head slightly in an upright posture and calling. Several unusual vocalizations were associated with courting.

A total of 33 hours of observations was collected on 14 different nests during the egg-laying phase. This period lasted from 2 to 66 days (15.9 ± 15.0 n = 18). For 9 of them, the nest was finally abandoned without incubation, in one case, new materials were added and the nest incubated. This occurred for four nests built by pairs of black birds and six nests built by pairs composed of at least one bird in orange/mixt plumage.

During normal egg-laying phases, birds visited the nests at a rate of 4.7 ± 0.4 trips per hour and mean nest attendance time was 59 ± 6 % of observation time with no significant difference of both criteria between sexes and pairs (black/black vs. orange/other).

Incubation

A total of 53 hours of observations was collected on 16 different nests during the incubation phase: 22 hours on pairs of undetermined birds and 31 hours on sexed pairs. During this period which lasted 13.7 ± 0.5 days (n=8), birds visited the nest at a rate of 4.6 ± 0.1 trips per hour and mean nest attendance time was 96 ± 1 % (Table). Both sexes incubated the eggs. During this period females spent 55 ± 2 % of observation time incubating and male 38 ± 2 % only ($P = 0.0003$, Wilcoxon test).

The number of trips per hour (5.07 ± 0.23 vs 4.35 ± 0.21 $p < 0.2$, Z= Mann-Whitney U test) was different through the stages of the incubation period and similar through the hours of data collection.

A positive correlation was found between the number of trips per hour and the number of interactions observed between other birds and the incubating pair (Kendall' correlation test; Tau = 0.21, $Z = 2.2$, $P < 0.03$).

Complete incubation spells and incubation recesses were collected during a total of 44,5 hours. Mean incubation spells were 15.5 ± 0.6 min. and incubation recesses averaged 0.7 ± 0.1 min. Incubation spells were longer in female than in male (19.1 ± 1.1 vs. 10.9 ± 0.7 min.; $p < 0.0001$, $Z= - 5.78$, Mann-Whitney U test), and in pairs of black birds than in pairs including at least one bird in orange plumage (16.8 ± 0.9 vs. 14.8 ± 0.8 min.; $p < 0.05$, $Z = - 2.05$, Mann-Whitney U test). Durations of incubation spells were similar among the incubation stages and hours of data collection.

Incubation recesses during which interactions with other birds were observed were longer than those occurring without any interactions (3.2 ± 0.8 vs. 0.4 ± 0.1 min.; $p < 0.0001$, $Z = - 5.47$ Mann-Whitney U test).

Nestling period

A total of 76 hours of observations was collected on 27 different nests during the nesting period: 44 hours on pairs of undetermined birds; 32 on sexed pairs. During this period, which last from 12-17 days (14.2 ± 0.6 days, n=9), birds visited the nest at a rate of 9.7 ± 0.6 trips per hour (Table 6). The nest attendance time proved to be affected significantly by nestling age ($P < 0.0001$; Kruskall-Wallis test; Fig. 2) and varied from 70 % to 23 % from 1-2 to 7-8 days after birth, then dropped under 10 % to 0% from 9-17 days after birth. The number of trip per hour was similar throughout the age of the young and the hour of data collection. A significant negative correlation was found between the number of trips per hour and the number of interactions observed (Kendall' correlation test; Tau = - 0.18, $Z = - 2.32$, $P < 0.02$). Male and female trips per hour were similar (5.02 ± 0.6 for male vs 4.5 ± 0.4 for female) but they were both significantly affected by the number of interactions, (Wilcoxon correlation test; $Z = - 3.31$, $P = 0.001$ for male; $Z = - 4.07$, $P<0.0001$ for female).

Independence

Chicks disappear from parent's territory 70 ± 23 days after fledgling (between 48 – 132 days) after being feed by them 56.6 ± 6.9 days. Dispersal of juveniles is often local, although individual birds sometime disappeared several months or forever after independence

Stage of nest failure, impact of parental investment and interactions on breeding success

The main stage of nest failure occurred at the egg-laying period: only 50 % of nests built were incubated. Predation by rats on nests built early in the breeding season, before the start of nest protection in each valley or nest built in inaccessible valley ridges, for 1998-2002 period may represent one cause of nest failure at this stage. Only 10 % of unprotected nests produced fledgling against 50 % of protected nests. Abnormally long egg-laying durations suggest that some mates are too young or too old for perform more reproductive effort, or that proximate or ultimate factor was impacting on reproduction in this particular case. Some nests may have been abandoned because of poor nest-site selection, poor building, and too much nest disturbance by introduced birds. Nests built for pair-bonding reason only is also common.

On the 80 nests incubated, 83 % of them produced nestlings, 88 % of nestlings fledged and only 73-80 % of fledglings survived the first week after fledging, a period which proved to be critical for young.

In order to assess the impact of parental investment on breeding success, different parameters in the incubation and nestling periods (interaction/hour, trip/hour, nest attendance time...) were compared in case of incubation failure and nestling or fledgling death or in case of success (Table 3). During the incubation period nests which were successful and allowed fledgling survival experienced 10 fold fewer interactions during the incubation period than the other ones. During the nestling period, successful breeding attempts (including fledgling survival) corresponded to nestlings being fed at a higher frequency (with more trips per hour) than the nests who failed, they also experienced 3.6 fold fewer interactions than the other ones. Interestingly, male but not female's trips/hour was significantly different during breeding success or failure.

Table 3: Difference between interactions, trips/hour, nest attendance time during incubation and nestling stages, male and female's trips/hours during nestling stage on breeding success or failure

	Success	Failure	Man-U Whitney tests
Incubation stage	Incubation success	Incubation failure	
Interactions/hour	**0.1 ± 0.1**	**1.0 ± 0.2**	0.05
Trips/hour	4.1 ± 0.3	4.7 ± 0.2	ns.
Nest attendance time	96 ± 1	96 ± 1	ns.
Nestling stage	Successful fledging survival	Unsuccessful breeding attempts	
Interactions/hour	**0.5 ± 0.2**	**1.8 ± 0.2**	0.0005
Trips/hour	**12.2 ± 1.0**	**8.5 ± 0.6**	0.0009
Male's trips/hour	**8.5 ± 1.3**	**3.6 ± 0.4**	0.007
Female's trips/hour	4.1 ± 0.7	4.8 ± 0.4	ns.
Nest attendance time	26 ± 6	31 ± 5	ns.

Discussion

This work describes for the first time the breeding biology of the Tahiti Monarch and the impact of several factors (sex, age, interactions) on breeding efforts and success. Overall, our results suggest that five factors limited Tahiti Monarch nesting success and fledging survival: depredation from rats and from introduced birds, lower parental investment due to disturbance of the breeding pairs by other birds; climatic hazard, percentage of young birds present in the population (including breeders) when introduced bird control is not performed. Other factors that we did not study, but which may have been important, include food limitations (through season and habitat quality), and nonviable eggs.

Breeding biology of the Tahiti Monarch and impact of sex, age and interactions

This study describes breeding biology and survival of the Tahiti Monarch, which have never been studied before in this species. As expected from life-history theory (Ricklefts 1980, Kulesza 1990, Stearns 1992), the Tahiti Monarch shows the pattern typical of tropical passerines in having a low reproductive rate, with a small clutch and usually only one brood each year. The existence of a seasonal pattern of reproduction is more typical of temperate zone passerines (Perrin, 1970) and probably reflects the seasonal nature of the climate of Tahiti which lies just within the tropics (Saul *et al*. 1998). Both sexes cooperated during each phase of the reproductive activity but females spent more time in the nest than male during incubation. With increasing nestling age, the nest attendance time decreased. This probably reflects the increase of the chick thermoregulatory abilities (Royama 1966).

Pairs that included birds in immature plumage incubated their nests during shorter incubation spells than pairs of black birds, but no difference were detected during the nestling period.

Parents experiencing more interactions left the nest after shorter incubation spells and left nests unattended for longer periods during incubation than parents living in more quiet territories. In the same way, incubation spells and incubation recesses during which interactions occurred were respectively shorter and longer than those during which no interactions were recorded. In Seychelles Magpie Robin, *Copsychus sechellarum*, the incubation times of females disturbed by Mynah or floater birds was lower than that by females without disturbance (Komdeur 1995).

During the nestling period, a significant negative correlation was found between the number of trips per hour and the number of interactions. Male and female trips per hour were similar but they were both significantly affected by the number of interactions.

Impact of nest disturbance on breeding success

Our data show that breeding success in Tahiti Monarch was adversely related to number of interactions experienced each hour by the breeding pair (both during incubation and nestling periods) and positively related to feeding frequency.

Interestingly, male but not female's trips/hour was significantly lower in nest experiencing breeding failure than those experiencing breeding success. This suggest that male may be more implicated in nest protection from introduced birds and that the fact that he spent less time feeding the young have a negative feed-back on breeding success, or because the young is finally predated, or because the young is less feed so less healthy for support fledgling crisis or difficult weather situation. In Seychelles Magpie Robin, higher nest disturbance during incubation also resulted in higher proportion of nest failures (Komdeur 1995).

This study confirmed the existence of an impact of other birds on the reproductive success of the Tahiti Monarch. This may act through direct predation on nests which is highly suggested in the case of the Indian Mynah because of a higher number of encounters and interactions between Indian Mynah and Tahiti Monarch around nests containing eggs and chicks than in other situation (Blanvillain *et al.* 2003). In this first case, nest disturbance and decreased breeding effort may possibly only reflect the exposure of the nest to predation risks. However, a second impact could be that nest disturbance through interactions, by decreasing the feeding frequency during the nestling phase, leading to the nestling having lower fitness and lower chance of survival during the nestling and the post-fledging period. It is probable that both factors act together. Red-vented Bulbuls, which occur in Tahiti Monarch territories throughout the stages of reproduction and outside breeding, may act more as inter-specific competitors for nest sites, territories and food resources rather than as nest predators (Blanvillain *et al*. 2003). This species may, thus, inflict a lower fitness on young through regular nest disturbance. However, it is also possible that Red-vented Bulbuls directly attack fledglings and kill them. Birds faced with higher territory disturbance may have to leave their nest more often to interact, thus exposing their eggs or young to variable temperatures, rain and predators such as rats and introduced birds. Longer brooding spells in unsuccessful nests might be associated with an attempt from the parents to increase protection of their young or reflect the lower fitness of those young. The alternative explanation could be that unsuccessful nests experienced more adverse weather conditions that leaded parents to brood their nestling for longer periods.

Studies of many island bird species in the Pacific show the dramatic impacts of introduced mammals, especially rats on those populations (Robertson *et al*. 1994; Blanvillain *et al*. 2002). In contrast very few studies as show the impact of introduced birds on island species, except for bird of prey for which predation is much more evident (Penny 1974; Lever 1994).

Interactions that occurred during breeding activities documented the breeding birds and Red-vented bulbul in 46 % of cases, Indian Mynah in 34 % of cases and other Tahiti Monarch in 8 % of cases (Blanvillain *et al.* 2003). Other 8% occurred with 5 different species. To our knowledge, the only other study demonstrating the impact of nest disturbance caused by other birds, including conspecifics, on breeding success concern another island bird, the Seychelles Magpie Robin. In that study, both Indian Mynah and floaters birds established in high-quality areas caused disturbance and nest failure to breeding pairs (Komdeur 1995). This could suggest that nest disturbance by other birds in island birds, by inducing nest failure, could have been a regulatory mechanism of island bird's population dynamics. Particularly in predator-free tropical islands for which habitat saturation could have been a major limiting factor for bird populations.

Depredation

As for the Kakerori, the Tahiti Monarch was in declining because ship rats (*Rattus rattus*) preyed on eggs and nestlings. (Blanvillain *et al.* 2003; Robertson *et al.* 1994). Nestling and fledgling predation by Indian Mynah was strongly suspected in the case of the Tahiti

Monarch (Blanvillain *et al*. 2003) and confirmed the reputation of nest thievery of the species (Moon 1992; Cheke 1987).

Predation is commonly cited as the major factor limiting nesting success in arboreal open-cup nesting birds (Nice 1957, Wilcove 1985, Martin & Roper 1988). The absence of mammalian predators during Tahiti Monarch evolution suggests that the Tahiti Monarch may be particularly vulnerable to predation by introduced feral cats and rats. The very audible begging calls performed by some very healthy young at the nest may increase the vulnerability of nests to depredation during the nestling stage.

The degree of depredation on adults is unknown. However, the inaccessible placement of Tahiti Monarch nests make adults sitting on nests difficult prey for cats but not for rat and for introduced birds such as Swamp Harrier.

Percentage of young birds present in the population (including breeders)

Increasing proportion of orange and grey birds, of less than 4 years, present in the population or involved in reproduction coincided with a lower breeding success between 1999 and 2007. This correlation decrease or disappeared if all the recovery period is considered. In 1998, too many nests were left unprotected from rats and this limiting factor was decreasing the reproductive success of even experimented/undisturbed pairs while after 2008, the initiation of bird control may help pair containing younger, less experimented partners to concentrate on breeding effort thus to succeed more easily its reproduction or/and this may decrease the possible negative impact of young birds disturbing the breeding pairs. The impact of age in breeding success has been reported in numerous studies (Forslund & Pärt 1995, Pugesek & Diem 1983). Young Palila, *Loxioides bailleui* nested late in the season and had a tendency to abandon eggs due to inexperience (Pletschet & Kelly 1990). Young birds of many species breed later and are less successful than older birds (De Steven 1978, Reese & Kadlec 1985). The increase in reproductive performance with age could be explained by three possibilities: progressive appearance or disappearance of phenotypes; age related improvements of competence and optimisation of reproductive effort (Forslund & Pärt 1995).

Food availability, territory quality and Tropical rain

Our data show that breeding success in Tahiti Monarch was related to feeding frequency. Thus, an alternative hypothesis could be that lower food availability during the nestling period could decrease the fitness of young and result in lower breeding success. A greater number of interactions around nests could reflect greater competition for food and thus less food availability. Variation in the onset of breeding season from year to year may indicate that a seasonal factor may have been influential. Reproductive performance in birds is highly dependent on the availability of food (Arcese & Smith 1988, Hamer *et al*. 1993). Passerine birds are thought to adjust the timing and amount of investment in breeding to prevailing food levels (Perrins 1970; Martin 1987; Ims 1990). Eggs laid by poorly nourished birds may have lower hatchability (Martin 1987). Eggs formed at the time of poor food availability had reduced hatching success in the Pied Monarch, *Ficedula hypoleuca* (Järvinen & Väisanen 1984). A severe food shortage might cause Tahiti Monarchs to abandon viable eggs. In addition, birds faced with diminished food resources may have to leave their nests more often to forage, thus exposing their eggs or young to variable temperatures, rain or predators.

One of our findings also indicates that food resources may limit Tahiti Monarch productivity: variability of fledging age (12 to 18 days). When local food supply is favourable, nestlings probably develop more rapidly and fledge earlier than when food is scarce (Skagen 1988), thus could account for the variability of Tahiti Monarch fledging age. However, this may not be related to food availability in the territory but more to the food provisioning rate by the parents, which itself is affected by the number of interactions with other bird species.

Habitat quality may act though food availability and nest protection from predators (Hatchwell, Chamberlain & Perrins 1996) and the effect of habitat on nesting success has been assessed in several studies (Högstedt 1990; Ens *et al.* 1992).

Several nest failures coincided with huge rains coming at the start of the wet season which peaks in December at Paea district. Rain could cause direct death of weak nestling or fledgling and also bring about food shortages which could induce lower nestling and fledgling fitness. With bad weather conditions, strong winds have sometimes broken tree branch holding the nest, resulting in nest failure.

Hatching failure

Hatching failure, due to inviability or desertion, was the primary cause of nest failure in Palila (Pletschet & Kelly 1992). Koening (1982) analysed 155 nesting studies and found that a mean of 9.4 % of eggs were unhatchable. Low population size and isolation of the four sub-populations of Tahiti Monarch may have led to inbreeding resulting in reduced fertility and higher incidence of lethal recessives exposed during embryo development. Evidence that inbreeding reduces both fertility and embryo survival exists for domestic fowl (Shoffner 1948), Japanese Quail, *Coturnix japonica* (Sittmann, Abplanalp & Fraser 1966) and Great Tits, *Parus major* (Van Noodwijk & Scharloo 1981) However, even if a high degree of inbreeding may be suspected in Tahiti Monarch due to limited size of the remaining population and the isolation of the 4 sub-population, the genetic fitness of the population is unknown.

Comparison with Rarotonga Monarch

The Tahiti Monarch seasonal pattern of reproduction is more protracted than that of the Rarotonga Monarch, *Pomarea dimidiata* (Saul *et al.* 1998). This species also lives in eastern Polynesia, on Rarotonga, 21°, 14’ S; (Cook islands), but the Tahiti Monarch lives a little closer to the equator than the Rarotonga Monarch: 17°, 38’ S. The breeding season of the species living closer to the equator may be more protracted or governed by variation in rainfall (as with passerines in the Galapagos, Curry & Grant 1989). With lower clutch size (1 nestling versus 2 for the Rarotonga Monarch), similar incubation length (13.5 versus 13 days for the Rarotonga Monarch) but slightly higher brooding length (12-18 days versus 11-15 days for the Rarotonga Monarch) it seems that the Tahiti Monarch is much less fertile than the Rarotonga Monarch. This could reflect a longer adaptation process to predator-free tropical islands for the Tahiti Monarch population than that of the Rarotonga Monarch. This also may explain the lower recovery rate of the Tahiti Monarch than the Rarotonga Monarch (Robertson *et al.* 1994; Blanvillain *et al.* 2003). The impact of Mynah was never observed in Rarotonga Monarch (Mac Cormak, personal communication) while two species of Mynah are now present in Rarotonga. Mynah are never observed within Rarotonga Monarch populations. From our point of view, the high level of habitat perturbation of Tahitian forest, with many invasive tulip tree (*Spathodea campanulata*), very attractive for both Mynah and Bulbul may explain this situation.

In conclusion,
With only 44 individuals and no more than 13 pairs, the Tahiti Monarch is one of the more endangered bird species in the world. The recent regular increase in young production and breeding success of breeding pairs are first positive results in its recovery, even if its survival remains uncertain. Its low productivity as well as minimum management between 2002 and 2008 are at the origin of this situation. Among the causes that have played a direct or indirect role in this situation, the introduction of alien predators (rats, cats, and birds) has played a major role in depleting the local populations, as for many species in Polynesia (Robertson *et al*, 1994. Blanvillain *et al*. 2002). We show in this study that introduced birds species, by increasing nest disturbance, also reduce breeding success in Tahiti Monarch. This is an original finding in island bird whereas the impact of mammalian species has been widely documented. In New Zealand, Diamond & Veitch (1981) concluded that extinctions of native species were not due to competition from introduced species but to other factors (such as mammalian predators and habitat alteration) and that exotics birds could invade forest only after decimation of native species and forest alteration. In Fiji, competition with native land birds is suspected for the Red-vented Bulbul, living in the forest and in contact with indigenous species but not for the Indian Mynah, restricted to man-modified habitat (Walting 1977) as in Rarotonga (Robertson *et al*. 1994). Those conclusions, the fact that Indian Mynah are now whispered in forest habitat at least at Tahiti (Blanvillain *et al.* 2002) and the paucity of data existing on impact of introduced birds suggest that this problem has been underestimated in the causes of native bird extinctions.

This population is extremely vulnerable due to its minute size, the fragmentation of the remaining population, its low reproductive rate and the numerous threats that face the remaining birds. Control of introduced mammals and birds is a prerequisite for its survival. Clearly, only long-term recovery efforts will save the species from extinction. More research is needed to determine the importance of the introduced birds on native birds elsewhere and the importance of food availability factor in the case of the Tahiti Monarch whereas information on the amount of inbreeding and degree of genetic variability would help determine its genetic fitness.

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