Breeding success and predation on artificial nests of the endemic pigeons Bolle's Laurel Pigeon *Columba bollii* and White-tailed Laurel Pigeon *Columba junoniae* in the laurel forest of Tenerife (Canary Islands)

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Breeding success and nest predation effects on the two Canarian endemic pigeons, Bolle's Laurel Pigeon *Columba bollii* and White-tailed Laurel Pigeon *C. junoniae*, were studied during 1995 in five zones of laurel forest on Tenerife Island. Nest predation was the more important cause of nesting failure of both species (88%), but principally affecting the White-tailed Laurel Pigeon. Experiments using artificial nests showed a greater predation on the ground than in trees and a lower predation in the February–March period than in June–July and September–October. The abundance of predators, estimated by bait consumption, showed a similar seasonal pattern, while fruit availability decreased over time from the first to third period. Predators identified by automatic cameras showed that Black Rat *Rattus rattus* was the major nest predator of both pigeons. These general patterns of nest predation affect the White-tailed Laurel Pigeon, which breeds on the ground mainly during April–July, much more than Bolle's Laurel Pigeon, which breeds in trees, especially in February–June. All seems to indicate that rats are the key factor causing the scarcity of the White-tailed Laurel Pigeon on Tenerife.

Laurel forest of the Canary Islands harbours two endemic species of pigeon: Bolle's Laurel Pigeon *Columba bollii* and White-tailed Laurel Pigeon *C. junoniae* (Fig. 1). Both have been considered old elements of the Canarian avifauna (Volsøe 1955, Jaime *et al.* 1993). Drastic regression of laurel forest after the conquest of the archipelago (15th century) caused a reduction in numbers and distribution of pigeons, so that one species (probably Bolle's Pigeon) disappeared from Gran Canaria at the end of the last century (Bristram 1889). Furthermore, bone remains, so far unidentified at a specific level, show that these species (or species very closely related to them) inhabited the dry eastern islands of Lanzarote and Fuerteventura (Rando & Perera 1994). White-tailed Laurel Pigeon could have been present on Gran Canaria (Alcover & Florit 1989); the historical early account (1402–04) of 'large pigeons with white ends to their tails' on Fuerteventura may have referred to this species (Collar & Stuart 1985).

Nowadays, both Canarian pigeons inhabit the islands of Tenerife, La Gomera and La Palma, but there are also small numbers of Bolle's Pigeon on El Hierro (Martín 1985, Martín *et al.* 1993, Hernández & Martín 1994). As numbers of these pigeons in the Canaries are very low, they have been given special protection (Collar & Stuart 1985, Tucker & Heath 1994).

Little is known about their breeding biology (Bannerman 1963, Emmerson *et al.* 1986). Both species lay a single egg. Bolle's Pigeon breeds in trees throughout the year (particularly in February–June) whereas the White-tailed Pigeon nests on the ground, probably all year round (pers. obs.), with a peak in April–July. Introduced predators are very abundant in the laurel forest and have been suspected of severely affecting breeding success of the White-tailed Pigeon (Hernández & Martín 1994).

As ground-nests have traditionally been considered to suffer from higher predation than nests above-ground (Ricklefs 1969, but see Martín 1993a for opposite views), the Canarian pigeons offer an optimal framework to examine differential predation rates

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Figure 1. The two endemic species of pigeon: (a) White-tailed Laurel Pigeon *C. junoniae* and (b) Bolle's Laurel Pigeon *Columba bollii*.

according to nest-site in a forest habitat. We investigated the spatio-temporal patterns of breeding success of the two species of pigeons, to examine possible relationships between nest-sites and nesting success, and to identify the main nest predators.

STUDY AREA AND METHODS

The Canary Islands (27°37'–29°25'N and 13°20'–29°25'W) form an archipelago of volcanic origin and are made up of seven main islands, situated in the Atlantic Ocean some 100 km (at the closest point) from the African continent. Tenerife is the largest (2034 km²) and highest (3718 m asl) island and has clearly defined vegetation belts changing with altitude. The laurel forest, generally located on the northern slopes of the island (mainly at 500–1000 m asl), has an average annual rainfall of over 700 mm and the mean temperature is about 15°C. This habitat is dominated by trees and bushes such as *Laurus azorica*, *Persea indica*, *Apollonias barbujana*, *Picconia excelsa*, *Ilex canariensis*, *Myrica faya*, *Viburnum tinus* and *Erica arborea*. This native woodland is a relict flora that formerly covered the margins of the Tethys Sea during the Tertiary.

Fieldwork was carried out at 11 localities in the main five zones of the laurel forest according to their respective extensions: three in Anaga (Monte de Aguirre, Las Yedras and Las Vueltas de Taganana), one in Tacoronte (Bosque de Agua García), two in Santa Úrsula (Barranco de Las Calderetas and Barranco de La Fortuna), two in Los Realejos (Barranco del Garabato and Barranco de La Calera) and three in Los Silos (Barranco de Blas, Galería del Caudal and Lomo de Antonillo) (Fig. 2). The study of natural nests was

conducted between February and August 1995 and artificial nests were installed in three different trials (February–March, June–July and September–October), to coincide with the known main breeding periods of the two pigeons.

Natural nests

Nest searches were conducted in all the five selected zones but, in Tacoronte, occupied nests were not found. Nesting success was determined by periodic visits until either the chick fledged or breeding failed. Checks were made from a distance with binoculars to minimize the possibility of predation linked to disturbance. Breeding success was calculated not only as the

Figure 2. Map of Tenerife indicating location of zones.

percentage of total nests that were successful but by the Mayfield method, which permits comparisons with other studies.

The relationship between nest site and breeding success was studied by analysing several characteristics of Bolle's Pigeon nests after the young left. We recorded and measured: tree species, trunk perimeter, diameter of the branch supporting the nest, distance to trunk, nest height above the ground, distance of the nest to the superior, inferior and lateral canopy, tree species in a radius of 1 m from the nest, number of old nests in a radius of 10 m. In each of four random quadrats of 1 × 5 m around the tree-nest, we measured the number, perimeter and height of the trees and bushes (grouped in two categories: 0.5–2 m, and > 2 m), and linear vegetation cover (< 50 cm). Altitude, slope and orientation were also recorded at each nest site.

Low numbers of White-tailed Laurel Pigeon nests ($n = 7$) prevented us from carrying out consistent statistical inferences for the several variables measured for this species.

Artificial nests

Due to the fact that the two pigeon species occurred at different densities, with different breeding periods and nest detection, we considered it of value to conduct parallel artificial nest predation experiments, a technique widely utilized in the last two decades (see Major & Kendal 1996 for a review).

Artificial nests comprised a wire-netting 'cup' (20 × 20 × 2.5 cm deep) lined with twigs and dry leaves. Each nest was baited with one Quail *Coturnix coturnix* egg and exposed for 18 days to simulate the natural clutch size and incubation period of these insular pigeons. We used 810 artificial nests in each of the three periods, using a total of 2430 Quail eggs. We used 15 stations, at 25 m intervals, in each of the 11 localities studied. At each station, five nests were used; one on the ground (simulating White-tailed Pigeon nest sites) and the other four at about 4 m height in tree species (*Erica arborea*, *Ilex canariensis*, *Myrica faya* and *Laurus azorica*) commonly selected by Bolle's Pigeon as nest sites. The distance between nests varied, depending on the availability of suitable substrate trees.

Quail eggs differ in colour but are only slightly smaller than those of pigeons. Although egg colour has not been shown to affect predation rate (Major & Kendal 1996), we decided to carry out two complementary experiments to assess effects of egg variation on preference and detectability to predators. In a

different locality of Anaga, during May–June, we placed 60 nests (30 on the ground and 30 in trees) containing two eggs, one from Quail and another from domestic pigeon. We also set 30 nests with just one Quail egg and another 30 with one pigeon egg. In these experiments we followed the methodology above. No significant differences were found in preference or detectability ($\chi^2_1 = 0.03$, ns and $\chi^2_1 = 0.09$, ns, respectively).

Identification of predators

To record predators, we used two automatic camera units (Canon Sure Shot A-1) triggered by breaking a beam of infrared light. Photographic techniques have proved to be much more reliable than other predator-detection methods and have been utilized with slight design modifications by different authors (Laurance & Grant 1994, Major & Gowing 1994, Picman & Schriml 1994).

From May to December 1995, both units were installed in the five zones of laurel forest except in Tacoronte and Santa Úrsula (where there was risk of human disturbance). One camera system was mounted on a tree and the other on the ground, about 1 m from an artificial nest containing 8–12 Quail or domestic pigeon eggs (depending on availability). A delay circuit gave a minimum 20-s pause between successive photographs to minimize the number of pictures taken of a single event. A digital clock was positioned in the field to record the time of predation. After an average of 6 days, the cameras were moved to a new location approximately 30 m away from the original position and the eggs replaced, to reduce the effects of habituation by the same individual predator.

Abundance of predators

Bait units were composed of ten toasted-honey corn rings hung up by a wire 15 cm above the ground. To obtain an index of rat abundance, we put five bait units (at 5 m intervals) at all stations of every locality during the three periods, just after the experiments on artificial nests were finished. We used a total of 2475 units (75 units/locality/period). The baits were left overnight and we considered a bait eaten when one or more corn rings were consumed.

Fruit availability

Fruits from several tree species in the laurel forest are consumed by rats (pers. obs.). Numerous studies have

shown that changes in food availability may influence rodent predation rates on birds (Atkinson 1985, Sieving 1992). Due to the omnivorous habits of rats, nest predation may be inversely related to fruit abundance. Counts of fruit were therefore made on the ground, in a band of 10×0.5 m, at each station during the three study periods.

Statistical analysis

Categorical data analyses were performed, using chi-squared tests. For analysing temporal variation of fruit availability, we used ANOVA. A logistic regression (forward stepwise selection, likelihood-ratio test; Norusis 1992) was utilized for studying possible variables that could influence predation on natural nests. The variables considered were the first 14 listed above under the heading 'Natural nests'.

RESULTS

Natural nests

We located 68 Bolle's Pigeon nests, most of them (79%) in four species of trees (*E. arborea* 34%, *L. azorica* 19%, *I. canariensis* 16% and *M. faya* 10%). This pigeon did not select tree species for nesting ($\chi^2_3 = 2.53$, ns); breeding occurred in the most abundant tree species in each locality.

The simple percentage of overall nesting success was 47% (incubation 59% and nestlings 80%). Mayfield nest success for the whole nesting period was 41% (incubation 54% and nestlings 76%) ($n = 30$ and 39 nests, respectively). Predation was the most important cause of nesting failure (86%).

Breeding success of this species differed between

Table 1. Nest success (simple percentage) of Bolle's Laurel Pigeon and White-tailed Laurel Pigeon in different areas of Tenerife.

Zone	No. of nests	Success	Failure	% success
Bolle's Laurel Pigeon				
Anaga	16	5	11	31
Santa Úrsula	13	10	3	77
Los Realejos	17	5	12	29
Los Silos	22	12	10	55
White-tailed Laurel Pigeon				
Los Realejos	7	2	5	29

areas (Table 1), being higher in Santa Úrsula than in Los Realejos and Anaga ($\chi^2_2 = 8.3$, $P < 0.02$). No statistical differences in breeding success were recorded in the different months or among the main tree species ($\chi^2_2 = 1.5$, ns). When variables directly related to nest sites are considered (see methods), there was greater success in those nests located in areas with a low density of bushes (< 2 m), further away from the trunk, and at shorter distances from the lower canopy (Table 2).

Nests of the White-tailed Pigeon proved to be very difficult to find because they are often built in inaccessible places where ropes are frequently needed to gain access. Only seven occupied nests (all of them in Los Realejos) were located during 1995. The percentage breeding success was 29% and predation explained all of the nest failures. Due to the small sample size, we also considered all the nests found for the period 1993–97; from a total of 22 nests, a breeding success of 27% was found. Despite the differences in breeding success between the species, the difference was not significant ($\chi^2_1 = 1.9$, ns).

Table 2. Logistic regression analysis of the main variables (see methods) that could influence nesting success of Bolle's Laurel Pigeon in Tenerife.

Variable	Slope	se	Wald	DF	P	R ^a	exp (B) ^b
DF	-0.47	0.23	4.10	1	< 0.05	-0.15	0.62
DT	0.69	0.32	4.51	1	< 0.05	0.17	1.99
NB	-0.10	0.04	5.81	1	< 0.02	-0.21	0.90
Constant	1.36	0.61	4.90	1	< 0.05		

DF, distance to inferior canopy; DT, distance to trunk; NB, number of bushes (0.5–2 m). The significance of the coefficients (B) is based on the Wald statistics. Model $\chi^2 = 14.5$, df = 3, $P < 0.01$.

^aThe R-statistic shows the partial correlation of the dependent variable and each of the independent variables. Positive R indicates that as the variable increases, so does the probability of nesting success; negative R indicates the contrary.

^bExp (B) is the factor by which the odds (ratio of the probability that nesting success will occur to the probability that it will not) change when the *i*th independent variable increases by one unit.

Table 3. Artificial nest predation rates found in different areas and periods in Tenerife ($n = 165$ ground-nests and $n = 645$ tree-nests in each period).

Areas	Ground				Trees			
	Feb–Mar	June–July	Sept–Oct	Total	Feb–Mar	June–July	Sept–Oct	Total
Anaga	62.2	88.9	77.8	76.3	27.3	60.0	57.2	48.3
Tacoronte	26.7	66.7	60.0	51.1	31.7	91.7	83.3	68.9
Santa Úrsula	43.3	83.3	93.3	73.3	41.4	63.6	77.6	61.0
Los Realejos	43.3	83.3	80.0	68.9	35.0	65.0	63.3	54.6
Los Silos	22.7	45.5	35.6	34.6	12.1	33.3	33.9	26.5

Artificial nests

Overall, 50% of the eggs in the artificial nests were predated, being lower in Los Silos than in the other sites ($\chi^2_4 = 192$, $P < 0.001$). During February–March the predation rate was lower than in the other two periods ($\chi^2_2 = 154$, $P < 0.001$).

Eggs in nests on the ground were clearly predated more than those on trees ($\chi^2_1 = 27$, $P < 0.001$), not only when the data are considered as a whole but even in each period and site ($P < 0.05$), except for Los Silos ($\chi^2_1 = 3.04$, ns). However, the opposite trend was found at Tacoronte ($\chi^2_1 = 4.3$, $P < 0.05$). Table 3 shows the spatio-temporal variation for the ground and tree-nests. A total of 61% ground-nests had the eggs predated. Los Silos showed a lower predation rate than Anaga, Santa Úrsula and Los Realejos ($\chi^2_3 = 60.7$, $P < 0.001$). In February–March, the predation rate was lower than during the other two periods ($\chi^2_2 = 39.7$, $P < 0.001$). Predation of contents in nests placed in trees was 48%. Again, a lower predation was recorded at Los Silos ($\chi^2_4 = 156$, $P < 0.001$) and generally during the first period ($\chi^2_1 = 154$, $P < 0.001$). No significant differences between predation according to tree species were found, except for a low predation in *L. Azorica* compared with *M. faya* and *I. canariensis* ($\chi^2_2 = 11.9$, $P < 0.01$).

Identification of predators

We obtained 411 identifiable photographs of animals visiting artificial nests, of which 405 were predators (321 on the ground and 84 on trees). All were mammals and 99.5% of them were Black Rat *Rattus rattus*. The remaining cases were one photo of a rat (either *R. rattus* or *R. norvegicus*) and one of a feral Cat *Felis catus*. In the latter case, the eggs were not consumed. Detailed analysis showed that individual animals were photographed repeatedly, but at least 48 different Black Rats were involved in attacking the eggs

(Fig. 3). Predation occurred almost exclusively at night (99%).

Abundance of predators

Overall, 70% of baits were consumed by rats. Higher consumption took place at Anaga while the lowest rates occurred at Santa Úrsula ($\chi^2_2 = 469$, $P < 0.001$). Furthermore, Los Realejos had a higher proportion of baits taken than the rest of the areas, except Anaga ($\chi^2_3 = 111$, $P < 0.001$). Overall, a higher proportion of baits was taken in June–July than in September–October ($\chi^2_1 = 8.0$, $P < 0.01$), and in September–October compared to February–March ($\chi^2_1 = 9.5$, $P < 0.01$).

Fruit availability

A total of 19 154 fruits was counted in the three study periods. Fruits belonged to 12 different tree species and bushes, but 99% were those of five species (*M. faya* 48%, *V. tinus* 37%, *I. canariensis* 8%, *P. excelsa* 4%, and *L. azorica* 2%). Overall, fruit availability showed a progressive decrease from

Figure 3. Black Rat *Rattus rattus* visiting experimental ground-nest in the laurel forest of Tenerife.

February–March to September–October (ANOVA, $F_{2,402} = 25$, $P < 0.001$).

DISCUSSION

Breeding success and artificial nest predation

Nest predation was the most important cause of nesting failure for both Canarian pigeons. No statistical differences were found between the species despite the average breeding success of Bolle's Laurel Pigeon being nearly twice that of the White-tailed Laurel Pigeon. Nevertheless, artificial nest experiments confirmed the appreciably higher risk to a ground-nester.

Black Rats are known to be an arboreal rodent (Tobin *et al.* 1996, Hooker & Innes 1995) so that Bolle's Laurel Pigeon nesting closer to the trunk and over a thick field layer of vegetation may prove to be more accessible and more at risk to predation. The higher predation observed in those zones with high (< 2 m) bush density around a tree-nest is more difficult to explain. However, movements of Black Rats also occur frequently on the ground and they show preferences for areas with a denser understorey. Other studies measuring vegetation characteristics around the nest site did not show consistent patterns of nest predation (Major & Kendal 1996), possibly due to different predator type.

Bolle's Laurel Pigeon nested mainly in the heath *E. arborea*, the most abundant tree in the different laurel forest zones. The results of several studies (Martin & Roper 1988, Martin 1993b) suggest that this may reduce the risk of nest predation, because the predator's search time is increased and the foraging efficiency decreased. No differences in the rate of predation between tree species were recorded.

The use of artificial nests to measure real predation rates has been long criticized (Major & Kendal 1996). However, our purpose was to compare relative nest predation rates among the different zones and emplacement (ground versus trees). We assumed that predators (mostly rats) forage in a similar manner at different zones and therefore comparison of relative nest predation among them would be valid (Loiselle & Hoppes 1983, Storch 1991, Ritchie *et al.* 1994).

Although greater nest predation rates in ground-nesting birds than in tree-nesting birds had been assumed (Ricklefs 1969), some studies have not detected consistent trends with respect to the effect of nest location (Major & Kendal 1996), and Martin (1993a) stated that even in forest habitats the opposite pattern can occur. This last predation pattern was not

detected in our study of either natural or artificial nests. These differences may be more related to the kind of predators (mammals or birds), rather than with intrinsic habitat characteristics. Mammals seem to exploit ground-nests more while tree-nests are more frequently predated by birds (Laurance *et al.* 1993, Nour *et al.* 1993, Seitz & Zegers 1993).

Overall, artificial nest contents were more often predated on the ground than in trees, but in Tacoronte the opposite trend was recorded. This locality is the smallest study zone (Fig. 2) and the differences observed could be related to small sample size or an effect on predator behaviour arising from human disturbance.

In Los Silos, a low artificial nest predation rate coincides with a high nesting success in natural nests and relatively low consumption of baits. All these facts indicate a low rat density in the area. However, in Santa Ursula, where the highest nesting success and the lowest consumption of baits were observed, a surprisingly high predation rate of artificial nests occurred.

It has been suggested that repetition of trials in the same artificial nests might result in increased predation rates over time due to habituation by predators or development of search images (Martin 1987, Picman 1988, Seitz & Zegers 1993). However, several studies show no consistent trends (Loiselle & Hoppes 1983, Sieving 1992, Nour *et al.* 1993). In our case, at least three months elapsed between trials, so we do not think that repetition influenced the results.

Our data show that artificial nest predation and consumption of baits present similar seasonal patterns, with lower values during the first trial (February–March) while the other two periods did not differ between them. This tendency coincides with a gradual decrease of fruit availability (Fig. 4), which would have forced rats to turn increasingly to alternative food. In this sense, the small sample size of natural nests studied in each period has not allowed us to detect statistical differences between them, although a tendency for greater nest predation during the summer was observed.

Identification of predators

The use of automatic cameras can produce a misleading view of the importance of predators because some may be frightened or become accustomed to the systems (Laurance & Grant 1994, Major & Gowing 1994). Although artificial nests differ from natural pigeon nests, the appearance of Black Rat on 99.5% of pictures clearly indicates that this introduced species

Figure 4. Seasonal changes in artificial nest predation (▼), bait consumption (■) and fruit density (●) on the global zones.

represents the major nest predator of both pigeons. Although we have occasionally detected feral Cat and Sparrowhawk *Accipiter nisus* attacking chicks of both pigeons, numerous signs of rat incidence on natural nests (egg shells, bones and feathers gnawed, droppings in nest) and the greater abundance of the Black Rat than that of the Norway Rat in the laurel forest, agree completely with the predator identification.

The date when the Black Rat was introduced to the Canaries is unknown but probably occurred between the 15th and 17th centuries. Prior to this, a large, now extinct, endemic and omnivorous rat (*Canariomys bravoi*) inhabited Tenerife and probably lived in the laurel forest (López Martínez & López Jurado 1987). There are no data on whether this rodent preyed upon pigeons; if it did, it would have minimized the impact of alien rats arriving later (Atkinson 1985, Burger & Gochfeld 1994).

On the other hand, the Black Rat has been considered the main predator responsible for the decline of bird fauna in insular environments (King 1985), sometimes producing catastrophic effects (Atkinson 1985). This process has been considered very important in forest bird communities (Moors *et al.* 1992, Lever 1994).

Nowadays, the White-tailed Laurel Pigeon is clearly less abundant than Bolle's Laurel Pigeon in Tenerife, and also shows a more restricted distribution. Furthermore, zones where the former is very scarce (Anaga and Santa Úrsula) showed higher artificial ground-nest predation than those areas where the species is more numerous (Los Realejos and Los Silos) ($\chi^2_1 = 32.6$, $P < 0.001$). The results obtained in the present study indicate that coexistence of Black Rat with Bolle's Laurel Pigeon is more feasible than with

White-tailed Laurel Pigeon. This probably arises from the different breeding biology of these two species; Bolle's pigeon (breeding in trees especially in February–June) and the White-tailed Laurel Pigeon (breeding on the ground and mainly during April–August). The Black Rat is probably the key factor determining the survival or extinction of the White-tailed Laurel Pigeon on Tenerife.

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