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Habitat requirements of the Seychelles Black Paradise Flycatcher *Terpsiphone corvina*: a re-evaluation of translocation priorities

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The critically endangered Seychelles Black Paradise Flycatcher *Terpsiphone corvina* was once found on at least five of the inner (granitic) islands in the Seychelles archipelago, western Indian Ocean. Currently, it is only found on two islands, with *c.* 98% of the world population (*c.* 150–200 individuals) occurring on the 10-km^2 island of La Digue. Creation of additional island populations is therefore considered crucial in improving its conservation status. The presence of native broad-leaved plateau forest in proximity to wetland areas is proposed as an important selection criterion when considering the suitability of other islands for translocation, due to the presumed importance of insect prey (dependent on water) in the diet. We quantified habitat use, territory composition, the effect of water on invertebrate abundance, and foraging and breeding success to determine the importance of native broad-leaved woodland and wetland areas for Flycatchers. Flycatcher territories contained significantly more native broad-leaved woodland (88%) than its availability on the plateau (43%); Flycatchers used native tree species significantly more for both foraging (81%) and nesting (95%) than their availability within territories (71%); and territory size varied inversely with the density of native broad-leaved tree species. Native broad-leaved forest was associated with semipermanent and permanent water bodies and availability of native forest habitat was a good predictor of territory distribution. The number of aerial insects trapped was higher close to water, but there was no effect of the proximity to water on the number of insects counted on foliage. The majority of identified prey species in adult diet were not dependent on water: Orthoptera and Lepidoptera were the most common prey groups, comprising 66% of identified prey items. There was no effect of proximity to water on foraging or breeding success (*c.* 35%): depredation was the major factor determining breeding success, and accounted for the majority of nest failures. The importance of wetland areas to Flycatchers therefore appears to have been over-emphasized. The implications for translocation and conservation of the Flycatcher are discussed.

The world population of the Seychelles Black Paradise Flycatcher *Terpsiphone corvina* (Newton 1867) (hereafter Flycatcher) is found almost exclusively on the 10-km^2 island of La Digue in the Republic of the Seychelles, western Indian Ocean. It is currently listed as critically endangered (BirdLife International 2000), with a current population estimate of *c.* 150–200 individuals (Rocamora 1997): a small number of individuals (*c.* 3–5) were recently discovered after an apparent absence of 60 years on Marianne (0.9 km^2) in 1998 (Parr & Shah 2000).

The Flycatcher was historically recorded on at least five granitic islands in the Seychelles archipelago: Aride, Félicité, Marianne, Praslin and La Digue (see Fig. 1). A viable population is now found only on La Digue and the restoration of populations on other islands is considered crucial in ensuring the bird's long-term survival (Watson 1984, 1991, Marshall 1997, Rocamora 1997). Prior to translocation it is essential to have a comprehensive understanding of a species' habitat requirements (IUCN 1998), as demonstrated by the

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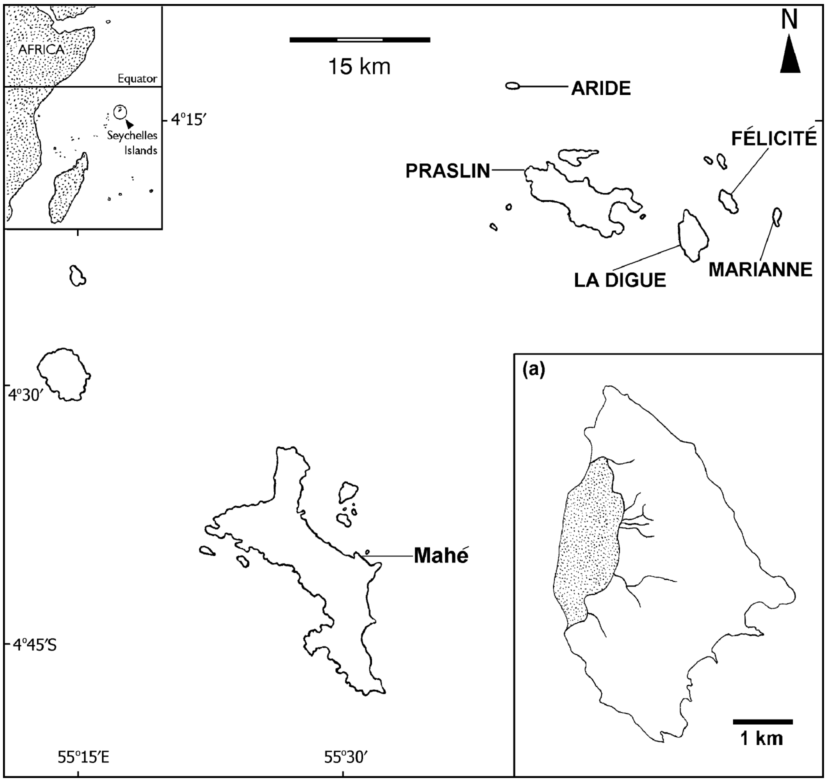

Figure 1. The documented historical range of the Seychelles Black Paradise Flycatcher. Terpsiphone corvina (Collar and Stuart 1985, Diamond 1984, and Watson 1991). Map shows Seychelles inner-archipelago: islands titled in bold upper-case were within the flycatcher's documented historical range. Insef (a) shows La Digue and the 161-ha stugy area (Shaded) encompassed by the canal, and the seven rivers which run into it.

successful translocations of the Seychelles Warbler *Acrocephalus seychellensis* (Komdeur *et al.* 1991) and Seychelles Magpie Robin *Copsychus seychellarum* (Lucking 1996).

There is a well-documented, but not exclusive, association between the Flycatcher and (i) native plateau broad-leaved woodland, primarily Badamier *Terminalia catappa* and Takamaka *Calophyllum inophyllum*; and (ii) marsh/wetland areas (Watson 1991, see also Rocamora 1997). However, their relative importance has yet to be quantified. Paradoxically, the Flycatcher population on La Digue has more than doubled in the last 12 years, from *c.* 25 pairs (*c.* 60 individuals) in 1978–1988 (Watson 1991) to 69 confirmed territories in the 1996/97 season (Rocamora 1997). This increase has occurred during a period of extensive land development, and a documented increase in fragmentation and reduction of native broad-leaved woodland habitat (Watson 1991, Marshall 1997, Rocamora 1997, Neufeld 1998), and in the presence of introduced (potential) adult and nest predators, including Black Rat *Rattus rattus*, Brown Rat *R. norvegicus*, Domestic Cat *Felis catus*, Barn Owl *Tyto alba affinis* and Common (or Indian) Mynah *Acridotheres tristis*. This marked increase in the population is difficult to explain, but may be associated with: (i) heightened public awareness and species protection via reduced nest disturbance and adult mortality – catapults were banned in 1991; (ii) an increase in the height of the water table as a result of the damming of a river on the plateau in the mid-1980s, which may indirectly have increased food availability (cited in Watson 1991) and possibly breeding success (see Rocamora 1997); and (iii) improved habitat management, although this has been limited primarily to the purchase of an 8-ha reserve in 1981 (which increased to 21 ha by 2001) and the control of felling of Takamaka and Badamier trees on the coastal plain through licensing.

The lack of understanding of the increase in the Flycatcher population over the last decade highlights the need for a systematic approach to identify factors affecting Flycatcher population dynamics, both to improve the management of the La Digue population and to identify suitable islands on which to establish populations. In this paper we quantify territory composition and habitat use to re-examine the importance of broad-leaved woodland and wetland areas in Flycatcher habitat requirements. We examine the effect of water (semipermanent and permanent) on invertebrate abundance, and foraging and breeding success. Specifically, we test whether invertebrate availability was higher in proximity to water, and whether this resulted in increased foraging and/or breeding success.

METHODS

Study area

The study was conducted from March 1999 to June 2000 on 161 ha of the *c.* 220-ha western coastal plateau of La Digue (*c.* 4°S, 55°E), being that part of the plateau that is encompassed by the canal (Table 1, Fig. 1). This is the same area in which Watson conducted intensive research between 1978 and 1988 (Watson 1981, 1988, 1991).

Study species

The Seychelles Flycatcher is a small (*c.* 18-g), insectivorous, socially monogamous, sexually dimorphic passerine (Newton 1867). Nests are usually located at the end of thin branches, predominantly in either Takamaka or Badamier. The clutch size is almost always one egg (Watson 1991). Breeding can occur throughout the year, although the peak in nesting occurs during the north-west monsoon (November–April; Watson 1991).

Habitat mapping

From a recent aerial photograph (1997, Ministry of Habitat and Land use, scale 1 : 2000) and ground survey six habitat types were identified in the study area: (i) native broad-leaved woodland (predominantly Takamaka and Badamier); (ii) mixed native broad-leaved and non-native broad-leaved woodland; (iii) non-native woodland; (iv) urban (including houses, gardens and cleared areas/grassland); (v) marsh (non-wooded) and (vi) others, e.g. exposed bedrock. The area of each habitat was calculated to the nearest hectare. Woodland areas were calculated using canopy cover.

Mapping of Flycatcher territories

The boundaries of 32 territories were mapped accurately on the aerial photograph (magnified to 1 : 1000). Boundaries were defined by observations of colour-ringed birds. The general locations of other non-study plateau territories within the study areas were marked on the same map (1 : 2000) using the location of singing males and/or nest locations (after Watson 1991, Rocamora 1997): unringed males were identified by variation in their conspicuous long central tail feathers (after Watson 1991, Rocamora 1997).

The locations of semipermanent or seasonal water (defined as areas of standing water, typically pools and marshes, which were present throughout most

Table 1. Documented historical range of the Seychelles Black Paradise Flycatcher *Terpsiphone corvina* showing dates of last known records and population estimates.

Island	Population	Year	Reference
Felicité	–	1906$^{EX.}$	Nicol (1906)
Marianne	–	1936	Vesey-Fitzgerald (1940)
	c. 3	1998	Parr and Shah (1998)
	c. 3	2000	Hill (2001)
Aride	–	1907$^{EX.}$	Diamond (1984)
Praslin	*c.* 3	1978	Watson (1984)
	c. 3	1989$^{EX.}$	Gerlach (1997)
La Digue	28	1965	Gaymer *et al.* (1969)
	50–90	1971	Beamish (1972)
	66	1977	Watson (1981)
	73	1988	Watson (1988)
	138 (150–200)	1996–97	Rocamora (1997)

– no data; sporadic reports of solitary individuals 1970s–1990s; $^{EX.}$ extinct thereafter.

of the wet season) were accurately plotted on the same photograph (1 : 2000). Territories were classified as one of the following types: (1) territories containing or bordering onto permanent water (canal); (2) territories containing or bordering onto semipermanent pools or marsh; and (3) territories that neither contained nor bordered onto water. Distances (in metres) were also measured to both the nearest semipermanent and the nearest permanent water.

Territory composition

The composition of 29 of the 32 territories was quantified as follows (three territories were not described owing to major habitat alterations occurring in them during the study). All trees over 10 cm dbh (diameter at breast height) were identified to species counted, and grouped into 10-cm size categories. Trees with multiple limbs were measured at their origin. A 300-m transect was run through each mapped territory (after Komdeur *et al.* 1991). Every 10 m the following were estimated: (i) canopy height to the nearest 5 m; (ii) understorey density (measured as the number of contacts within 0–1 m, 1–2 m and 2–3 m height intervals); (iii) percentage total canopy cover and percentage cover of each tree species above 3 m, estimated by looking vertically upwards through a 5-cm-diameter cardboard tube at each point. One observer (R.B.) made all measurements. From these 30 points we then calculated: (i) a mean canopy height for each territory, (ii) an index of understorey density (total number of contacts/number of points within woodland on the transect) and (iii) a mean canopy cover for all tree species and native tree species. We also calculated a fragmentation index for each territory, expressed as: length of forest edge within a territory (m)/forest area within territory (m^2).

Invertebrate abundance

We measured invertebrate abundance on 21 of the 32 territories (seven of each of territory types 1, 2 and 3) using aerial counts and counts of invertebrates on foliage. Leaf and aerial insects were sampled every 2 months. Leaf count data were collected from September 1999 to December 2000 and aerial counts were conducted from December 1999 to December 2000.

Leaf insect sampling

Invertebrate counts were conducted following the methods of Hill (2001). A representative selection of trees was made within each territory to allow for localized environmental variation. On each tree, counts of insects were made on individual leaves, 1–3 m above the ground. The numbers of individual invertebrates observed on the undersides of leaves were recorded in each of 19 taxonomic groups: spider (Araneae), mite (Acari), ant (Hymenoptera, Formicidae), other Hymenoptera, psocid (Psocoptera), soft bug (Hemiptera: Sternorrhyncha), leaf hopper (Hemiptera: Auchenorrhyncha), bug (Hemiptera: Heteroptera), fly (Diptera), cricket (Orthoptera), moth (Lepidoptera), cockroach (Blattodea), beetle (Coleoptera), lacewing (Neuroptera), earwig (Dermaptera), springtail (Collembola), bristletail (Thysanoptera), snail (Gastropoda) and unidentified. For some groups (Lepidoptera, Neuroptera, Coleoptera) the totals included both adults and larvae.

In each focal territory we counted the number of invertebrates on five Takamaka and five Badamier trees (20 leaves on each tree). In addition, we counted invertebrates on three non-native tree species (15 trees of each species, 20 leaves on each), both close to permanent water (< 50 m; Mango *Mangifera indica*, Breadfruit *Artocarpus altilis*, Jamblon *Syzygium cumini*) and in areas where there were no sources of water (Mango, Breadfruit and Kalis Dipap *Tabebuia pallida*), i.e. equivalent to territory categories 1 and 3, respectively. All insect counts were conducted from 08:00 to 11:30 hours and 15:30 to 17:00 hours, during relatively dry and calm conditions.

A mean number of invertebrates per unit area of leaf (m^2) was calculated for: (i) Takamaka and Badamier trees separately for each territory, (ii) Takamaka and Badamier together as a measure for native tree species on each territory and (iii) non-native broad-leaved tree species close to and far from water (territory types 1 and 3, respectively). On focal territories, two leaves from each Badamier and Takamaka tree were collected in September 1999. Leaf areas were measured by drawing the outline of each leaf onto 1 cm^2 of paper. Their respective length and breadths were also measured. From the leaf dimensions and area a formula to predict leaf area was calculated. Predicted leaf areas (PLA) were calculated from length and breadth measurements made on Takamaka and Badamier leaves collected in December 1999 and March 2000. There was no seasonal difference in PLA or differences in PLA between territory types (1–3) for either tree species (repeated measures ANOVA, all tests ns). Actual leaf areas calculated from September 1999 were used in future calculations. Mean ± se leaf area was: Takamaka = 128.84 ± 4.12 ($n = 210$); Badamier = 280.36 ± 17.46 ($n = 210$).

For non-native trees, leaf areas were measured as above, in December 1999 for Mango, Jamblon and Kalis Dipap, and in March 2000 for Breadfruit. Mean ± se leaf area was: Mango = 79.39 ± 4.23 ($n = 60$); Jamblon = 72.73 ± 3.21 ($n = 30$); Kalis Dipap = 41.45 ± 1.73 ($n = 30$); Breadfruit = 768.55 ± 39.71 ($n = 60$).

To calculate the number of invertebrates per unit area of leaf (m^2) we used the formula: number of invertebrates/(number of leaves × mean leaf area [m^2] × number of trees), and these data were expressed as total number of invertebrates, total excluding ants, and total excluding ants and soft bugs. A diversity index was calculated as the mean number of taxa per leaf per tree species.

Aerial insect counts

Aerial invertebrates were sampled using a malaise type flight intercept trap 1 m × 1 m × 1 m (McGavin 1997) suspended in the canopy at *c.* 5 m height located approximately in the middle of each territory. The sides and central partition of the trap were made of black mosquito netting, and the roof was made of denser white netting. This was left on each focal territory for 96 h (five nights). Samples were collected and stored in 70% ethanol and invertebrates were later counted and identified to Order. Aerial invertebrate counts were expressed as total number of invertebrates (excluding ants) caught over five nights. A diversity index for each aerial trap (number of taxa per trap, excluding ants) was also calculated.

Behavioural observations – habitat use and foraging

Observations of foraging behaviour were made for each sex once a month on 21 territories (for which invertebrate abundance was measured) between August 1999 and the end of May 2000. Observations commenced 1 min after finding the focal bird. The observer spent a maximum of 1 h on the territory. Behavioural observations were made using 10 × 25 binoculars, and were dictated directly onto tape using a hand-held recorder and transcribed later. For each 1-min sample period that a focal individual was observed, the following data were noted: (i) the number and species of tree the individual landed in and used for foraging (trees were classed as one of five types: Takamaka, Badamier, other broad-leaved tree species [native and non-natives], and non broad-leaved species [Casuarina *Casuarina equisetifolia* and Coconut *Cocos nucifera*]); (ii) the foraging strategy of each attempted and successful feeding attempt – the Flycatcher exhibits two general modes of feeding, namely (a) hawking, in which aerial prey species are taken on the wing, and (b) gleaning (or sally gleaning), in which prey species are taken from the surface of leaves/branches either on the wing or while perched (Bullock *et al.* 1988, Watson 1991); (iii) the presence/absence of understorey under each tree; (iv) tree height (m); (v) foraging height (m); (vi) the number of attempted and successful gleans/hawks on each tree; (vii) prey size (small = 0.5 × bill length, medium *c.* 1 × bill length, and large > 1 × bill length; where bill length [tip to gape] is *c.* 2 cm); and, when possible, (viii) prey type. We excluded minutes from the analyses when a focal bird was not observed for the complete minute or was incubating. All trees were included in the analyses except when an individual was clearly observed to be returning to the same tree for a purpose other than foraging, e.g. nest-building, incubation and provisioning of a nestling or young fledgling. In these instances the tree was only considered once during a given watch. In total, 335 observations were collected, over a mean duration of 17.3 min (se = ±0.42 min). All data were collected by one observer (R.B.).

It was not possible to measure the time spent foraging per tree due to the rapidity of Flycatcher feeding behaviour. We therefore express foraging success as number of successful feeds per total observation time, having first ensured that there was no difference in rates of feeding between territory classes or with distance to water (repeated measures ANOVA, all tests, ns). Data were grouped on a 2-month basis for each sex on each territory, giving six repeated observations of foraging success per sex per territory to avoid missing cells in the data set.

Breeding success

Thirty-two territories (including the 21 for which foraging and invertebrate abundance was also measured) within the study area were monitored every 1–2 weeks from 1 June 1999 until 1 June 2000. Each active breeding attempt, defined as when an egg was laid in a nest, was recorded. Once found, nests were monitored every third day. When a bird was first observed to be sitting on a nest, its contents were observed; this was done using a mirror on a pole, when there were no adults at the nest, usually the same day, to ensure egg-laying had actually occurred and to check clutch-size. When a nest was presumed to have failed, it was also checked in an identical way. Date of failure was taken as the mid-point between inspections. A nest could only be checked with the mirror if it was less than 7 m high ($n = 120$; 78%). Date of hatching was determined by observing the behaviour of the parents at the nest. Nests found on non-focal territories were monitored as above and assigned as territory types 1, 2 or 3 (see above). Distance to semipermanent, permanent, and nearest water sources was also measured.

Breeding success was expressed as: $(1\text{-daily failure rate})^{31.92} \times 100$, where 31.92 is the mean number of days between laying and fledging ($n = 47$; BirdLife Seychelles unpubl. data), and daily failure rate is the number of failed nests/total number of observation days (Mayfield 1961, 1975). Observation days were calculated from first egg date (FED) or from the date of finding an active nest. Standard errors for daily failure rates and z-tests for comparisons of daily failure rates for each territory type (1–3) and actual distance to semipermanent, permanent and nearest water (at 100 m intervals) were calculated after Johnson (1979) and Hensler and Nichols (1981).

Chicks were ringed and weighed (to the nearest 0.1 g) on average 2.09 days (se = ±0.20; $n = 54$) before fledging. Unlike many other passerine nestlings, Flycatchers do not leave the nest prematurely in response to disturbance.

Analyses

Statistical tests follow Sokal and Rohlf (1981) and Siegel and Castellan (1988). Data were analysed using SPSS (Norusis 1992). Statistical tests are two-tailed and corrected for ties when appropriate. Repeated measures ANOVAS were used to analyse foraging success and aerial and leaf counts as repeated observations were made on the same territories. Invertebrate counts (leaf and aerial) and number of successful feeds per minute (total, hawks and gleans) were log transformed, and proportions were arcsine transformed. In tests examining the effect of proximity to water on various dependent variables, territory class (1, 2 or 3) was not entered simultaneously with distances to semipermanent, permanent or nearest water (which were entered as constant co-variates in separate analyses). All interactions were non-significant unless otherwise stated and all tests were two-tailed.

RESULTS

Habitat composition of study area

In the 161-ha study area there were 69 ha (42.7%) of Takamaka–Badamier-dominated forest. This comprised 124 discrete blocks: 80 < 0.1 ha, 30 between 0.1 and 1.0 ha, and 11 greater than 1 ha. The remainder of the study area comprised 60 ha (37.1%) urban, 20 ha (12.4%) non-native woodland (predominantly coconut), 9 ha (5.7%) mixed woodland stands (native and non-native trees), 4 ha (2.5%) marsh (non-wooded) and 1 ha (0.7%) others (e.g. bedrock).

Territory size, composition and distribution

Sixty-two confirmed territories were identified in the study area (Fig. 2); 41 out of 62 (65%) territorial males had been colour-ringed within the study area by July 1999, and 90% of territories had at least one member of the pair ringed by June 2000.

Mean territory size was 1.04 ha (se = ±0.07, range 0.4–2.46 ha, $n = 32$); mean territory size only including woodland was 0.92 ha (se = ±0.05). Territories comprised predominantly native broad-leaved woodland, the proportion of which was significantly higher than in 50 randomly selected points of mean territory size (mean woodland area: territories = 0.87, se = ±0.05 ha [84%], $n = 29$; 'random territories' = 0.47, se = ±0.05 ha [45%], $n = 50$; Mann–Whitney U-test, $z = 3.63$, $P < 0.01$).

The best predictor of territory size (excluding non-woodland habitats) was the density of Takamaka and Badamier combined (number of trees per hectare; Stepwise multiple regression, $t = -3.99$, $P = 0.0013$). Territories also tended to be larger further from permanent water (Stepwise multiple regression, $t = 2.22$, $P = 0.0357$).

In addition to the marked overlap in distribution of territories with that of native broad-leaved (Takamaka and Badamier) forest (see Fig. 2), the number of Flycatcher territories in the study area was also highest close to permanent water (Kendall rank correlation, number of pairs vs. distance to water [grouped in 100-m intervals], $r_k = -0.92$, $P < 0.01$, $n = 9$). However, the area of native broad-leaved forest also correlated negatively with increasing distance to permanent water (Kendall rank correlation,

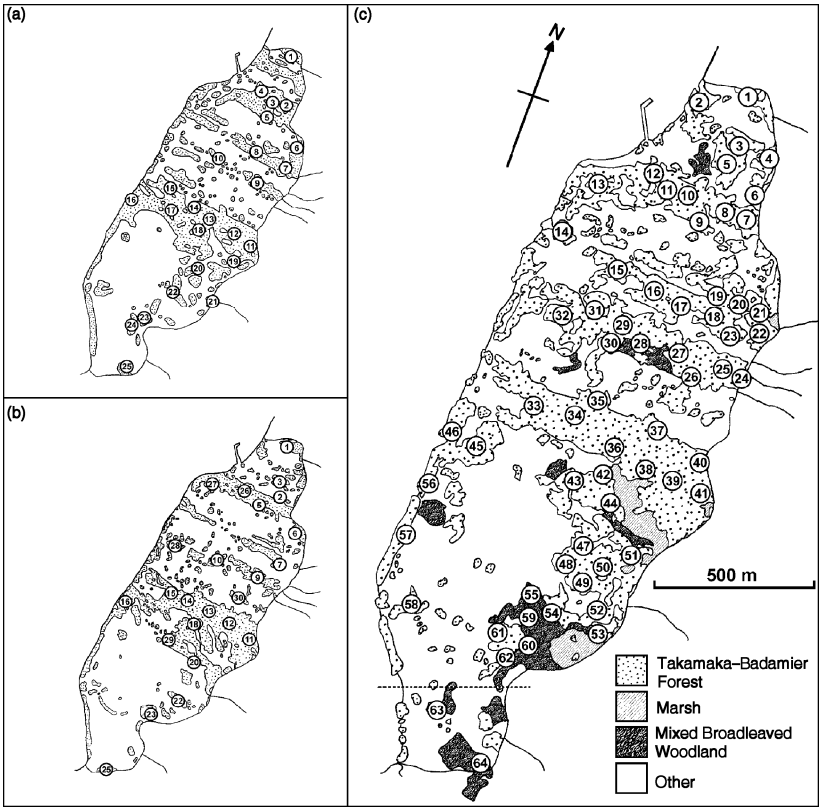

Figure 2. Distribution of territories and Takamaka–Badamier woodland in the 161-ha study area on La Digue's western plateau in (a) 1978, (b) 1988 (both from Watson 1991) and (c) 1999–2000. The 13 ha of plateau below the dotted line in (c) was not intensively surveyed, but was known to contain at least two territories (63 and 64).

area of native broad-leaved forest vs. distance to water [grouped in 100-m intervals], $r_k = -0.99$, $P < 0.001$, $n = 9$). On controlling for this confounding factor there was no correlation between territory density and distance to permanent water (Kendall partial correlation, number of territories vs. distance from water, $r_k = -0.20$, $P = 0.63$, $n = 9$). This is further highlighted in Figure 3, which shows that there was no difference between the number of expected and observed Flycatcher territories with respect to distance from permanent water (canal).

Eighty-four per cent (52/62) of territories occurred within 200 m of semipermanent water. However, 47 out of 106 random (50-m × 50-m) squares plotted on the plateau, which comprised predominantly native broad-leaved woodland, were significantly closer to semipermanent water (pools and marsh) than random squares ($n = 59$) containing other (non-broad-leaved woodland) habitats (mean distance to semipermanent water: native forest = 96.28, se = ±16.09, $n = 46$; other habitats = 127.34, se = ±13.79, $n = 46$; Mann–Whitney *U*-test, $z = 2.51$, $P < 0.05$). The association between broad-leaved woodland and semipermanent pools is unsurprising as 83% (75/90) of semipermanent pools were found either in ($n = 56$) or adjacent to ($n = 19$) native broad-leaved woodland habitat. There was no difference in distance to permanent water between random squares containing either broad-leaved or non-broad-leaved habitats (mean distance to permanent water: native forest = 383.67, se = ±29.05, $n = 56$; other habitats = 350.11, se = ±38.39, $n = 60$; Mann–Whitney *U*-test, $z = 0.85$, ns).

Territory utilization

On average, 71.9% of tree species within study territories ($n = 29$) were natives (range = 38.7–94.2%), the majority of which were Takamaka and Badamier (98.2%, se = ±0.70; 52% Takamaka and 47% Badamier).

Eighty-six per cent of trees within focal territories ($n = 21$) used for foraging were native species, the majority of which were Takamaka and Badamier (98.5%). Native tree species were used significantly

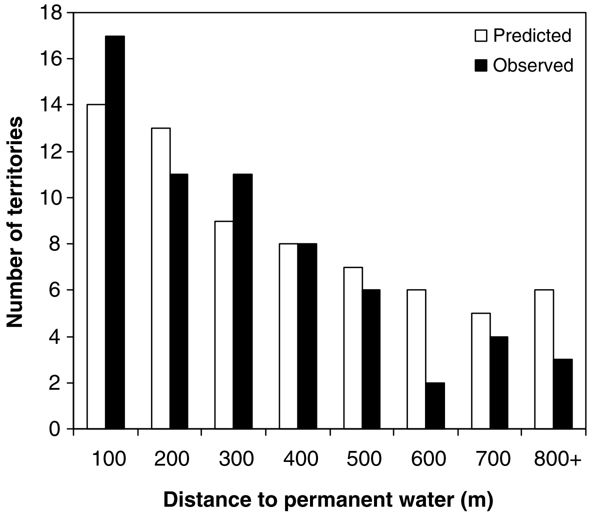

Figure 3. Predicted and observed number of Flycatcher territories with respect to distance to permanent water (grouped at 100-m intervals). Data exclude 13 ha not intensively surveyed (see Fig. 1). Expected number of territories was calculated by dividing the area of broad-leaved woodland in each distance category by the mean territory size (1.04 ha). Chi-squared test, number of observed pairs vs. the number of predicted pairs, $x_7^2 = 3.58$, $P = 0.83$.

more for foraging than their availability within a territory (Wilcoxon pair sign rank test, proportion of native trees in a territory vs. proportion of native trees used for foraging, $z = 3.91$, $P < 0.01$, $n = 21$).

Ninety-five per cent of all active nests (from 52 territories) found were in native tree species, the majority in Badamier (54.5%) and Takamaka (37.8%). This pattern was repeated for all the focal ($n = 32$) territories, with 94% of nests being built in native species: 60% in Badamier and 32% in Takamaka. Nests were more likely to occur in native species than their availability in territories suggested (Chi-square test, number of non-native and native trees vs. number of nests in non-native and native trees, $x_2^2 = 28.55$, $P < 0.001$). Badamier was used for more nesting attempts than expected from its availability than Takamaka ($x_2^2 = 11.25$, $P < 0.001$).

Invertebrate abundance

Invertebrates on leaves

Native tree species had higher counts of insects than the selected non-native tree species (repeated measures ANOVA, territory class and native/non-native species; total number of invertebrates, $F_{1,43} = 43.75$, $P < 0.001$; invertebrates excluding ants, $F_{1,43} = 70.80$, $P < 0.001$; invertebrates excluding ants and soft bugs, $F_{1,43} = 79.28$, $P < 0.001$; see Appendix 1). For native tree species, counts of insects were higher on Takamaka than on Badamier (repeated measures ANOVA, territory type and Takamaka/Badamier; total invertebrates, $F_{1,36} = 9.4$, $P = 0.004$; excluding ants, $F_{1,36} = 25.71$, $P < 0.001$; excluding ants and soft bugs, $F_{1,36} = 23.99$, $P < 0.001$; see Appendix 1). Similarly, native tree species also had higher levels of diversity (number of taxa per leaf per tree) than introduced tree species (repeated measures ANOVA, $F_{1,43} = 25.52$, $P < 0.001$, whereas Takamaka was higher than Badamier (repeated measures ANOVA, $F_{1,36} = 5.44$, $P < 0.05$; see Appendix 1).

Total counts of insects (including ants and soft bugs) on native trees (data for Takamaka and Badamier combined) differed between territory types and were lower on territories furthest from water (i.e. Type 3; repeated measures ANOVA, $F_{2,18} = 3.99$, $P < 0.05$; see Appendix 1). However, there was no difference between territory type when ants and/or soft bugs were excluded (repeated measures ANOVA, territory type vs. number of invertebrates: excluding ants, $F_{2,18} = 0.50$, ns; excluding ants and soft bugs, $F_{2,18} = 0.02$, ns). Similarly, total leaf counts varied with distance to water (semipermanent water, $t = -3.25$, $P < 0.01$; permanent water, $t = -1.78$, $P = 0.091$; nearest water, $t = -2.81$, $P < 0.05$), but there was no effect of actual distance to water on leaf counts excluding ants and/or soft bugs (repeated measures ANOVAS, all tests, ns).

Apart from ants and soft bugs, the most common taxa found on native tree species were arachnids, coleopterans and orthopterans (although their respective frequencies differed between species), and arachnids, coleopterans and dipterans were the three most common taxa found on non-native trees (Table 2).

There was no difference between territory types in invertebrate diversity (number of taxa per leaf per tree) on either Takamaka and Badamier, although diversity was influenced by actual distance to water and was generally higher closest to water (semipermanent water, $t = -2.96$, $P < 0.01$; permanent water, $t = -1.51$, $P = 0.13$; nearest water, $t = -2.75$, $P < 0.01$).

Counts of aerial insects

Invertebrates trapped in aerial intercept traps ranged in size from 2 mm to 30 mm. The most frequently caught taxonomic group was Lepidoptera, comprising 65% of specimens (Table 2). There was no difference between territories in number of aerial invertebrates caught (repeated measures ANOVA, territory type vs. aerial insect counts, $F_{2,18} = 1.37$, ns; see Appendix 1). However, there was an indication that distance to

Table 2. Invertebrate composition of insects counted on foliage (natives and non-native trees) and aerial traps. Superscripts (1–3) show the three commonest invertebrate groups (excluding ants and soft bugs).

	Leaf counts			
Taxa	Takamaka	Badamier	Non-natives	Aerial counts
Orthoptera	18.5 (286)^3	33.8 (667)^1	5.4 (36)	4.6 (560)
Lepidoptera	10.2 (157)	4.4 (87)	3.8 (25)	65.6 (8057)^1
Araneae	25.7 (397)^1	16.2 (320)^3	28.3 (188)^2	1.8 (221)
Diptera	5.5 (85)	8.5 (169)	33.8 (224)^1	8.1 (998)^2
Blattodea	12.9 (200)	6.5 (129)	1.8 (12)	0.7 (83)
Hymenoptera	0.9 (14)	0.7 (13)	1.5 (10)	1.4 (172)
Coleoptera	18.6 (287)^2	25.9 (493)^2	21.3 (141)^3	6.7 (822)^3
Others	7.6 (117)	4.9 (98)	3.9 (26)	8.8 (1364)
Total^a	14 414	18 203	25 844	12 584
Total^b	3 288	4 121	3 394	12 277
Total^c	1 543	1 976	665	–

Total^a = total number of invertebrates.
Total^b = total number of invertebrates excluding ants.
Total^c = total number of invertebrates excluding ants and soft bugs.

Table 3. Identified adult Flycatcher diet (both sexes combined, $n = 341$) July 1999–May 2000. This also shows the percentage of prey items that were taken by hawks or gleans (including sally gleaning).

Taxa	Frequency	% in diet	% glean	% hawks
Orthoptera	140	41.1	87.9	12.1
Lepidoptera*	88	25.8	73.9	26.1
Araneae	36	10.6	100	0
Diptera	28	8.2	64.3	35.7
Blattodea	27	7.9	92.5	7.5
Hymenoptera	8	2.3	50.0	50.0
Odonata	8	2.3	37.5	62.5
Neuroptera	5	1.5	80.0	20.0
Phasmatodia	1	0.3	100	0

*Includes both larvae and adults.

water affected the total number of aerial insects caught, with fewer being caught further from water (repeated measures ANOVA: semipermanent water, $t = -3.11$, $P < 0.01$; permanent water, $t = -1.94$, $P = 0.067$; nearest water, $t = -3.33$, $P < 0.01$). There was no effect of water on the frequency of Lepidoptera caught, the commonest order trapped (repeated measures ANOVA, territory type, $F_{2,18} = 0.32$, ns; semipermanent water, $t = -0.81$, ns; permanent water, $t = -0.435$, ns; nearest water, $t = -1.08$, ns).

The invertebrate diversity in aerial traps (number of taxa, excluding ants) did not differ significantly between territory class (repeated measures ANOVA, $F_{2,18} = 1.13$, ns; see Appendix 1), but correlated negatively with distance to water (semipermanent water, $t = -3.24$, $P < 0.01$; permanent water, $t = -2.29$, $P < 0.05$; nearest water, $t = -3.50$, $P < 0.01$).

Diet

The majority of prey items taken were small: 2869/3241 (88.5%). The remainder was made up of 271 medium (8.4%) and 101 large (3.2%) items. In total, 341 prey items (10.5%) were identified. Although only 2.3% (67/2869) of small prey items were identified, 66% (178/271) of medium-sized items and 94% (95/101) of large items were identified. The two most common orders identified as prey (July 1999 to May 2000) were Orthoptera and Lepidoptera, which comprised 66% of identified prey items (Table 3). Although we were unable to identify the majority of small items in the diet with certainty during feeding observations, ants (Hymenoptera: Formicidae) or soft bugs (Hemiptera: Sternorrhyncha, with the possible exception of psyllids) did not appear to comprise a significant part of Flycatcher diet.

Foraging

Gleaning (taking prey from a leaf surface either while on the wing or while perched) was the most common feeding method exhibited by both sexes, accounting for 81% (2614/3241) of successful feeds. There was no effect of territory class or distance to water on foraging success (repeated measures ANOVA, sex and territory class vs. successful feeds per min: territory class, $F_{2,14} = 0.11$, ns; semipermanent water, $t = 0.07$, ns; permanent water, $t = 1.24$, ns; nearest water, $t = 0.06$, ns; territory class and sex vs. successful gleans per min: territory class, $F_{2,14} = 0.10$, ns; semipermanent water, $t = 0.31$, ns; permanent water, $t = 1.48$, ns; nearest water, $t = 0.31$, ns; repeated measures ANOVA, sex and territory class vs. successful hawks per minute: territory class, $F_{2,5} = 0.11$, ns; semipermanent water, $t = –0.70$, ns; permanent water $t = –0.28$, ns; nearest water, $t = –0.74$, ns; see Table 4).

There was no effect of territory class or distance to water on frequency of either foraging strategy (repeated measures ANOVA, territory type vs. proportion of successful feeds that were hawks, $F_{2,14} = 0.55$, ns; see Table 4; semipermanent water, $t = –0.77$, ns; permanent water, $t = –1.45$, ns; nearest water, $t = –0.76$, ns).

Breeding success

On average there were 3.4 (se = ±0.24, range 0–6) breeding attempts per focal territory ($n = 32$) over a 12-month period. Breeding success was 35% for the 32 focal territories and 36% for all ($n = 52$) territories. The majority of nest failures were due to nest predation, characterized by the absence of an egg or chick from a nest. There was no difference in breeding success between territory types (Table 4). Furthermore, breeding success did not differ significantly between whether it was less than or more than 100 m from (i) semipermanent water (40.8% vs. 33.1%, $z = 0.91$, ns); (ii) permanent water (41.4% vs. 37.3%, $z = -0.51$, ns); or (iii) nearest water (39.3% vs. 34.9%, $z = -0.18$, ns).

Nestlings were lighter in territories far from water (one-way ANOVA, territory class vs. mean fledging weight, $F_{2,37} = 3.59$, $P < 0.05$; Table 4), although there was no difference in date of weighing chicks (relative to fledging) between territory class (one-way ANOVA, territory class vs. days prior to fledging, $F_{2,50} = 0.73$, ns).

DISCUSSION

This study has emphasized the importance of native broad-leaved (Takamaka–Badamier) plateau forest in the habitat requirements of the Seychelles Black Paradise Flycatcher: territories contained significantly more native broad-leaved woodland (88%) than its general availability on the plateau (43%); Flycatchers used native tree species significantly more for both foraging (81%; invertebrate abundance was 2–5 times higher on native than on non-native tree species) and nesting (95%) than their availability within territories (71%); and the density of native plateau tree species was the major factor in determining territory size. The importance of wetland areas in Flycatcher requirements was less clear.

The density of Flycatcher territories was certainly highest close to permanent water (the canal; see also

Table 4. Territory class vs. mean foraging success (successful feeds per minute: min^{-1}) ± se, mean proportion of successful feeds that were hawks (% hawks) ± se, daily failure rate ± se, breeding success (%), and mean fledging weights (g). Sample sizes are given in parentheses. For statistics see text.

	Territory class		
	1	2	3
Total feeds min^{-1}	0.57 ± 0.03	0.60 ± 0.03	0.57 ± 0.25
Gleans min^{-1}	0.46 ± 0.23	0.47 ± 0.21	0.45 ± 0.20
Hawks min^{-1}	0.11 ± 0.09	0.13 ± 0.10	0.12 ± 0.10
%Hawks	0.23 ± 0.02	0.20 ± 0.02	0.25 ± 0.02
Daily failure rate	0.029 ± 0.012 (40)	0.031 ± 0.009 (71)	0.034 ± 0.013 (40)
Breeding success (%)	38.8 (40)	37.0 (71)	33.4 (40)
Fledging weight (g)	17.24 ± 0.29 (7)	17.39 ± 0.21 (24)	16.45 ± 0.19 (9)

Watson 1991) and the majority of territories were in close proximity (< 200 m) to standing semipermanent water (see also Rocamora 1997). However, the significant negative correlation between density of pairs (per 10 ha of woodland) and distance to permanent water shown by Watson (1991), used to justify the importance of water and also observed in this study (Kendall correlation coefficient, $r_k = -0.56$, $P < 0.05$, $n = 9$), does not control for the underlying distribution of woodland area relative to water within the study area. A larger area of plateau (and hence woodland) is close to permanent water, and the current distribution of territories on La Digue's western plateau can be explained by: (i) the distribution of preferred native broad-leaved woodland with respect to permanent water (the canal), and (ii) a non-random association between the distribution of native broad-leaved woodland and semipermanent water. The only evidence from this study of an effect of permanent water on Flycatcher distribution was that territories located further from permanent water were generally larger and that chick fledging weights were higher in proximity to water.

Flycatcher diet

Although the Flycatcher is known to be insectivorous, the composition of its diet prior to this study was based to a large extent on casual observations (e.g. Gaymer *et al.* 1969, Watson 1981). We identified 75% of medium and large items, and considering prey species by volume, this probably represents a significant proportion of total prey quantity. The association between Flycatchers and wetland areas has been explained through the assumption that many of its prey species were dependent on water (Watson 1991, Gerlach 1997). However, identified Flycatcher diet (July 1999 to May 2000) was dominated by species that were not directly dependent on water (Orthoptera and Lepidoptera comprised 66% of identified prey items) and in general paralleled the prominence of non-water-dependent invertebrates in both foliage counts and traps (see Tables 2 and 3). Only *c.* 10% of identified prey items comprising two orders, Odonata and Diptera, can be considered to be either directly dependent (Odonata) or possibly dependent (Diptera) on water at some stage in their life cycle. There may also be a secondary effect of water, with the density of arachnids and predatory insects affected by availability of invertebrate species that are dependent on water.

The invasive water lettuce *Pistia stratiotes* has been blamed for a 'collapse' in the population of aquatic invertebrate prey species (Gerlach 1996), but the predicted accompanying decline in Flycatcher numbers has not occurred: in fact, the population has increased, which provides further credence to the suggestion that there has been an over-emphasis of water-dependent prey species in Flycatcher diet.

Effect of water on foraging success, breeding success and population trends

Under conditions of high prey availability there is an expectation of increased foraging efficiency and (if prey availability is the major determining factor) enhanced breeding success. Although there was some evidence that the proximity to water affected the total number of aerial insects, there was no evidence of a parallel effect on the number of invertebrates (excluding ants and soft bugs) counted on leaves. Because the predominant mode of feeding involved taking prey items directly from the surface of leaves (accounting for 80% of successful feeds) the lack of a water-effect on foraging success was, in hindsight, perhaps not unexpected. Similarly, breeding success was unaffected by proximity to water. Depredation appeared to be the principal cause of nest failures, levels of which were probably sufficiently high to mask any effect of water. However, fledging weights were lower in territories far from water, a fact that may be related to food availability and ultimately to territory quality.

The water-table of the western plateau increased significantly (by *c.* 30 cm) after the damming of the canal in 1984. Part of the dam was removed in 1992 (documented in Marshall 1997) and this is presumed to have resulted in a lowering of the water-table, although this remains unquantified. Interpretation of census data is ambiguous as to the impact of water-table changes on Flycatcher numbers. There was no immediate effect on Flycatcher numbers as a result of raising the water-table and the plateau population was characterized by a period of stasis between 1978 and 1988, 4 years after the dam was built (Watson 1991), whereas Flycatcher numbers increased post 1992 after removal of part of the dam.

Implications for conservation and translocation

Early work on a smaller, more restricted Flycatcher population (Watson 1981, Watson 1988, 1991; see

Fig. 2), and subsequent qualitative observations on territory distribution (e.g. Marshall 1997, Rocamora 1997) led to the supposition that woodland close to wetland areas was the primary factor in accounting for Flycatcher distribution. This observation ultimately drove Flycatcher conservation policy on La Digue and the prioritization of islands to receive translocated populations. Quantitative data from this study warrant a re-assessment of Flycatcher habitat requirements, specifically the relative importance of wetland areas.

Native broad-leaved woodland is clearly important for Flycatchers (see also Watson 1991); the presence of such habitat is clearly a major selection criterion in choosing other islands for translocation, and continued conservation of this habitat on La Digue is essential. However, the relative importance of wetland areas in Flycatcher habitat requirements appears to have been over-emphasized; the distribution of territories can be explained by a non-random association between preferred habitat and water bodies. To an extent, this association is a consequence of land development post-colonization that probably occurred preferentially, at least at the outset, in drier areas, allowing persistence of native vegetation in wetland areas.

The lack of quantifiable benefits to Flycatchers living in proximity to wetland areas is supported by the observation that individuals survive and breed successfully in dry plateau woodland (as well as on low slopes off-plateau) on La Digue, albeit probably requiring larger territories. Therefore to link all future conservation strategies with extensive freshwater wetlands may unnecessarily restrict options for the bird's conservation. Certainly, the historic distribution of Flycatchers included islands without extensive or numerous marsh systems, e.g. Marianne, Félicité and Aride (Nicol 1906, Vesey-Fitzgerald 1940, Diamond 1984). However, in light of the unique topographical and hydrological characteristics of La Digue, resulting in relatively damp conditions over most low-lying areas, it would be sensible to adopt a precautionary approach to the prioritization of islands to receive translocated populations, initially considering islands that provide the largest area of suitable habitat in proximity to wetlands (water may be especially important on smaller drier islands with more seasonal wetlands). This study highlights the difficulties in using remnant, possibly atypical, populations as a basis for future conservation and management decisions.

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Appendix 1. Territory class and invertebrate abundance on foliage (mean m^2 ± se), mean foliage diversity (± se), mean number of aerial insects (trapped over 5 nights ± se), and aerial invertebrate diversity ± se. For statistics see text.

		Territory class		
		1	2	3
Insect counts[1]	Natives	58.50 ± 5.05	64.01 ± 4.93	34.23 ± 3.45
	Introduced	55.13 ± 9.91	–	27.02 ± 3.96
	Takamaka	71.84 ± 6.06	79.18 ± 6.44	48.65 ± 5.60
	Badamier	45.17 ± 7.70	48.84 ± 6.92	21.80 ± 3.18
Insect counts[2]	Natives	13.01 ± 1.88	11.72 ± 1.06	11.08 ± 1.69
	Introduced	6.51 ± 1.84	–	7.89 ± 1.82
	Takamaka	16.06 ± 2.78	13.1 ± 11.27	16.30 ± 3.18
	Badamier	9.97 ± 2.48	10.34 ± 1.79	5.93 ± 7.26
Insect counts[3]	Natives	5.75 ± 0.44	5.89 ± 0.43	5.59 ± 0.43
	Introduced	1.50 ± 0.35	–	3.7 ± 1.08
	Takamaka	7.75 ± 0.70	6.86 ± 0.59	6.87 ± 0.59
	Badamier	3.76 ± 0.37	4.91 ± 0.59	4.31 ± 0.54
Leaf diversity	Natives	2.40 ± 0.05	2.64 ± 0.06	2.34 ± 0.07
	Introduced	1.49 ± 0.20	–	1.43 ± 0.19
	Takamaka	2.28 ± 0.08	2.42 ± 0.10	2.31 ± 0.13
	Badamier	2.68 ± 0.10	2.68 ± 0.11	2.31 ± 0.10
Aerial counts		85.35 ± 13.38	73.39 ± 11.60	71.61 ± 14.42
Aerial diversity		6.10 ± 0.23	6.06 ± 0.22	5.35 ± 0.31

[1] Total number of invertebrates per m^2 on leaves.
[2] Number of invertebrates per m^2 on leaves excluding ants.
[3] Number of invertebrates per m^2 excluding ants and soft bugs.