



Impact of the invasive crazy ant *Anoplolepis gracilipes* on Bird Island, Seychelles

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Abstract

The crazy ant (*Anoplolepis gracilipes*) invaded Bird island, Seychelles, in the 1980s. In 1997, its range expanded and population densities increased. The impacts of this change were studied in 2001 using a combination of arthropod collecting methods. The ant population excluded larger invertebrates (principally the large ant *Odontomachus simillimus* and the crabs, principally *Ocypode* spp.). Cockroaches, however, remained abundant in ant-infested areas and tree-nesting birds (Lesser Noddy *Anous tenuirostris*) appear to be able to breed successfully in the presence of the crazy ant. The ants are only abundant in areas of deep shade which provide cool nesting areas, yet enabling them to forage in the open when ground temperatures fall. The expansion of the ants was correlated with the regeneration of woodland on the island. Recommendations are made for the management of the woodland which may reduce the impacts of the crazy ant.

Introduction

The threat from alien invasive species is widely perceived as one of the major contributions to present-day high-extinction rates, affecting an estimated 30% of threatened birds, 15% of threatened plants and 10% of threatened mammals (Hilton-Taylor 2000). Invasive predatory ant species may be particularly problematic (Williams 1994; Moller 1996; Tsutsui and Suarez 2003) as exemplified by the spread of the ants *Linepithema humile* (Mayr), *Pheidole megacephala* Fabricius, *Solenopsis wagneri* Santschi (= *S. invicta*) and *Wasmannia auropunctata* (Roger) in the North America, the Galapagos and Hawaii islands (Haskins and Haskins 1965; Clark et al. 1982; McGlynn 1999) and widespread invasions by the crazy ant *Anoplolepis gracilipes* (F. Smith) (= *A. longipes*). This tropical tramp species has been widely introduced and is now found throughout much of

Africa, Asia, America and Australia (Dorow 1996). This species has been recorded as excluding other ant species (Greenslade 1971) and recently has been implicated in a population crash in the red crab *Gecarcoidea natalis* on Christmas Island (O' Dowd et al. 1999). It has been listed as one of the 100 'worst invasive alien species' (Lowe et al. 2001).

A. gracilipes is believed to have been introduced to Mahé island in the Seychelles islands in about 1962, remaining in the Maldivé area of the island until 1970, and then having colonized most lowland areas by 1975 (Haines and Haines 1978b). Praslin island was colonized in 1975; the population appeared to have died out by the late 1970s without intervention (Haines and Haines 1978b). However, it is now known to be well established on the island (Dorow 1996) and it is now present on nine islands (Mahé, Anonyme, St. Anne, Praslin, Petite Soeur, Marianne, Felicite, La Digue and

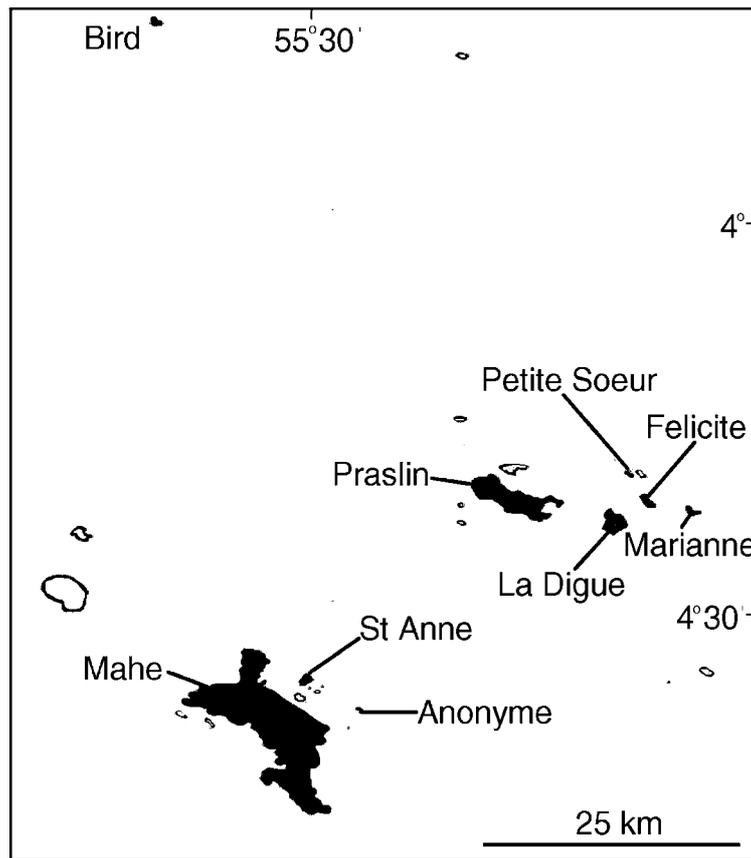


Figure 1. Central islands of the Seychelles group, with *A. gracilipes* invaded islands shaded.

Bird island; Gerlach 2003) (Figure 1). The impact of *A. gracilipes* on Mahé in the 1970s resulted in significant declines in the abundance of other ants, several other insect groups, millipedes and spiders (Lewis et al. 1976; Haines and Haines 1978a).

The most recently reported invasion of *A. gracilipes* in Seychelles has been on Bird island. While the species colonized the island in the 1980s, probably in building materials imported from Mahé island, it remained restricted to buildings until 1997 (Robert 1998a; Feare 1999). In that year, the ant spread into the island's colony of nesting sooty tern (*Sterna fuscata* Linnaeus), occupying 16% of the colony's range in 1998 and 50% in 1999 (Robert 1998c, 1999a). This caused the failure of tern breeding in 1999 due to the ants swarming over the ground, disturbing the chicks and causing them to shake their feet constantly. This is normally a behaviour used to dislodge ticks but the numbers of ants resulted in constant repetition of

the movement, leading to excessive energy expenditure, reduced feeding, and ultimate exhaustion and death (Robert 1999b). Attempts at control have included a range of chemical baits and sprays. Currently control relies on cypermethrin-based insecticidal sprays combined with burning to clear ants from the area used by the sooty tern colony (Robert 1999a). This has successfully prevented the ant from occupying the area of the tern colony since 2000.

Bird island is the most northerly of the Seychelles islands and is a coral island, resting on the edge of the Seychelles plateau. As a small (101 ha) coral island, all its habitats can be described as coastal, with a strong maritime influence on all areas. Originally the island was probably a mixture of open habitat used by the nesting terns and *Pisonia grandis* R.Br. woodland. Most of the habitat of the island was modified in the 1900s by the establishment of a coconut (*Cocos nucifera* L.)

plantation. This is now abandoned and *P. grandis* woodland is regenerating. The vegetation includes many introduced species, few of which are significant components of any habitat. The exception is *Carica papaya* L. which is widely dispersed (and increasing locally) by birds. There is no significant agriculture or gardening and habitat management and chemical input are restricted to seasonal burning and insecticide spraying of one area to maintain open habitat for the sooty tern colony. This has no detectable impact on other parts of the island. Bird Island has been visited by biologists on several occasions since 1905. Available data on the island's biota are largely concentrated on the sooty tern colony but scattered observations exist (Fryer 1909; Benoit 1978; Feare 1979; Stoddart and Fosberg 1981). Surveys of the island's ecosystems were made in April and October 2001 and October 2002. These complement the data accumulated on the spread of the crazy ants (Gerlach 2003) providing an evaluation of the impact of this species on Bird island.

Methods

Distribution of the crazy ant

Since 1997, the distribution of the crazy ant has been monitored by residents of the island and during attempts to control the species and eradicate it from the sooty tern colony. These observations were compiled to provide an approximate rate of expansion. The island was divided into a grid of 40 squares, each measuring approximately 150 m, using the runway and main path for orientation and measured by pacing. In each square 20 randomly positioned 1 m² quadrats were studied. In these quadrats, the number of ants active on the surface of the leaf litter at mid-day was counted and the canopy cover estimated visually. Counting ants at mid-day provided a comparative measure of activity and abundance for each square. The square was observed from a distance of 2 m to ensure minimal disturbance to the ants. The association between crazy ant numbers and habitat factors was analysed using a multiple analysis of covariance of canopy cover (leaf litter depth was found to be directly correlated ($F = 10.2$, $P < 0.0001$) to canopy cover and was excluded from analysis) and

minimum distance from the sea. In each grid square the presence or absence of potential nest sites (logs, piles of leaves or rocks or man-made structures) was recorded.

Biodiversity

Arthropod diversity on Bird island was surveyed on 4th and 5th April 2001, 21–23rd October 2001 and 20–22nd October 2002. During each visit, 10 samples of leaf litter, each covering 1 m², were collected from an *A. gracilipes* free area and an infested area (points A and B in Figure 2). These sites differed primarily in the presence or absence of the crazy ant. Both were areas of woodland, details of comparisons of vegetation and tree cover are given in Table 3. All leaf litter types were sampled, for samples from coconut woodland the superficial layers of leaves were removed and the partially decomposed sub-surface leaves used. The superficial layers did not support invertebrate life as revealed by careful examination of leaves outside of the sample quadrats. These samples were sieved and placed in Tullgren funnels for 24 h. Sweep netting of 10 m² was also carried out in these two areas. In October 2002, no *A. gracilipes*-free woodland could be found, and 20 leaf litter samples were collected from randomly selected grid squares. For each sample, the invertebrate composition, litter depth, canopy cover and distance from the sea were recorded. The association between invertebrate numbers and crazy ants was analysed using a multiple analysis of covariance of crazy ant numbers, canopy cover and minimum distance from the sea.

The numbers of nesting terns in ant-invaded and ant-free areas were investigated by recording the number of active lesser noddy (*A. tenuirostris* (Temminck)) nests on *P. grandis* trees. Ten trees with estimated heights of 10–45 m were examined in the ant invaded area and adjacent to it. Observations were made between 10:00 and 12:00 h for comparative data. Trees infested with ants were easily identified by the trails of ants on the trunks, trees without ants were double checked by disturbing the leaf litter around the base of the tree and fissures in the bark. If no ants could be located by this method, the tree was concluded to be ant-free.

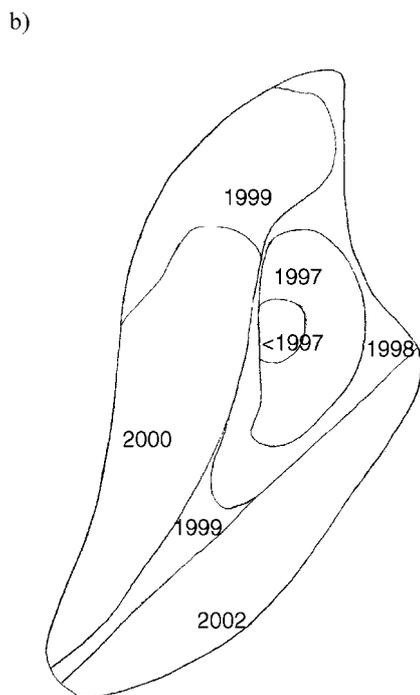
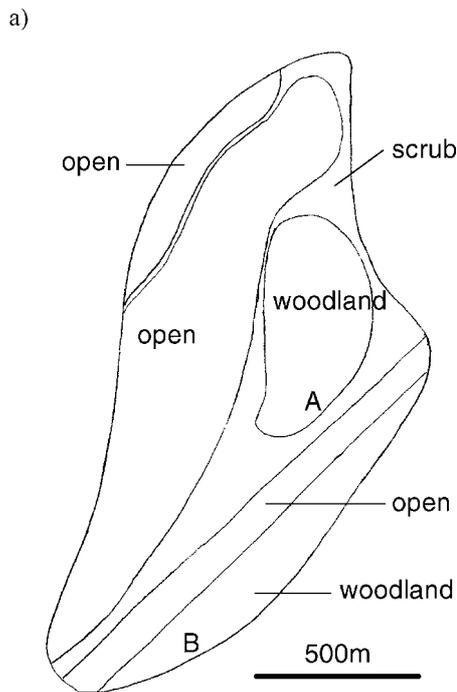


Figure 2. Habitats and the crazy ants on Bird island: (a) habitats on Bird island (habitat comparison points A and B marked); (b) crazy ants range expansion since 1997 (based on reports from island residents).

Crazy ant behaviour

The behaviour of the crazy ant visible on the surface of the ground was observed at irregular times throughout the day by counting the maximum number of workers foraging on the surface at any one time in a 1-min observation period. Observations were made between 11:00 and 13:00 h in each grid square. In one grid square (point A), these observations were repeated hourly from 6:00 to 18:00 h. In each case, the square was observed from a distance of 2 m, where possible from a rock or area of open ground, to minimise disturbance to the ants. Night-time observations required close approach to the ants and disturbance could not be prevented, thus reliable comparative night-time observations could not be obtained.

Results

Distribution of the crazy ant

The ant has spread from the buildings on the west of the island into the central woodland areas and the open ground of the tern colony in the north. In 2001, 70 ha of the island were occupied by the ant, with the southern and eastern parts of the island remaining ant free (Figure 2). By October 2002, the ant had spread over the whole island. A significant association was found between the numbers of ants, distance from the sea and canopy cover (Table 1; Figure 3). The effect of canopy cover was observed in the activity data but could not be accurately analysed in leaf litter data as the heat from the lamps used in the Tullgren funnels killed all crazy ant individuals collected (but did not have any such effect on other taxa). The ant was only observed during the middle of the day where canopy cover exceeded 75%, although disturbance or observations at other times revealed their presence in all grid squares in 2002. Potential nest sites were found to be uniformly distributed across the island, with no association with areas of high or low crazy ant abundance.

Crazy ant behaviour

The crazy ant is crepuscular. Activity on the surface of the ground was observed between 6:00 and

Table 1. Results of statistical testing (MANCOVA) of the effect of habitat and *Anoplolepis gracilipes* abundance on the abundance of invertebrates

| Taxon | Variable | df | Seq. SS | Adj. SS | Adj. MS | F | P |
|--|--|----|---------|---------|---------|-------|--------|
| <i>Anoplolepis gracilipes</i> (F. Smith) | Cover | 6 | 1213.34 | 1454.59 | 242.43 | 20.58 | <0.01 |
| | Distance to sea | 2 | 315.20 | 315.20 | 157.60 | 13.38 | <0.01 |
| | Error | 31 | 365.23 | 365.23 | 11.78 | | |
| | Total | 39 | 1893.78 | | | | |
| Dictyoptera <i>Lobopterella dimidiatipes</i> (Bolivar) | Cover | 1 | 19.39 | 39.79 | 39.79 | 4.50 | <0.05 |
| | <i>Pycnoscelus indicus</i> (Fabricius) | 1 | 38.00 | 33.57 | 33.57 | 3.80 | NS |
| | <i>Anoplolepis</i> | 1 | 8.56 | 8.56 | 8.56 | 0.97 | NS |
| | Error | 36 | 318.44 | 318.44 | 8.85 | | |
| Nematoda Unidentified sp. | Total | 39 | 384.40 | | | | |
| | Cover | 1 | 27.06 | 39.37 | 39.27 | 17.25 | <0.001 |
| | Distance to sea | 1 | 7.41 | 7.85 | 7.85 | 3.05 | NS |
| | <i>Anoplolepis</i> | 1 | 4.03 | 4.03 | 4.03 | 1.85 | NS |
| Annelida Unidentified sp. | Error | 36 | 81.61 | 81.61 | 2.54 | | |
| | Total | 39 | 120.09 | | | | |
| | Cover | 1 | 32.08 | 32.08 | 35.768 | 17.02 | <0.001 |
| | Distance to sea | 1 | 15.23 | 15.23 | 15.121 | 5.12 | <0.05 |
| Mollusca <i>Gastrocopta tripunctata</i> Morelet | <i>Streptosela acicula</i> Morelet | 1 | 3.29 | 3.29 | 3.001 | 2.17 | NS |
| | <i>Opeas pumilum</i> Pfeiffer | 1 | 3.00 | 3.00 | 2.925 | 2.10 | NS |
| | Error | 36 | 76.01 | 76.01 | 11.240 | | |
| | Total | 39 | 134.14 | | | | |
| Araneae <i>Heliophanus activus</i> (Blackwall) | <i>O. aphanes</i> (Thorell) | 1 | 0.00 | 0.08 | 0.084 | 0.09 | NS |
| | <i>Oedignatha mogamoga</i> Marples | 1 | 3.91 | 4.61 | 4.613 | 4.82 | NS |
| | <i>Opopaea lena</i> Suman | 1 | 2.59 | 2.59 | 2.592 | 2.71 | NS |
| | Error | 36 | 34.47 | 34.47 | 0.957 | | |
| Schizomida <i>Ovozomus similis</i> (Hirst) | Total | 39 | 40.98 | | | | |
| | Cover | 1 | 29.06 | 29.06 | 29.001 | 9.75 | <0.001 |
| | Distance to sea | 1 | 5.30 | 5.30 | 5.295 | 4.23 | NS |
| | <i>Anoplolepis</i> | 1 | 4.00 | 4.00 | 3.999 | 3.78 | NS |
| Diplopoda <i>Dalodemidae</i> sp. | Error | 36 | 66.17 | 66.17 | 6.615 | | |
| | Total | 39 | 104.51 | | | | |
| | Cover | 1 | 35.80 | 35.80 | 33.111 | 22.24 | <0.001 |
| | Distance to sea | 1 | 4.17 | 4.17 | 3.902 | 3.56 | NS |
| Chilopoda <i>Cryptops</i> sp. | <i>Anoplolepis</i> | 1 | 3.21 | 3.21 | 3.100 | 2.98 | NS |
| | Error | 36 | 88.87 | 88.87 | 12.234 | | |
| | Total | 39 | 132.05 | | | | |
| | Cover | 1 | 12.34 | 12.34 | 9.223 | 11.23 | <0.05 |
| Psocoptera Unidentified sp. | Distance to sea | 1 | 3.78 | 3.78 | 3.548 | 3.34 | NS |
| | <i>Anoplolepis</i> | 1 | 2.29 | 2.29 | 2.290 | 2.00 | NS |
| | Error | 36 | 84.12 | 84.12 | 9.121 | | |
| | Total | 39 | 103.53 | | | | |
| Isopoda <i>Trichorhina tomentosa</i> (Budde-Lund) | Cover | 1 | 27.60 | 27.60 | 26.124 | 15.77 | <0.001 |
| | Distance to sea | 1 | 12.13 | 12.13 | 12.125 | 5.55 | <0.05 |
| | <i>Anoplolepis</i> | 1 | 3.00 | 3.00 | 2.998 | 2.01 | NS |
| | Error | 36 | 84.16 | 84.16 | 2.234 | | |
| Isopoda <i>Trichorhina tomentosa</i> (Budde-Lund) | Total | 39 | 126.88 | | | | |
| | Cover | 1 | 28.00 | 39.77 | 39.768 | 17.75 | <0.001 |
| | Distance to sea | 1 | 17.85 | 15.78 | 15.784 | 7.05 | <0.05 |
| | <i>Anoplolepis</i> | 1 | 3.93 | 3.93 | 3.925 | 1.75 | NS |
| Isopoda <i>Trichorhina tomentosa</i> (Budde-Lund) | Error | 36 | 80.65 | 80.65 | 2.240 | | |
| | Total | 39 | 130.38 | | | | |

Continued on next page

Table 1. Continued

| Taxon | | Variable | df | Seq. SS | Adj. SS | Adj. MS | F | P | |
|--------------------------|-------------------------------------|---------------------------------------|--------------------|---------|---------|---------|--------|--------|--------|
| Dermaptera | <i>E. annulipes</i> (Lucas) | Cover | 1 | 17.11 | 17.11 | 15.232 | 11.23 | <0.05 | |
| | | <i>Gonolabis electra</i> Burr | Distance to sea | 1 | 7.22 | 7.22 | 6.889 | 3.05 | NS |
| | <i>Anoplolepis</i> | | 1 | 2.20 | 2.20 | 2.194 | 1.85 | NS | |
| | | Error | 36 | 88.97 | 88.97 | 12.240 | | | |
| | | Total | 39 | 115.49 | | | | | |
| Diptera | (larvae) | Cover | 1 | 36.00 | 36.00 | 33.242 | 21.25 | <0.001 | |
| | | Distance to sea | 1 | 17.00 | 17.00 | 12.174 | 9.15 | <0.05 | |
| | <i>Anoplolepis</i> | | 1 | 2.99 | 2.99 | 2.992 | 0.75 | NS | |
| | | Error | 36 | 90.16 | 90.16 | 0.224 | | | |
| | | Total | 39 | 146.15 | | | | | |
| Coleoptera | Anobiidae | Cover | 1 | 1.47 | 0.76 | 0.758 | 2.53 | NS | |
| | | Ptiniidae | Distance to sea | 1 | 0.97 | 1.16 | 1.161 | 3.88 | NS |
| | Staphylinidae | <i>Anoplolepis</i> | 1 | 0.75 | 0.75 | 0.751 | 2.51 | NS | |
| | | Error | 36 | 10.78 | 10.78 | 0.299 | | | |
| | | Total | 39 | 13.98 | | | | | |
| Hymenoptera (Formicidae) | <i>B. cordemoyi</i> Forel | Cover | 1 | 5.49 | 9.45 | 9.452 | 17.98 | <0.001 | |
| | | <i>P. megacephala</i> (Fabricius) | Distance to sea | 1 | 2.08 | 1.54 | 1.538 | 2.93 | NS |
| | <i>S. seychellensi</i> Forel | <i>Anoplolepis</i> | 1 | 2.89 | 2.89 | 2.888 | 5.49 | <0.05 | |
| | | <i>Strumigenys emmae</i> (Emery) | Error | 36 | 18.92 | 18.92 | 0.526 | | |
| | <i>T. albipes</i> (F. Smith) | Total | 39 | 29.38 | | | | | |
| | <i>T. lanuginosum</i> Mayr | <i>O. similimus</i> (F. Smith) | Cover | 1 | 2.33 | 2.12 | 2.123 | 5.33 | <0.01 |
| | <i>T. simillimum</i> (F. Smith) | | Distance to sea | 1 | 1.89 | 1.32 | 1.320 | 3.03 | NS |
| | <i>O. similimus</i> (F. Smith) | | <i>Anoplolepis</i> | 1 | 363.52 | 363.52 | 11.982 | 23.23 | <0.001 |
| | Error | | 36 | 109.67 | 109.67 | 2.987 | | | |
| | Total | | 39 | 477.42 | | | | | |

Data are taken from all 40 grid squares in 2002. Native species are highlighted in bold.

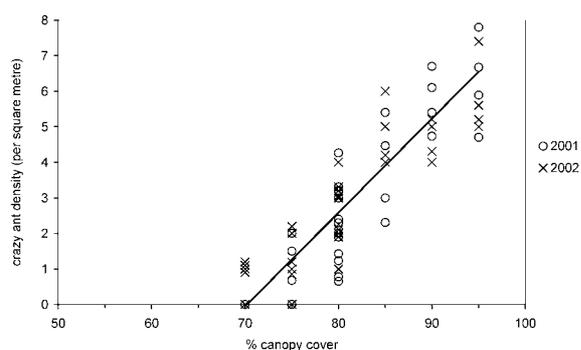


Figure 3. The relationship between crazy ant activity at mid-day and canopy cover (ant density = 0.257 (canopy cover) – 18.545; $R^2 = 0.888$; $P < 0.001$) in the visual sample quadrats in 2002.

9:30 h and between 16:30 and 18:00 h. During the middle of the day, no ants were observed until the leaf litter was disturbed when large numbers emerged from under leaves and out of rotten logs. The crazy ant was observed to forage on the

beaches at 17:00 h down to the water's edge. Night-time observations (18:00 to 23:30 h) in the ant-infested areas revealed only small numbers of foraging ants. No comparative measures of activity could be obtained at night due to the difficulty of making night-time observations without disturbing the ants.

When active, ants were seen foraging on the surface and tending a species of aphid on *Scaevola sericea* Vahl bushes. Ants were observed on *Pisonia grandis* and *Cordia subcordata* Lam. trees with heavy infestations of larvae of the indigenous moth *Ethmia nigroapicella* Saalmüller. The larvae were protected by silk webs and no direct predation was observed. The ants were observed to feed on the freshly broken surfaces of the leaves eaten by the caterpillars. Items carried by crazy ants included scale insects (*Pulvinaria urbicola* Cockerell) and cydnid bugs. Freshly dead ghost crabs (*Ocypode ceratophthalma* (Pallas)) were observed on the northern beach, the large numbers

Table 2. Significant regressions predicting invertebrate abundance (derived from the data analysed in Table 1)

| | Regression | <i>t</i> | <i>P</i> |
|-----------|--|----------|----------|
| Cockroach | $Y = 6.275 - 0.036$ (cover) | -2.12 | <0.05 |
| Spider | $Y = 3.423 - 0.582$ (sea) | -2.19 | <0.05 |
| Ants | $Y = 2.772 - 0.017$ (cover) + 0.044 (<i>Anoplolepis</i>) | 5.89 | <0.001 |
| | <i>B. cordemoyi</i> Forel | | |
| | <i>P. megacephala</i> (Fabricius) | | |
| | <i>S. seychellensis</i> Forel | | |
| | <i>S. emmae</i> (Emery) | | |
| | <i>T. albipes</i> (F. Smith) | | |
| | <i>T. lanuginosum</i> Mayr | | |
| | <i>T. simillimum</i> (F. Smith) | | |
| | <i>O. simillimus</i> (F. Smith) | | |
| Beetles | $Y = 0.152 + 0.012$ (cover) - 0.122 (<i>Anoplolepis</i>) | -2.22 | <0.05 |
| Woodlice | None | | |
| | $Y = 4.946 - 0.036$ (cover) - 1.077 (sea) | -4.21 | <0.05 |

Table 3. Woodland composition and cover at points A and B

| Plant Habit | Plant species | Status | Number per hectares | | | |
|-------------|--------------------------------|--------------------------|---------------------|------|------|------|
| | | | A | | B | |
| | | | 1999 | 2002 | 1999 | 2002 |
| Open tree | <i>Carica papaya</i> | Introduced crop plant | 320 | 310 | 400 | 1240 |
| Canopy tree | <i>Casuarina equisetifolia</i> | Native | 0 | 0 | 80 | 60 |
| Canopy tree | <i>Cocos nucifera</i> | Native (largely planted) | 1120 | 1110 | 0 | 0 |
| Canopy tree | <i>Pisonia grandis</i> | Native | 640 | 660 | 640 | 720 |
| Shrub | <i>Scaevola sericea</i> | Native | 0 | 0 | 400 | 300 |
| % cover | | | 90 | 90 | 30 | 70 |

of ants on these crabs and the unusually high density of fresh (<24 h old) remains (50 per hectare) may be indicative of predation by the ants. Ten nests of crazy ants contained remains of individuals of eight earwigs (*Euborellia annulipes* (Lucas)), two ants (*Odontomachus simillimus*), two crickets (*Zarceus fallaciosus* Bolivar), one cockroach (*Periplaneta americana* (Fabricius)) and one beetle (*Uloma* sp.). In addition, live individuals of *E. annulipes* and woodlice (*Cubaris murina* Brandt) were found in crazy ant nests.

Biodiversity

No significant crazy ant-related invertebrate distribution patterns could be detected except for ants and one species of paussine carabid beetle (the first record of this ant parasite subfamily from Seychelles) (Tables 1 and 2). The single species of paussine beetle was positively associated with the

crazy ant whilst other ant species were reduced in areas with abundant crazy ant. Most ant species were widespread, but the largest species, *O. simillimus* (F. Smith) did not coexist with crazy ants.

In the woodland area the mean level of crazy ant activity at mid-day was 5.4 active ants per square metre, with the highest density in the densest woodland. Leaf-litter samples (which also include ants below the surface of the litter) contained over 10 times more ants (mean density of 60 m⁻²). The crazy ant was scarce in open woodland although it does forage in open habitats at dusk. Differences in woodland composition and cover in ant invaded and ant-free areas are summarised in Table 3.

Active Lesser Noddy nests were found in ant invaded and ant-free areas with no significant difference between the two areas (in the 10 trees studied in each area ant-infested trees supported 49 nests, whilst ant-free trees had 45 nests). Nest success was difficult to determine, but approximately 50% of nests in both areas

contained visible chicks (49% in ant-infested trees, 51% in ant-free trees), suggesting that success was comparable.

Discussion

Distribution of crazy ant

The spread of the crazy ant over Bird island since 1997 is estimated at 146–294 m per year, which is considerably lower than the rate of 402 m per year calculated on Mahé (Haines and Haines 1978a). This may suggest that factors other than the intrinsic rate of colony expansion are important on Bird island. Density in the invaded woodland on Bird island (as indicated by leaf litter sampling with Tullgren funnels) is approximately 0.6 million ants per hectare (with a range of 0.08–0.79 million). This is comparable with densities estimated for parts of Mahé in 1978 (Union Vale 0.25–0.5 and Mamelles 0.9 million) but is lower than the introduction focus on Mahé (1.3 million ha⁻¹; Haines and Haines 1978b). The highest densities were in the mature woodland, and no pattern of a high density leading invasive edge could be detected. This suggests that habitat characteristics are the primary determinant of crazy ant abundance on Bird island.

Woodland on Bird island has expanded considerably over the past 10 years. In 1994, it was restricted to a small area of dense *P. grandis*, spreading from about 5 ha in 1997 to its current extent of approximately 70 ha (35 ha with permanent colonies). The expansion of the woodland in the mid 1990s has resulted in improved conditions for woodland-inhabiting invertebrates, including the crazy ant. Their 2001 distribution reflects their preference for shaded habitats, with colonies restricted to the dense woodland. The woodland that was not occupied by the crazy ant had a much more open structure. Although the total number of plants over 2 m ha⁻¹ was similar in ant-free and ant invaded areas (1920 compared to 2160, respectively), the number of canopy forming trees was 60% lower (720 compared to 1840). The crazy ant-invaded areas were principally the overgrown coconut plantation, the abundant coconut trees (1120 per hectare) providing dense shade and also abundant rotten wood for nest construction.

Areas free of the crazy ant were more exposed and have a thin humus layer unsuitable for nesting.

Crazy ant behaviour

The behavioural observations indicate that the crazy ant is limited (spatially or temporally) by high temperatures. It has been reported that *A. gracilipes* activity is limited by temperature, being restricted to temperatures in the range of approximately 25–30 °C (Dammerman 1929). These are the normal shade temperatures experienced by the islands, although noon temperatures above 30 °C are frequent and in full sun temperatures would be expected to rise much higher. Consequently, it is to be expected that crazy ant activity will be reduced in the middle of the day and that activity (particularly colony establishment) will concentrate on shaded areas, such as the woodland.

The crazy ant has been recorded preying on blind snakes (*Ramphotyphlops braminus* Daudin), turtle (*Eretmochelys imbricata* (Linnaeus)) hatchlings and fairy tern (*Gygis alba* Sparrm) chicks that had fallen from their nests (Robert 1998a; Feare 1999). Disturbance to the sooty tern colony was noted in 1998 (Robert 1998b) ultimately resulting in the terns abandoning part of the colony (Robert 1998c). The disturbance caused to the nesting terns and their chicks appears to be principally aggravation rather than direct predation. The ants swarm over the ground and the terns, causing the adults to preen frequently and the chicks to stamp their feet, a behavioural mechanism that normally serves to reduce tick infestations (Feare and Gill 1997). The swarming of the crazy ant results in the tern chicks constantly stamping their feet, causing excessive energy expenditure and reduced feeding, ultimately resulting in exhaustion and death (Robert 1999b). Tree-nesting terns (and possibly other birds) appear to be able to coexist with crazy ants, although there is a high degree of irritation caused by the ants running over the birds. At present, there is no evidence that this irritation causes high levels of mortality in tree-nesting terns.

Biodiversity

The impact of crazy ants on Bird island may be highly significant as has been suggested in the past,

although previous reports have not distinguished the impact of the ants from habitat effects, in particular some interpretations may be misleading due to the close association between the ants and the densest areas of vegetation. Reports of significant impacts may reflect observations made at a different stage in the invasion process or temporary phenomena resulting from other, unrelated ecological processes. This includes reports of die-back of *P. grandis* caused by coccoid bugs *P. urbicola* cultured by crazy ants (Hill 2002). *P. grandis* die-back is a temporary phenomenon and it may be too simplistic to attribute this to a *Pulvinaria*-ant interaction alone. Crazy ants do tend the coccoids and infestations can be locally extremely high. However, throughout 2001–2002, heavily-infested trees remained healthy and any study of such die-back should also consider climatic variation. Similarly reports of the decline of reptiles and *Polistes olivaceus* (De Geer) wasps following the crazy ant range expansion (Hill 2002) are not supported by more recent observations.

The Tullgren funnel data indicate that crazy ants do not have a significant effect on the abundance of invertebrates, with the exception of other ant species and paussine beetles. All ant species were positively correlated with crazy ant numbers other than *O. simillimus*. The small ants may share the microhabitat preferences of the crazy ant but the large predatory *O. simillimus* is excluded and directly fed upon by crazy ants. The paussine beetles are generalist ant parasites and their positive association with the crazy ant reflects this parasitism. Similarly, the flowerpot snake *R. braminus* was found to be locally abundant in ant-infested areas and was observed feeding on ants (*P. megacephala*).

The limited data available on crazy ant diet suggest that a large part of the faunal differences are not due to direct predation by crazy ants. Haines and Haines (1978a) identified Hymenoptera (unspecified but implied to be mostly ants) as the main food component (18.5% of food items), followed by cockroaches (15%), termites (11%), bugs (11%), woodlice (10%), beetles (7%), plant material (6%) and myriapods (5%). Other items totalled less than 5%. Direct predation by crazy ants may be expected to be most significant for other large ant species (e.g., *O. simillimus*) and may be significant for the large invertebrates apparently excluded by

the ants. Cockroaches may be expected to be affected by crazy ants on this basis but the high local densities of cockroaches in crazy ant habitat may obscure any predation impacts. Alternatively, the cockroaches may benefit from ants reducing the numbers of other predators as appear to be the case in agricultural habitat in La Réunion (M. Samways, pers. commun.). It should also be noted that in 2001, areas not invaded by crazy ants were occupied by the native predatory ant *O. simillimus*. This species is slightly larger than the crazy ant and possesses powerful jaws. It is likely to have as significant an impact on leaf-litter inhabiting invertebrates as the crazy ant does. The principal difference in the effects of these species is that the colonies of *O. simillimus* are smaller and more scattered and the species is predominantly terrestrial, whilst crazy ants frequently forage on vegetation (pers. observ.). A comparison of the fauna of areas on Mahé with heavy crazy ant infestations with areas with few crazy ants by pitfall trapping indicated that few other ant species coexisted with the crazy ant. Beetle, fly millipede, spider and collembolan numbers were reduced, but that cockroaches, hemipteran bugs, moths and woodlice were more abundant (Haines and Haines 1978a). These data are difficult to interpret, however, as unrecorded ecological factors may have caused the differences in abundance in both the crazy ants and the other invertebrates.

The current management of crazy ants on Bird island comprises the spraying of insecticide around habitations and the open area of the sooty tern colony to keep the terns' nesting area largely free of ants during the nesting season. This affects only the open areas and no management is carried out in the woodland areas studied. Extension of the insecticidal spraying could result in eradication of the ants but at potentially great cost to the invertebrate fauna. The majority of the invertebrates are widespread species but there are some endemics of conservation significance (such as a new dalodemid millipede species so far located only on Bird island). The impact of crazy ants may be reduced if the ant density declines. Such a decline can be expected in future, as ant predators become more abundant (principally the paussine beetles and the ant lion *Myrmeleon obscurus*). Further reduction in crazy ant abundance could be effected by habitat management. The current composition of the woodland

is heavily biased towards coconuts in crazy ant areas. These provide ideal nesting places for the ants and dense shade. The natural woodland would originally have been dominated by *P. grandis*, which has an open structure. If the remnants of the old coconut plantation were eliminated, the density of trees would be reduced by 54% and the tree canopy opened out by at least 30%. This habitat structure would be less suitable for the crazy ant than the current coconut dominated habitat. The woodland is likely to become more open naturally as the high rhino beetle population kills the mature coconuts (mortality currently running at 5–10% annually), but the process could be greatly enhanced by manual cutting of the young palms.

The crazy ant is believed to have colonised Bird island and all the Seychelles islands it inhabits as a result of accidental introduction in supplies imported from crazy ant infested islands (probably Mahé in most cases). It is the most obvious introduced species on Bird island, although the invertebrate fauna include several introduced species. The ant species include three native species (*O. simillimus*, *S. seychellensis* Forel and *Brachymyrmex cordemoyi* Forel) and four cosmopolitan species: *Strumigenys emmae* (Emery), *Tetramorium lanuginosum* Mayr, *T. simillimum* (F. Smith), *Technomyrmex albipes* (F. Smith) (a tramp species of uncertain origin) and *P. megacephala*. *T. albipes* is common in woodland and is present on both the ground and on vegetation. *P. megacephala* and the *Tetramorium* species are more restricted on Bird island and only found on the ground. Both species are generally regarded as introductions although their status in the Seychelles fauna is currently uncertain (being among the first ants recorded from the islands in the 19th century). If these species are introduced it is possible that any ant facilitated ecological change has already taken place, obscuring any impacts of crazy ant invasion.

Invasive ants have been reported to disrupt entire ecosystems (Porter and Savignano 1990; Vinson 1991) with direct impacts on plants (Bond and Slingsby 1984) and other ant species (Clark et al. 1982; de Kock and Giliomee 1989; Brandão and Pavia 1994; Holway 1995; Human and Gordon 1996). Of these direct impacts, it has been found that ant species categorised as non-cryptic above-ground foragers are most significantly affected

(Holway 1995; Human and Gordon 1996). The exclusion of the large surface feeding *O. simillimus* by *A. gracilipes* on Bird island is in accordance with this finding. The findings of this study suggest that the impacts of invasion by introduced species may be obscured by the ecological processes of the biological system concerned and habitat effects, especially when there is a significant change in the habitat. This results in the frequently confusing picture of alien ants coexisting with native species and unpredictable outbreaks of invasives. This complexity of species change has long been recognised (Haskins and Haskins 1965; Wilson and Taylor 1967), although rarely reported in recent reviews of ant invasions.

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